Seed arrival in tropical forest tree fall gaps

CAROLINA PUERTA-PIÑERO,[1] HELENE C. MULLER-LANDAU, OSVALDO CALDERÓN, AND S. JOSEPH WRIGHT

Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Panamá, República de Panamá

Abstract. Tree deaths open gaps in closed-canopy forests, which allow light to reach the forest floor and promote seed germination and seedling establishment. Gap dependence of regeneration is an important axis of life history variation among forest plant species, and many studies have evaluated how plant species differ in seedling and sapling performance in gaps. However, relatively little is known about how seed arrival in gaps compares with seed arrival in the understory, even though seed dispersal by wind and animals is expected to be altered in gaps. We documented seed arrival for the first seven years after gap formation in the moist tropical forests of Barro Colorado Island (BCI), Panama, and evaluated how the amount and functional composition of arriving seeds compared with understory sites. On average, in the first three years after gap formation, 72% fewer seeds arrived in gaps than in the understory (207 vs. 740 seeds·m^{-2}·yr^{-1}). The reduction in number of arriving seeds fell disproportionately on animal-dispersed species, which suffered an 86% reduction in total seed number, while wind-dispersed species experienced only a 47% reduction, and explosively dispersed species showed increased seed numbers arriving. The increase in explosively dispersed seeds consisted entirely of the seeds of several shrub species, a result consistent with greater in situ seed production by explosively dispersed shrubs that survived gap formation or recruited immediately thereafter. Lianas did relatively better in seed arrival into gaps than did trees, suffering less of a reduction in seed arrival compared with understory sites. This result could in large part be explained by the greater predominance of wind dispersal among lianas: there were no significant differences between lianas and trees when controlling for dispersal syndromes. Our results show that seed arrival in gaps is very different from seed arrival in the understory in both total seeds arriving and functional composition. Differential seed arrival in gaps will help to maintain wind-dispersed, explosively dispersed, and possibly other understory species in the community of plants that regenerate in gaps.

Key words: *animal-dispersed species; Barro Colorado Island; canopy gaps; dispersal syndrome; gap dependence; lianas; Panama; tropical forest; wind-dispersed species.*

INTRODUCTION

The degree to which regeneration depends on light availability and thus tree fall gaps defines a fundamental axis of life history variation among plant species in closed-canopy forests (Denslow 1987, Pacala et al. 1996). Understanding how gaps differentially influence recruitment of different species is essential to understanding how tree falls contribute to this life history variation. Species differ in their ability to colonize gaps through a seedling bank, a seed bank, or by seed arrival after gap formation, as well as in their responses to gap microenvironments. Many studies have evaluated how species differ in seed and seedling banks, seedling establishment, and in later growth and survival in gaps (e.g., Brokaw 1987, Garwood 1989, Kitajima 1994, Dalling et al. 1998). In contrast, relatively little is known about seed arrival into newly formed gaps (Augspurger

and Franson 1988, Schupp et al. 1989, Loiselle et al. 1996, Dalling et al. 2002, Jones et al. 2005, Du et al. 2011), and, to the best of our knowledge, there are no data in the literature concerning changes in seed arrival as gaps recover and close.

Seed deposition is expected to differ between gaps and understory for several reasons (Schupp et al. 1989). Differences in solar heating of gaps vs. the surrounding canopy and changes in canopy height at gap edges combine to alter wind patterns and seed deposition by wind (Augspurger and Franson 1988, Bohrer et al. 2008). The loss of canopy cover and perch sites within gaps reduces seed deposition by most arboreal animals, birds, and bats; however, other species are attracted to the occasional tree or dead trunk that survives gap formation or to the dense tangles of vegetation found near the ground in many newly formed gaps (Schemske and Brokaw 1981, Blake and Hoppes 1986, Levey 1988, Wenny 2000). In situ seed production increases among herbs, shrubs, and treelets that survive gap formation, escape light limitation, and increase reproductive effort (Schnitzer and Carson 2001). As gaps close, environmental conditions change rapidly, leading to further changes in wind patterns, animal movements, seed

production, and seed deposition. In the long term, seed deposition returns to the pattern for tall forest; however, in the short term, seed deposition may differ from both new gaps and tall forest, and from a linear interpolation between these two endpoints. Schupp et al. (1989) predicted (1) more wind-dispersed and fewer animal-dispersed seeds would arrive in the center of a newly formed gap than in the nearby understory; (2) more small, but not large, animal-dispersed seeds would arrive in gaps than in the understory during the early stages of gap regeneration; and (3) seed arrival in gaps would converge on understory values as gap vegetation matured and the gap closed.

Schupp et al. (1989)'s prediction that new gaps would have more wind-dispersed and fewer animal-dispersed seeds arriving has been evaluated several times, with mixed results. In a three-month study of paired gap and adjacent understory traps on Barro Calorado Island (BCI), Augspurger and Franson (1988) observed nonsignificant trends for wind-dispersed species to show higher seed arrival in gaps than understory, and animal-dispersed species to show the opposite. A study of paired gap and understory traps at La Selva, Costa Rica, found fewer wind-dispersed seeds, but more wind-dispersed species arrived in gaps than in the understory (Loiselle et al. 1996). Analyses of 14 BCI species by Dalling et al. (2002) and Jones et al. (2005) found no significant differences in seed arrival between gap and understory sites in 13 species; however, the bird-dispersed shrub *Palicourea guianensis* had higher seed arrival in gaps. Gap and understory sites in a subtropical forest in China did not differ in the density of all arriving seeds, or the density of wind-dispersed seeds (Du et al. 2011). Finally, in a frugivore-centric analysis, four bird species tended to disperse seeds to the understory, while a fifth species tended to disperse seeds to gaps at Monteverde, Costa Rica (Wenny and Levey 1998). The other predictions of Schupp et al. (1989) have yet to be evaluated.

An additional prediction concerns plant life-forms. Lianas might do relatively better than trees with respect to seed arrival into gaps for two reasons. First, lianas are more likely to be wind-dispersed, and wind-dispersed seeds might be more likely to arrive in gaps (Augspurger and Franson 1988, Schupp et al. 1989, Loiselle et al. 1996; but see Bohrer et al. 2008). Dispersal mode and life-form covary in the neotropics (Gentry 1988, Hammond and Brown 1995). BCI is typical with wind-dispersed seeds characterizing 60% of liana species, 25% of canopy tree species; and <10% of treelet and shrub species (Muller-Landau and Hardesty 2005). Second, lianas might prosper in gaps because of their plastic growth. Lianas can grow laterally into gaps from the nearby understory and can survive after being dragged to the forest floor as gaps form (Putz 1984, Schnitzer et al. 2000, Schnitzer and Carson 2010, Schnitzer and Bongers 2011, Dalling et al. 2012). The density of individual lianas and, after correcting for numbers of individuals, the density of liana species are greater in gaps than in paired understory sites on BCI (Schnitzer et al. 2000, Dalling et al. 2012). Because life-form, dispersal mode, and growth plasticity are confounded and might influence seed arrival, we will consider factorial combinations of life-form (lianas vs. freestanding) and seed dispersal mode (wind vs. animal vs. explosive). One combination (explosively dispersed lianas) is absent from our data. We will refer to the five remaining combinations as functional groups.

Gap conditions might influence the number, mass, and diversity of seeds arriving both in absolute terms (total amount arriving) and in relative terms (proportion of total). More than 700 seeds arrive per square meter per year on BCI, with many dropping from the plants directly overhead (Harms et al. 2000, Muller-Landau et al. 2008). Because there are no plants directly overhead in new tree fall gaps, we predict absolute seed arrival will be lower in gaps than in the understory for all functional groups and all three metrics: total seed number, total seed mass, and total seed species number. Nonetheless, the predictions of Schupp et al. (1989) might still be realized in relative terms, with gaps favoring wind-dispersed species relative to animal-dispersed species and, among animal-dispersed species, small-seeded species relative to large-seeded species. We quantified relative success as the proportions of seed number, seed mass, and species number arriving and absolute success as the density arriving. Thus, we considered the effects of gaps and gap age for absolute and relative values of three seed metrics (species number, seed number, and total seed mass) and five functional groups.

We quantified seed arrival during the first seven years after gap formation on BCI and evaluated the following predictions:

1) Absolute seed arrival is lower in first-year gaps than in the understory for all seed metrics and functional groups and converges smoothly on understory values in subsequent years.
2) Relative seed arrival in gaps is lower for animal-dispersed seeds and greater for wind-dispersed seeds (Augspurger and Franson 1988, Schupp et al. 1989).
3) Among animal-dispersed species, relative seed arrival in gaps is lowest for large-seeded species (Schupp et al. 1989). Therefore, total seed mass arriving in gaps declines more than total seed number.
4) Relative seed arrival in gaps is greater for lianas and lower for freestanding species (henceforth trees) (Schnitzer et al. 2000, Dalling et al. 2012).
5) In new gaps, the mechanism for prediction 4 is the higher frequency of wind dispersal among lianas (Gentry 1988, Muller-Landau and Hardesty 2005). Therefore, wind-dispersed trees and lianas experience the same relative increase, and animal-dispersed trees and lianas experience the same relative decrease in newly formed gaps.

6) In older gaps, the mechanism for prediction 4 is growth of lianas into gaps and gap edges providing in situ seed sources (Schnitzer et al. 2000, Dalling et al. 2012). Therefore, seed arrival recovers more rapidly for lianas than for trees with the same dispersal syndrome.

METHODS

Study site and species

Barro Colorado Island (BCI), Panama, (9°10′ N, 79°51′ W) supports moist tropical forest. Annual rainfall averages 2600 mm, with a pronounced dry season from mid December to mid April. Frugivores are protected from hunters, and the frugivore community is largely intact, with the only missing species being macaws and white-lipped peccaries (Muller-Landau and Hardesty 2005). This study was conducted in the 50-ha forest dynamics plot (Condit 1998), where the forest has been little disturbed for at least 1500 years, with the exception of a small (<2 ha) patch of ~150-year-old secondary forest (Piperno 1990). We classified woody species as liana (L) or freestanding (T, trees) and animal-dispersed (A), wind-dispersed (W), or explosively (ballistically) dispersed (E) based on published records (Croat 1978) and unpublished observations of Osvaldo Calderón, Bonifacio DeLeon, and S. J. Wright.

Seed trap census

We quantified seed production using 200 seed traps set in a systematic random design along 2.7 km of trails within the 50-ha plot in January 1987 (Wright and Calderón 2006). We placed 50 additional traps in the centers of newly formed canopy gaps between June 2002 and June 2004 (Appendix: Fig. A1). The 50 additional traps were placed within three weeks of gap formation in large gaps created by the deaths of two or more canopy trees. We refer to the 200 randomly placed traps as "understory" traps, because the vast majority of them were in the understory at any given time, and we lack useful information on which, if any, might have been in gaps. We censused all 250 traps weekly. Our analyses include censuses from 12 June 2002 through 31 December 2010.

Each seed trap consists of a square, 0.5-m² Polyvinyl chloride (PVC) frame supporting a shallow, open-topped, 1-mm mesh bag suspended 0.8 m above the ground on four PVC posts. All seeds and fruits that fall into the traps are identified to species and counted. Because the seed traps are located above the ground, they capture fruits and seeds falling directly from plants, as well as those dropped, spat, or defecated by birds, bats, and arboreal mammals. The traps do not record secondary dispersal of fallen seeds. For each species, trap, and year, seed number was calculated as the sum of the number of simple seeds and the number of fruits multiplied by species-specific mean seed-to-fruit ratios.

Seed mass was then calculated by multiplying seed number by species-specific mean fresh diaspore mass.

Analyses

To characterize changes in seed arrival between gaps and understory as gaps age, we calculated annual seed rain metrics for each year after gap formation. Because most species fruit at a characteristic time of year (Zimmerman et al. 2007) and levels of seed production vary widely among years (Appendix: Fig. A2; Wright and Calderón 2006), we based all comparisons of seed arrival in gaps and understory on contemporaneous censuses. As an example, the first five gap traps were established on 12 June 2002. We calculated annual seed rain metrics starting on the week of 12 June for these five traps, with the first year after gap formation ending after 52 weeks, the second year after 104 weeks, and so on. We repeated this calculation for every gap trap, replacing 12 June 2002 with trap-specific start dates. We also calculated annual metrics for all 200 understory traps for each start date associated with a gap trap.

We then pooled the annual metrics by year after gap formation and bootstrapped (sampled with replacement) to determine 95% confidence intervals. The bootstrap algorithm controlled the proportional representation of trap start dates to compare contemporaneous seed rain. To do this, we first drew 50 gap traps and tallied the proportional representation of each start date. We then applied the same proportional representation of start dates to a random draw of 200 understory traps. For each year after gap formation, we then calculated a gap : understory ratio as the mean value of the metric in gaps divided by the mean value in understory. Ratios less than 1 indicate lower values in gaps than in the understory. We performed 1000 bootstraps to calculate 95% confidence intervals for gap : understory ratios for each metric. Predictions were significant when 95% confidence intervals did not overlap.

We calculated gap : understory ratios and 95% confidence intervals for six metrics for the five functional groups, the two life-forms pooled over dispersal modes, and the three dispersal modes pooled over life-forms. The six metrics were the number and proportion of species, the number and proportion of individual seeds, and the fresh mass and proportion of total fresh mass of arriving seeds. The functional groups combined life-form (trees [T] vs. lianas [L]) and dispersal modes (animal [A], explosive [E], and wind [W]). The five functional groups were the combinations AT, AL, ET, WT, and WL (there were no explosively dispersed lianas). The six predictions can now be restated for specific metrics and functional groups (using the same numbers used in the Introduction):

1) Gap : understory ratios for absolute metrics (number of species, number of seeds, and fresh mass) are predicted to be significantly less than 1 for the first year after gap formation and to increase smoothly

toward 1 during the first seven years after gap formation for all five functional groups.

2) Gap : understory ratios for relative metrics (proportions of species, seeds, and fresh mass) are predicted to be significantly smaller for animal-dispersed seeds than for wind-dispersed seeds (and for AT vs. WT and AL vs. WL).

3) For animal-dispersed species, the gap : understory ratio for seed mass is predicted to be significantly smaller than the gap : understory ratio for number of seeds.

4) Gap : understory ratios for relative metrics (proportions of species, seeds, and fresh mass) are predicted to be significantly greater for lianas than for trees.

5) Gap : understory ratios for relative metrics (proportions of species, seeds, and fresh mass) are predicted to be similar for WT and WL, similar for AT and AL, and significantly greater for wind-dispersed seeds than for animal-dispersed seeds in the first year after gap formation (WT > AT, WL > AL, and pooled wind-dispersed > pooled animal-dispersed).

6) Gap : understory ratios for all six metrics are predicted to recover (approach 1) more quickly with years since gap formation for liana seeds than for tree seeds (AL > AT, WL > WT, and pooled liana > pooled tree).

RESULTS

Composition of the seed rain

The 250 traps captured 816 281 seeds representing 363 woody species between 12 June 2002 and 31 December 2010. The 363 species included 193 animal-dispersed trees (AT), 58 animal-dispersed lianas (AL), 26 wind-dispersed trees (WT), 76 wind-dispersed lianas (WL), and 10 explosively dispersed trees (ET). Because there are just 10 explosively dispersed species, their results are relegated to the Appendix: Figs. A8 and A9. The understory traps, which serve as our baseline for comparison, averaged 10.6 seed species·trap^{-1}·yr^{-1}, 740.4 individual seeds·m^{-2}·yr^{-1}, and 65.6 grams fresh mass of seeds·m^{-2}·yr^{-1}.

Two of the five functional groups dominated seed arrival. There were more species of animal-dispersed trees than of the four remaining functional groups combined. Animal-dispersed trees also dominated total seed mass (63.9 kg vs. 2.7 kg for the remaining groups); however, wind-dispersed trees dominated seed number, with just four wind-dispersed tree species (*Alseis blackiana*, *Jacaranda copaia*, *Luehea seemannii*, and *Terminalia amazonia*) comprising 38% of total seed number. Thus, temporal patterns of seed arrival for all woody plants over time since gap formation closely matched animal-dispersed trees for species number (compare Figs. 1A and 2B) and seed mass (Figs. 1C and 2J) and were intermediate between animal- and wind-dispersed trees for seed number (Figs. 1B, 2E, and 2F).
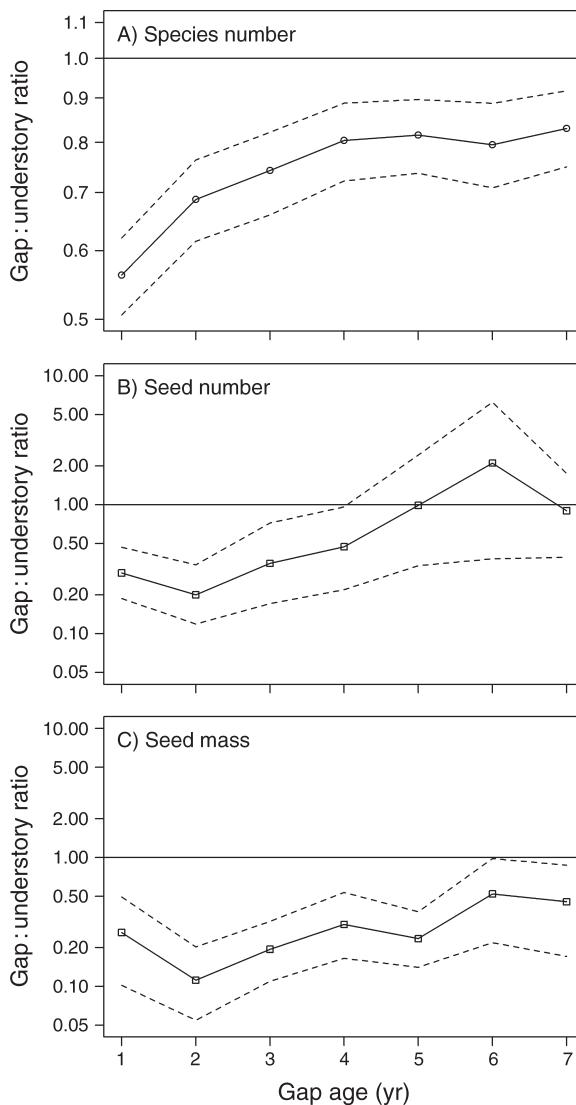

FIG. 1. The effects of gap age on (A) species number, (B) seed number, and (C) seed mass arriving for all woody species combined for the first seven years after gap formation in the moist tropical forests of Barro Colorado Island (BCI), Panama. Gap : understory ratios (open symbols and solid lines; note the log scale) were calculated as the mean value per trap and year in gaps divided by the corresponding mean value in the understory, and 95% confidence intervals (dashed lines) were obtained by bootstrapping over traps.

Prediction 1: Absolute seed arrival

In the first year after gap formation, about half as many species arrived in gaps as in the understory (Fig. 1A). As gaps aged, the species richness of arriving seeds approached that of understory sites; however, the gap : understory ratio remained significantly below 1 through year 7 (Fig. 1A and Appendix: Fig. A7A, Table A1A). The Shannon diversity index with species weighted by number or by mass of arriving seeds was significantly lower for gaps than for understory sites in
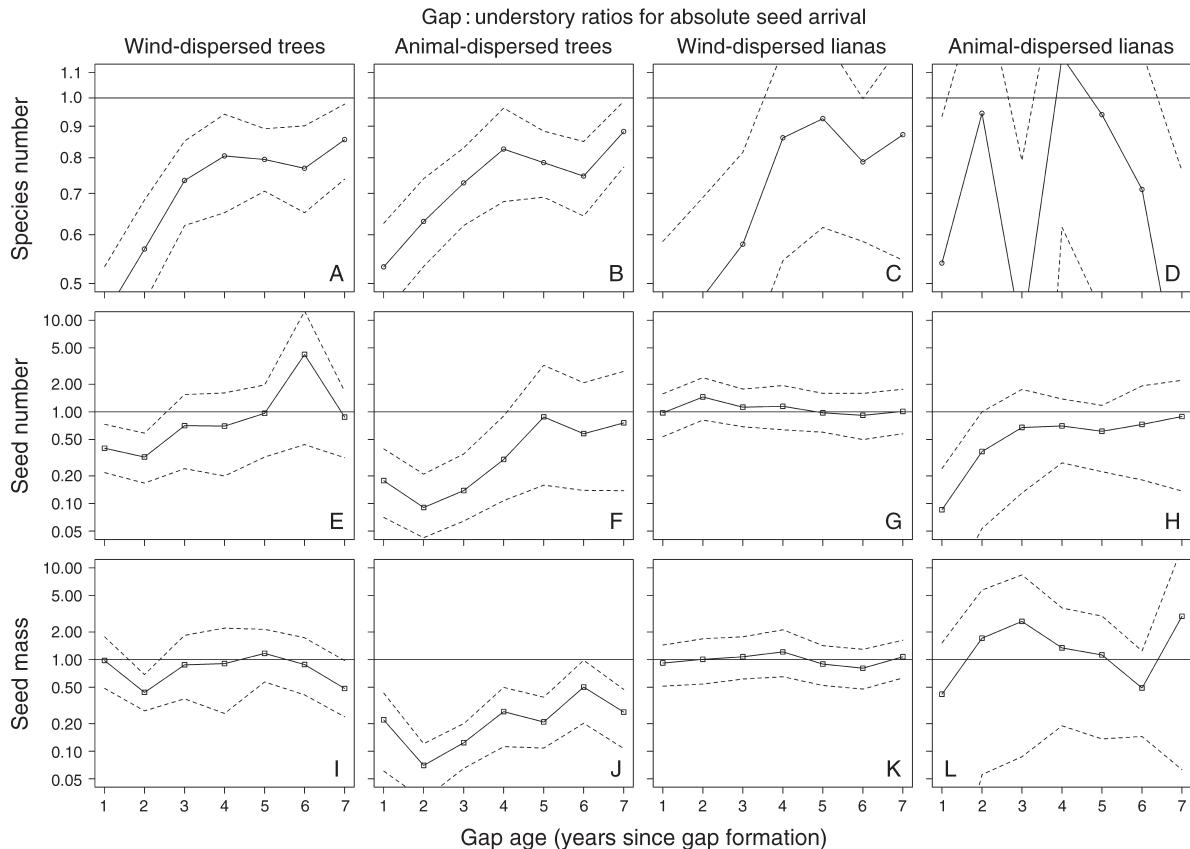
Fig. 2. The effects of gap age on the (A–D) absolute numbers of species and (E–H) seeds and (I–L) seed mass arriving for four functional groups: (A, E, I) wind-dispersed trees, (B, F, J) animal-dispersed trees, (C, G, K) wind-dispersed lianas, and (D, H, L) animal-dispersed lianas. Gap : understory ratios (open symbols and solid lines) were calculated as the mean value per trap and year in gaps divided by the corresponding mean value in the understory, and 95% confidence intervals (dashed lines) were obtained by bootstrapping over traps.

only the first year after gap formation (Appendix: Fig. A7B, C).

The total number of seeds arriving in gaps was just 30% of the number arriving in the understory in the first year after gap formation (Fig. 1B; Appendix: Table A1B). Gaps continued to receive significantly fewer seeds than understory sites for the first four years after gap formation, with a gradual increase over this period and a return to understory levels in year 5 (Fig. 1B; Appendix: Table A1B). Differences were greater for seed mass, with gap traps receiving <25% of the seed mass of understory traps through five years and significantly lower seed mass throughout all seven years (Fig. 1C; Appendix: Table A1C).

Absolute seed rain was significantly lower in first-year gaps than in the understory for 9 of 15 combinations of seed metrics and functional groups (Fig. 2 and Appendix: Fig. A8, Table A1B). All five functional groups had fewer species arriving in first-year gaps than in the understory, three (WT, AT, and AL) had lower seed number, and one (AT) had lower seed mass. The first year gap : understory ratio did not differ significantly from 1 for the six remaining combinations of seed

metrics and functional groups (Fig. 2 and Appendix: Fig. A8, Table A1B). With increasing gap age, the observed gap : understory ratios for absolute seed arrival tended to return to 1 for most functional groups and metrics, and there were fewer and fewer cases that were significantly different from 1.

Prediction 2: Relative seed arrival of animal- and wind-dispersed seeds

Animal-dispersed species contributed a significantly lower proportion of species number, seed number, and seed mass in new gaps, while wind-dispersed species contributed a significantly higher proportion, with these effects declining with gap age (Figs. 3 and 4, Table 1). This pattern was especially pronounced among trees: Animal-dispersed trees had relative gap : understory ratios significantly less than 1 for species number, seed number, and seed mass for seven, three, and seven years after gap formation, respectively, while wind-dispersed trees had ratios significantly larger than 1 in all but two of these same years (Fig. 4). Lianas showed much the same trends, although results were less often statistically significant. Animal-dispersed lianas had gap : understory
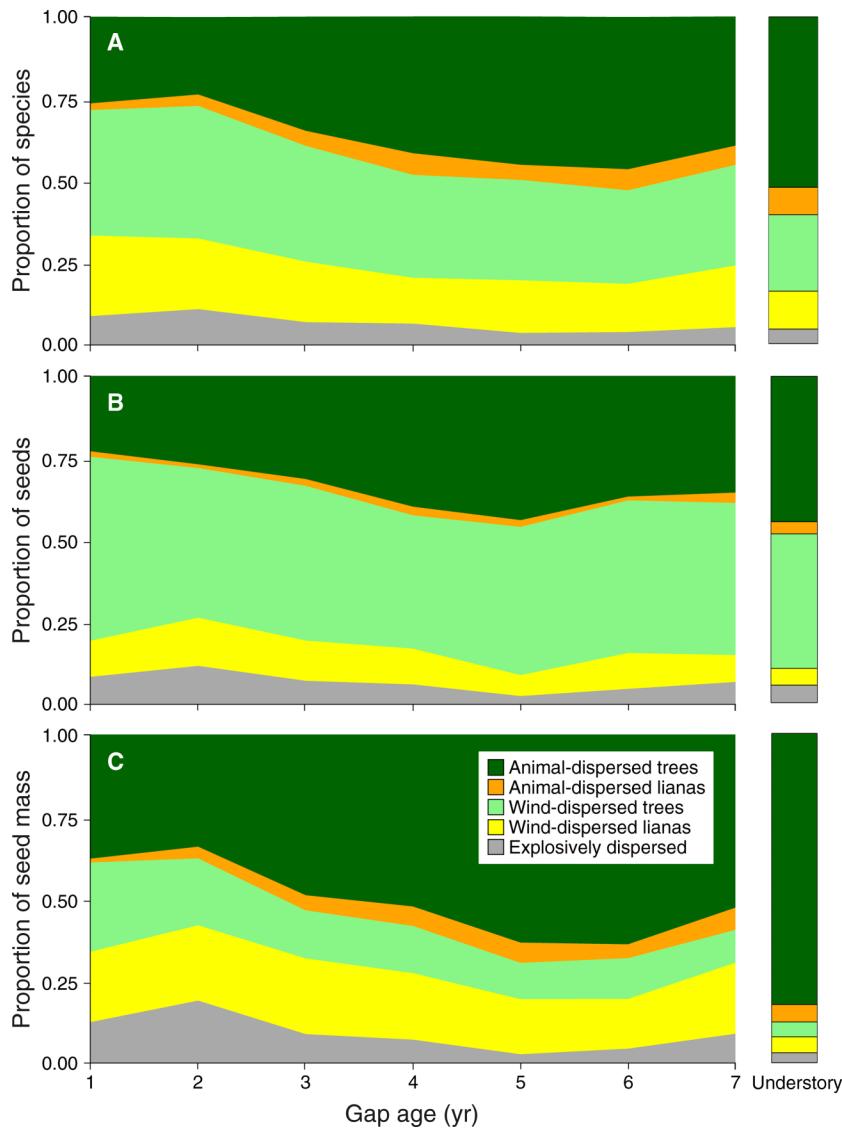
FIG. 3. Proportional contribution of five functional groups (wind- and animal-dispersed trees and lianas, and explosively dispersed species) to (A) the number of species, (B) the number of seeds, and (C) the mass of seeds arriving in the first seven years after gap formation (left-hand panels) and in the understory for the corresponding period (right-hand panels).

ratios significantly less than 1 for seven, two, and one years for species number, seed number, and seed mass, respectively, while ratios for wind-dispersed lianas were significantly larger than 1 for seven, one, and seven years, respectively (Fig. 4). The results for trees and lianas combined largely matched those for trees of the same dispersal syndrome (Appendix: Table A2).

Prediction 3: Seed mass vs. seed number
for animal-dispersed seeds

There was a trend for animal-dispersed trees to suffer a greater reduction of seed mass than of seed number in gaps, while the opposite trend was observed among lianas (Fig. 3). Specifically, the gap : understory ratio for absolute seed mass was smaller than the gap : understory

ratio for absolute seed number in six years for animal-dispersed trees, just one year for animal-dispersed lianas, and four years for both life-forms combined (Appendix: Table A1B, C). None of these differences were statistically significant.

Prediction 4: Relative seed arrival of lianas and trees

Lianas as a group tended to have higher relative seed arrival in gaps than did trees for most years and metrics. In terms of relative species number and relative seed number, lianas had gap : understory ratios larger than 1 in six and five years, respectively, but these differences were never statistically significant (Table 1). In terms of relative seed mass, lianas had gap : understory ratios ranging from 1.51 to 2.17, which were significantly

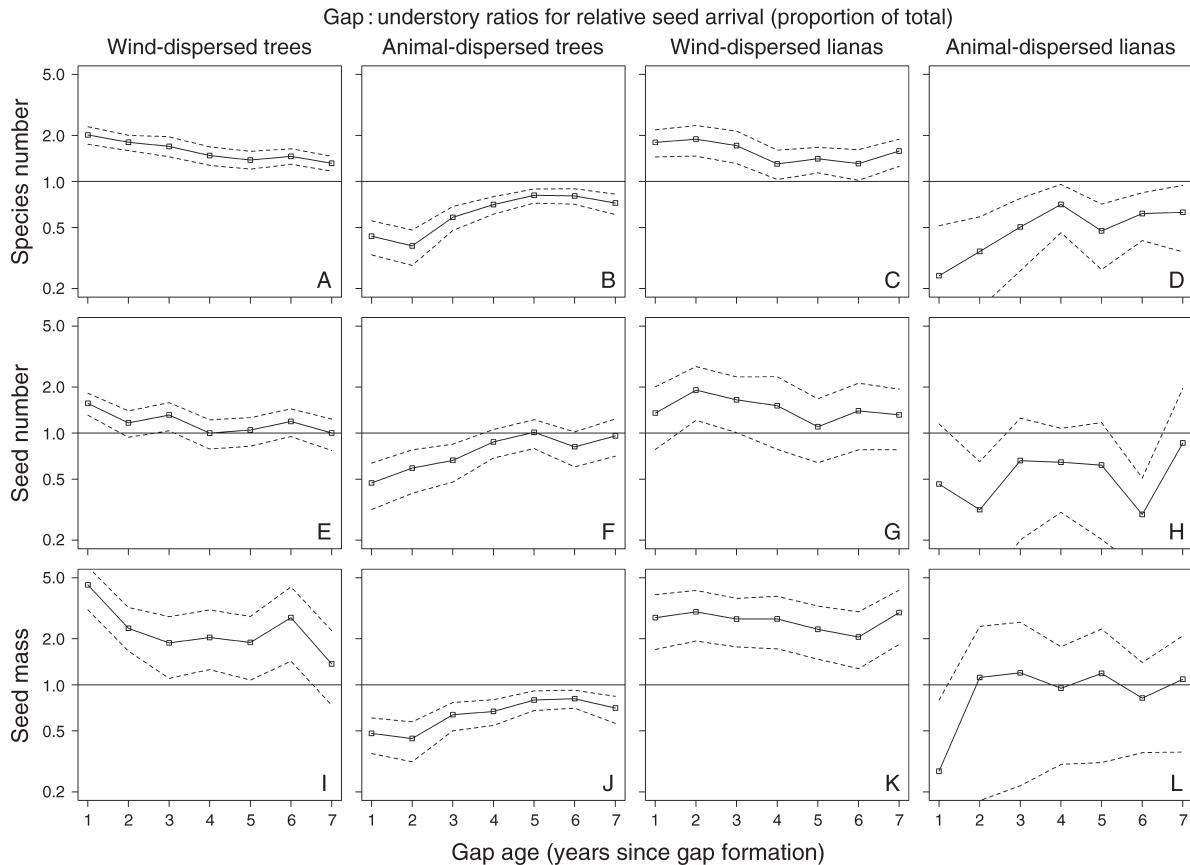Gap : understory ratios for relative seed arrival (proportion of total)

FIG. 4. The effects of gap age on the relative proportions of (A–D) species, (E–H) seeds, and (I–L) seed mass arriving for four functional groups: (A, E, I) wind-dispersed trees, (B, F, J) animal-dispersed trees, (C, G, K) wind-dispersed lianas, and (D, H, L) animal-dispersed lianas. Gap : understory ratios (open symbols and solid lines) were calculated as the mean value per trap and year in gaps divided by the corresponding mean value in the understory, and 95% confidence intervals (dashed lines) were obtained by bootstrapping over traps.

larger than 1 in all seven years, while trees had gap : understory ratios ranging from 0.83 to 0.92, which were significantly less than 1 in all seven years (Table 1).

Prediction 5: Relative seed arrival of lianas and trees within dispersal modes

When lianas and trees were compared within dispersal modes, they showed very similar relative seed arrival in gaps, across all years (Fig. 4; Appendix: Table A2). Indeed, within dispersal syndromes, the gap : understory ratios for relative seed arrival of lianas and trees were never significantly different (Appendix: Table A2); however, confidence intervals were quite large, especially for animal-dispersed lianas, reflecting low statistical power.

Prediction 6: Recovery of seed arrival of lianas and trees with gap age

There was a nonsignificant trend for absolute seed arrival to return to understory values more quickly for animal-dispersed lianas than for animal-dispersed trees

(Fig. 2; Appendix: Table A1). Wind-dispersed lianas and wind-dispersed trees showed roughly similar recovery patterns (Fig. 2). Absolute seed arrival of lianas in gaps never overshot understory values; gap : understory ratios were never significantly greater than 1, for wind-dispersed lianas, animal-dispersed lianas, or lianas as a group (Fig. 2, Table 1). This was not simply an issue of wide confidence intervals: the observed mean itself was less than 1 (albeit usually not significantly) in a majority of cases.

Explosively dispersed species

We did not make predictions about explosively dispersed species; however, relative gap : understory ratios were significantly greater than 1 for species number, seed number, and seed mass through the first four, two, and four years after gap formation, respectively (Appendix: Fig. A9). The importance of explosively dispersed species in gaps declined with time after gap formation (Appendix: Fig. A9).

DISCUSSION

We documented seed arrival for the first seven years after gap formation in the moist tropical forest of Barro Colorado Island (BCI), Panama, and evaluated six predictions concerning associations between seed arrival and three plant traits. The traits included life-form, seed dispersal mode, and seed mass. Combinations of life-form and dispersal mode comprised five functional groups (animal- and wind-dispersed trees, animal- and wind-dispersed lianas, and explosively dispersed trees). Our seven-year data set enabled the first evaluation of predictions concerning seed arrival as gap vegetation recovers and understory conditions are re-established. Our conclusions regarding differences between gap and understory are conservative as our "understory" traps almost certainly included some traps in gaps.

Schupp et al. (1989) predicted absolute seed arrival would be greatest in newly formed gaps for wind-dispersed seeds, in maturing gaps for small animal-dispersed seeds, and in the understory for large animal-dispersed seeds. In contrast, we predicted absolute seed arrival would be greatest in the understory for all functional groups (Prediction 1). We based this prediction on previous analyses of understory seed arrival. The tree or liana directly overhead dominates understory seed arrival (Harms et al. 2000, Muller-Landau et al. 2008). Newly formed gaps lack reproductive plants directly overhead. For this reason, we predicted absolute seed arrival would be lower in gaps than in the understory. Nine of 15 analyses provided significant results consistent with this prediction, and not one analysis found significantly greater absolute seed arrival in gaps than in the understory (Fig. 2 and Appendix: Fig. A8).

Augspurger and Franson (1988), Schupp et al. (1989), and Loiselle et al. (1996) predicted greater arrival of wind-dispersed seeds in gaps than in the understory. They reasoned that the broken canopy at gap edges and solar heating of gaps would alter winds and enhance deposition of wind-dispersed seeds in gaps. Atmospheric physicists now predict the opposite, with forest gaps enhancing wind sweeps, updrafts, and ejection of seeds above the surrounding canopy (Bohrer et al. 2008). Thus, absolute seed arrival should be lower in gaps than in the understory for wind-dispersed species. Five of nine analyses for wind-dispersed species provided significant results consistent with this latter prediction: Seed number per trap was significantly lower in young gaps for wind-dispersed species overall (Table 1) and for wind-dispersed trees (Fig. 2E), and species number was significantly lower for wind-dispersed trees, wind-dispersed lianas, and wind-dispersed species overall (Table 1, Fig. 2A, C). This contrasts with the results of Augspurger and Franson (1988) in the same site, who report higher seed arrival of wind-dispersed species in gaps. However, the difference they observed was not statistically significant, and reflects just 12 weeks of data

from 86 traps with a total area of 9.5 m^2, a much smaller sampling effort than our study (7 years of data from 250 traps with a total area of 125 m^2).

Wind-dispersed seeds do comprise a larger proportion of all seeds arriving in gaps than in the understory, reflecting a greater absolute decline in seed arrival in gaps for animal-dispersed than for wind-dispersed seeds (Fig. 4; Prediction 2; Augspurger and Franson 1988, Loiselle et al. 1996, Du et al. 2011). There is a simple explanation. Wind-dispersed seeds tend to disperse further than animal-dispersed seeds, and, more importantly, a smaller proportion of wind-dispersed seeds fail to disperse, ending up on the ground under their seed parent (Muller-Landau et al. 2008). Thus, dispersal tends to bring relatively more wind-dispersed than animal-dispersed seeds into gaps simply because a larger proportion of wind-dispersed seeds disperses beyond the parent crown. This effect would be reinforced if gaps had a larger negative impact on seed deposition by animals than by wind (Prediction 2), but our analyses cannot discriminate between these two mechanisms.

Lianas were significantly overrepresented among seeds arriving in gaps relative to trees (Prediction 4; Table 1). Two compatible mechanisms might contribute. First, liana seeds might be overrepresented in gaps because 60% of BCI liana species are wind-dispersed, and wind-dispersed seeds are overrepresented in gaps (Prediction 5). Second, lianas might flourish in and near gaps and in situ seed production might also contribute (Prediction 6). We found that seeds of wind-dispersed lianas were overrepresented in gaps, at levels similar to wind-dispersed trees, while animal-dispersed lianas were generally underrepresented in gaps, at levels similar to animal-dispersed trees (Fig. 4; Appendix: Table A2B). This suggests that the association between life-form and dispersal mode largely explains the relative importance of liana seeds in gaps.

We observed significant increases in the relative importance of explosively dispersed seeds in gaps, a result we did not anticipate (Appendix: Fig. A9). Explosively dispersed species included four abundant understory shrubs (*Hybanthus prunifolius*, *Acalypha macrostachya*, *Rinorea sylvatica*, and *Anaxagorea panamensis*). The traps capture large numbers of seeds of two of these species (*Hybanthus* and *Acalypha*), despite the fact that these short-statured species are probably systematically underrepresented because they may release their seeds at or below the height of the traps. Release from light limitation might have permitted increased in situ seed production in tree fall gaps by surviving adults of these abundant understory species (Schnitzer and Carson 2001). The short dispersal distances characteristic of explosively dispersed species (Muller-Landau et al. 2008) would ensure that most seeds remained in the gap. Disproportionate declines in the absolute number of animal-dispersed species in gaps (Fig. 2F, H) would reinforce absolute increases in arrival

TABLE 1. Gap:understory ratios for mean seed arrival metrics for the first seven years after gap formation for both life-forms (lianas vs. freestanding species) and the two main dispersal modes (animal and wind) in the moist tropical forests of Barro Colorado Island (BCI), Panama.

	Years after gap formation		
Functional group	1	2	3
A) Absolute species number per trap per year			
Animal (A)	*0.60* (0.52–0.68)	*0.69* (0.59–0.80)	*0.79* (0.70–0.89)
Wind (W)	*0.50* (0.41–0.59)	*0.59* (0.49–0.69)	*0.74* (0.62–0.86)
Lianas (L)	*0.43* (0.29–0.60)	*0.52* (0.35–0.73)	*0.56* (0.35–0.82)
Trees (T)	*0.66* (0.60–0.72)	*0.71* (0.63–0.80)	*0.78* (0.71–0.85)
B) Absolute seed number per trap per year			
Animal (A)	*0.18* (0.07–0.39)	*0.09* (0.04–0.22)	*0.14* (0.06–0.37)
Wind (W)	*0.43* (0.24–0.78)	*0.40* (0.23–0.70)	0.76 (0.30–1.77)
Lianas (L)	*0.61* (0.34–0.97)	1.06 (0.67–1.56)	1.01 (0.67–1.46)
Trees (T)	*0.31* (0.19–0.50)	*0.20* (0.12–0.33)	*0.34* (0.16–0.71)
C) Absolute seed mass per trap per year			
Animal (A)	*0.22* (0.07–0.44)	*0.09* (0.04–0.18)	*0.16* (0.07–0.28)
Wind (W)	0.99 (0.61–1.50)	*0.68* (0.47–0.94)	1.00 (0.62–1.57)
Lianas (L)	0.67 (0.29–1.25)	1.39 (0.38–3.49)	1.79 (0.50–4.52)
Trees (T)	*0.25* (0.09–0.45)	*0.09* (0.04–0.13)	*0.14* (0.08–0.21)
D) Relative species number per trap per year			
Animal (A)	*0.41* (0.30–0.51)	*0.37* (0.28–0.47)	*0.57* (0.48–0.67)
Wind (W)	**1.92** (1.72–2.11)	**1.87** (1.70–2.03)	**1.69** (1.50–1.87)
Lianas (L)	1.17 (0.97–1.39)	1.24 (0.98–1.51)	1.21 (0.97–1.45)
Trees (T)	0.96 (0.90–1.02)	0.94 (0.88–1.01)	0.95 (0.90–1.00)
E) Relative seed number per trap per year			
Animal (A)	*0.47* (0.32–0.64)	*0.57* (0.39–0.75)	*0.66* (0.49–0.84)
Wind (W)	**1.52** (1.32–1.73)	**1.30** (1.11–1.50)	**1.33** (1.11–1.53)
Lianas (L)	1.07 (0.62–1.59)	1.33 (0.85–1.88)	1.34 (0.84–1.88)
Trees (T)	0.99 (0.92–1.05)	0.95 (0.89–1.02)	0.96 (0.91–1.02)
F) Relative seed mass per trap per year			
Animal (A)	*0.47* (0.34–0.61)	*0.47* (0.34–0.60)	*0.66* (0.53–0.79)
Wind (W)	**3.48** (2.65–4.29)	**2.73** (2.04–3.35)	**2.25** (1.68–2.85)
Lianas (L)	**1.78** (1.20–2.44)	**2.17** (1.48–2.90)	**2.16** (1.51–2.83)
Trees (T)	*0.89* (0.79–0.98)	*0.84* (0.73–0.93)	*0.83* (0.73–0.93)

Notes: Bootstrapped 95% confidence intervals are given in parentheses. Gap:understory ratios were calculated as the means per year per gap trap divided by the corresponding means per year per understory trap. Thus, for example, the gap:understory ratio for the absolute species number per trap per year equals (mean number of species per year per gap trap)/(mean number of species per year per understory trap). The ratio for relative species number, in contrast, is calculated as follows: (mean proportion of species per year per gap trap)/(mean proportion of species per year per understory trap). Boldface type highlights ratios significantly different from 1, with italics indicating significantly lower than 1. Table A1 in the Appendix provides corresponding values for all combinations of functional groups.

of explosively dispersed seeds (Appendix: Fig. A8), leading to highly significant increases in their relative importance in gaps (Appendix: Fig. A9).

Conclusions and future directions

Over the first three years after gap formation, many fewer seeds arrived in gaps (207 seeds·m^{-2}·yr^{-1}) than in the understory (740 seeds·m^{-2}·yr^{-1}). The reduction in gaps fell disproportionately on animal-dispersed seeds and, in particular, on large animal-dispersed seeds (compare Fig. 3B and C). In contrast, wind-dispersed and explosively dispersed seeds comprised a larger proportion of the seeds arriving in gaps than in the understory (Fig. 4 and Appendix: Fig. A9). Thus, differential seed arrival will favor regeneration by wind-dispersed and explosively dispersed species in gaps at the expense of animal-dispersed species. Further, seed and seedling banks are likely to be relatively more important for regeneration by animal-dispersed species in gaps. Finally, the mechanism that is likely to favor seed arrival in gaps by explosively dispersed species (increased in situ seed production associated with release from light limitation in gaps) might also favor other shrub and treelet species whose adults never reach the forest canopy and are usually light limited. Future work should evaluate the importance of seed rain and its composition for gap regeneration relative to contributions from the seed and seedling banks, which have quite different functional composition.

TABLE 1. Extended.

	Years after gap formation		
4	5	6	7
0.86 (0.73–0.99)	*0.76* (0.67–0.86)	*0.76* (0.66–0.87)	*0.89* (0.79–1.00)
0.80 (0.67–0.94)	*0.80* (0.71–0.89)	*0.75* (0.65–0.87)	0.89 (0.77–1.02)
0.77 (0.54–1.02)	*0.68* (0.48–0.88)	0.84 (0.63–1.06)	0.77 (0.52–1.05)
0.84 (0.75–0.93)	*0.85* (0.78–0.93)	*0.86* (0.77–0.96)	*0.89* (0.81–0.98)
0.31 (0.12–0.82)	0.88 (0.15–2.99)	0.58 (0.15–1.96)	0.76 (0.14–2.57)
0.75 (0.25–1.79)	1.01 (0.35–2.31)	4.10 (0.46–12.65)	0.90 (0.34–1.79)
0.99 (0.65–1.46)	0.80 (0.52–1.15)	0.86 (0.48–1.42)	0.96 (0.54–1.53)
0.45 (0.21–0.93)	0.91 (0.31–2.12)	1.97 (0.38–5.67)	0.81 (0.32–1.69)
0.29 (0.12–0.53)	*0.23* (0.12–0.38)	*0.50* (0.21–0.97)	*0.43* (0.14–0.86)
1.06 (0.56–1.78)	1.04 (0.69–1.53)	0.80 (0.52–1.18)	0.79 (0.52–1.20)
1.31 (0.56–2.68)	1.02 (0.41–2.18)	0.6 (0.31–1.09)	2.52 (0.23–10.99)
0.27 (0.12–0.45)	*0.22* (0.11–0.37)	*0.51* (0.19–0.94)	*0.28* (0.13–0.49)
0.71 (0.62–0.80)	*0.76* (0.68–0.85)	*0.78* (0.69–0.87)	*0.72* (0.62–0.81)
1.43 (1.26–1.60)	**1.39** (1.25–1.53)	**1.41** (1.26–1.56)	**1.41** (1.26–1.57)
1.06 (0.90–1.22)	1.00 (0.82–1.18)	1.01 (0.83–1.18)	**1.21** (1.02–1.42)
0.98 (0.95–1.02)	1.00 (0.96–1.04)	1.00 (0.95–1.04)	0.95 (0.90–1.00)
0.86 (0.67–1.04)	0.98 (0.77–1.18)	*0.77* (0.58–0.97)	0.95 (0.68–1.22)
1.09 (0.89–1.29)	1.04 (0.84–1.23)	**1.25** (1.05–1.45)	1.04 (0.81–1.29)
1.24 (0.81–1.78)	0.91 (0.56–1.33)	0.97 (0.57–1.39)	1.16 (0.74–1.68)
0.97 (0.90–1.02)	1.02 (0.98–1.05)	0.99 (0.93–1.05)	0.99 (0.94–1.03)
0.70 (0.57–0.82)	*0.82* (0.70–0.90)	*0.81* (0.70–0.91)	*0.73* (0.60–0.86)
2.39 (1.76–3.10)	**2.12** (1.53–2.80)	**2.26** (1.59–2.99)	**2.21** (1.52–2.95)
2.04 (1.41–2.74)	**1.82** (1.23–2.54)	**1.51** (1.06–2.00)	**2.14** (1.49–2.84)
0.84 (0.75–0.94)	*0.88* (0.79–0.97)	*0.92* (0.84–0.99)	*0.83* (0.73–0.93)

LITERATURE CITED

Augspurger, C. K., and S. E. Franson. 1988. Input of wind-dispersed seeds into light-gaps and forest sites in a Neotropical forest. Journal of Tropical Ecology 4:239–252.

Blake, J. G., and W. G. Hoppes. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. Auk 103:328–340.

Bohrer, G., G. G. Katul, R. Nathan, R. L. Walko, and R. Avissar. 2008. Effects of canopy heterogeneity, seed abscission and inertia on wind-driven dispersal kernels of tree seeds. Journal of Ecology 96:569–580.

Brokaw, N. V. L. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. Journal of Ecology 75:9–19.

Condit, R. 1998. Tropical forest census plots: methods and results from Barro Colorado Island, Panama and a comparison with other plots. Springer-Verlag, New York, New York, USA.

Croat, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Palo Alto, California, USA.

Dalling, J. W., S. P. Hubbell, and K. Silvera. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. Journal of Ecology 86:674–689.

Dalling, J. W., H. C. Muller-Landau, S. J. Wright, and S. P. Hubbell. 2002. Role of dispersal in the recruitment limitation of neotropical pioneer species. Journal of Ecology 90:714–727.

Dalling, J. W., S. A. Schnitzer, C. Baldeck, K. E. Harms, R. John, S. A. Mangan, E. Lobo, J. B. Yavitt, and S. P. Hubbell. 2012. Resource-based habitat associations in a Neotropical liana community. Journal of Ecology 100:1174–1182.

Dalling, J. W., M. D. Swaine, and N. C. Garwood. 1998. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. Ecology 79:564–578.

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. Annual Review of Ecology and Systematics 18:431–451.

Du, Y., X. Mi, and K. Ma. 2011. Comparison of seed rain and seed limitation between community understory and gaps in a subtropical evergreen forest. Acta Oecologica 44:11–19.

Garwood, N. C. 1989. Tropical soil seed banks: a review. Pages 149–209 in M. A. Leck, V. T. Parker, and R. L. Simpson, editors. Ecology of soil seed banks. Academic Press, San Diego, California, USA.

Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden 75:1–34.

Hammond, D. S., and V. K. Brown. 1995. Seed size of woody plants in relation to disturbance, dispersal, soil type in wet tropical forests. Ecology 76:2544–2561.

Harms, K. E., S. J. Wright, O. Calderón, A. Hernández, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404:493–495.

Jones, F. A., J. Chen, G.-J. Weng, and S. P. Hubbell. 2005. A genetic evaluation of seed dispersal in the Neotropical tree

Jacaranda copaia (Bignoniaceae). American Naturalist 166: 543–555.

Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. Oecologia 98:419–428.

Levey, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. Ecology 69: 1076–1089.

Loiselle, B. A., E. Ribbens, and O. Vargas. 1996. Spatial and temporal variation of seed rain in a tropical lowland wet forest. Biotropica *28*:82–95.

Muller-Landau, H. C., and B. D. Hardesty. 2005. Seed dispersal of woody plants in tropical forests: concepts, examples, and future directions. Pages 267–309 *in* D. F. R. P. Burslem, M. A. Pinard, and S. E. Hartley, editors. Biotic interactions in the tropics. Cambridge University Press, Cambridge, UK.

Muller-Landau, H. C., S. J. Wright, O. Calderón, R. Condit, and S. P. Hubbell. 2008. Interspecific variation in primary seed dispersal in a tropical forest. Journal of Ecology 96:653–667.

Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, Jr., R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecological Monographs 66:1–43.

Piperno, D. R. 1990. Fitolitos, arquelogia y cambios prehistoricos de la vegetacion en un lote de cincuenta hectareas de la Isla de Barro Colorado. Pages 153–156 *in* E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, editors. Ecologia de un bosque tropical. Smithsonian Institution Press, Washington, D.C., USA.

Putz, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. Ecology 65:1713–1724.

Schemske, D. W., and N. Brokaw. 1981. Treefalls and the distribution of understory birds in a tropical forest. Ecology 62:938–945.

Schnitzer, S. A., and F. Bongers. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. Ecology letters 14:397–406.

Schnitzer, S. A., and W. P. Carson. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology 82:913–919.

Schnitzer, S. A., and W. P. Carson. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. Ecology letters 13: 849–857.

Schnitzer, S. A., J. W. Dalling, and W. P. Carson. 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. Journal of Ecology 88:655–666.

Schupp, E. W., H. F. Howe, C. K. Augspurger, and D. J. Levey. 1989. Arrival and survival in tropical treefall gaps. Ecology 70:562–564.

Wenny, D. G. 2000. Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. Ecological Monographs 70:331–351.

Wenny, D. G., and D. J. Levey. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. Proceedings of the National Academy of Sciences USA 95:6204–6207.

Wright, S. J., and O. Calderón. 2006. Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. Ecology Letters 9:35–44.

Zimmerman, J. K., S. J. Wright, O. Calderón, M. A. Pagan, and S. Paton. 2007. Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: the role of annual changes in irradiance. Journal of Tropical Ecology 23:231–251.

SUPPLEMENTAL MATERIAL

Appendix

Figures showing (1) locations of traps, (2) temporal variation in seed rain, (3) proportion of traps for gaps and understory and number of species, seeds, and seed mass for every functional group, (4) effects of gaps on species diversity, and (5) gap : understory ratios for absolute and relative seed arrival (species number, seed number, and seed mass) for explosively dispersed species; and tables presenting gap : understory ratios for absolute and relative seed arrival for all functional groups (*Ecological Archives* E094-140-A1).