Small Tent-Roosting Bats Promote Dispersal of Large-Seeded Plants in a Neotropical Forest

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ABSTRACT

In Neotropical regions, fruit bats are among the most important components of the remaining fauna in disturbed landscapes. These relatively small-bodied bats are well-known dispersal agents for many small-seeded plant species, but are assumed to play a negligible role in the dispersal of large-seeded plants. We investigated the importance of the small tent-roosting bat *Artibeus watsoni* for dispersal of large seeds in the Sarapiquí Basin, Costa Rica. We registered at least 43 seed species > 8 mm beneath bat roosts, but a species accumulation curve suggests that this number would increase with further sampling. Samples collected beneath bat feeding roosts had, on average, 10 times more seeds and species than samples collected 5 m away from bat feeding roosts. This difference was generally smaller in small, disturbed forest patches. Species-specific abundance of seeds found beneath bat roosts was positively correlated with abundance of seedlings, suggesting that bat dispersal may influence seedling recruitment. Our study demonstrates a greater role of small frugivorous bats as dispersers of large seeds than previously thought, particularly in regions where populations of large-bodied seed dispersers have been reduced or extirpated by hunting.

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Key words: Costa Rica; defaunation; forest regeneration; frugivorous bats; seed dispersal.

FRUGIVOROUS BATS REPRESENT AN IMPORTANT PROPORTION of mammal biomass and diversity within the Neotropics (Emmons & Feer 1997). Frugivorous bats are at least as abundant as frugivorous birds, and they persist in relatively high abundances in medium to highly disturbed habitats (*e.g.*, Gorresen & Willig 2004, Faria 2006, Montiel *et al.* 2006). Neotropical bats are widely recognized as effective seed dispersers for small-seeded pioneer trees during early stages of forest regeneration (Medellin & Gaona 1999, Bernard & Fenton 2003, Lobova & Mori 2004). Because of their small body size, fruit bats of the Neotropics are thought to play a negligible role in dispersal of larger uningested seeds, however (see Muscarella & Fleming 2007). This assumption might stem from the fact that the studies evaluating the role of Neotropical fruit bats as seed dispersers are based on the collection of feces during bat captures, which limits records to endozoochoric seed dispersal (Kunz 1988). Few studies have documented epizoochorous events of seed dispersal by bats and very few report bat dispersal of large uningested seeds (but see Lopez & Vaughan 2004, Mello *et al.* 2005).

Tropical tree species present an astonishing range of up to six orders of magnitude in seed mass (0.001–100 g), and exhibit a wide spectrum of seed dispersal and recruitment strategies; approximately 90 percent are animal dispersed (Gentry 1982, Foster 1986). In Neotropical forests, small-seeded species in the genera *Cecropia*, *Vismia*, *Solanum*, and *Piper* are associated with early-successional areas and may have a wide range of seed dispersers available, from ants to monkeys, including many frugivorous bats in the

subfamily Stenodermatinae that scatter seeds widely while defecating during flight (Bonaccorso & Gush 1987). An important component of the flora of mature forests is comprised by large-seeded tree species (*e.g.*, those belonging to Lecythidaceae, Chrysobalanaceae, and Sapotaceae families) that are thought to be dispersed primarily by medium- to large-bodied animals (Poorter & Rose 2005, Wright *et al.* 2007a).

Deforestation causes both loss and alteration of natural habitats, converting large forested areas to mixed landscapes composed of isolated patches of forests and human-modified areas (Daily *et al.* 2003, Laurance 2004, Tabarelli *et al.* 2005, Mayfield *et al.* 2006). Faunal composition in such disturbed landscapes is affected by both reduction in area and overhunting that may strongly deplete populations of large-bodied vertebrates (Peres & Palacios 2007). Thus, the remaining disperser fauna of highly disturbed landscapes is often composed of a subset of the original fauna comprised mainly of small- to medium-sized rodents, small birds, and bats that are thought to disperse primarily small-seeded pioneer plants with few or no importance to disperse large-seeded plant species (Terborgh *et al.* 1997, Melo *et al.* 2006). As a result, extirpation of large frugivores was proposed to be the main cause of long-term extinction of a high percentage of the flora comprised by large-seeded (> 1.5 cm) trees species in Northeastern Brazil (Silva & Tabarelli 2000).

Few studies have documented the role of remaining small-bodied fauna, especially frugivorous bats, in the dispersal of large-seeded species. Because large-seeded fruits cannot be ingested by small-bodied bats, alternative methods are required to detect their dispersal. Such fruits are usually processed by bats in feeding roosts where seeds are deposited after the pulp is consumed (Rodriguez-

Herrera *et al.* 2007). One type of feeding roost is the modified leaves used by tent-roosting bats. In the Neotropics, tent-roosting bats comprise 17 species with both broad and restricted geographical distribution and represent about 22 percent of all Neotropical frugivorous bat species (Rodriguez-Herrera *et al.* 2007). Many tent-roosting bats belong to the genus *Artibeus* (47%; *N* = 8), one of the most abundant frugivorous bat genera in the Neotropics (Bonaccorso 1979, Medellin *et al.* 2000). Thus, it is reasonable to expect that if small-bodied Neotropical bats are important seed dispersers of large uningested seeds, we might encounter dispersed seeds of many species beneath feeding roosts.

In this study we suggest, contrary to what is commonly assumed in the literature, that Neotropical fruit bats can disperse a vast diversity of seeds they cannot ingest (large seeds). For this, we sampled the seeds deposited beneath leaf tents used for food processing by the small tent-roosting bat *Artibeus watsoni* (Thomas 1901) in a Costa Rican tropical wet forest. We first report the observed number of seed species > 8 mm found under leaf tents. Second, to evaluate how tent-roosting bats may influence overall patterns of large seed rain in the forest, we compare the abundance, richness, and composition of seeds present in samples under bat roosts with samples collected 5 m away from leaf tents. Furthermore, we compare bat-generated seed rain between large, undisturbed reserves and small, disturbed forest patches. Finally, we correlate species-specific abundance of seeds found under bat roosts with the respective abundance of seedlings in both mature and secondary forests. We provide evidence here that Neotropical fruit bats disperse a vast diversity of uningested large seeds, contrary to the common assumptions in the literature.

METHODS

STUDY SITES.—Our study was carried out in three disturbed, small forest patches and two large forest reserves of tropical wet forest in the Sarapiquí Basin, Costa Rica (Table 1; Fig. S1). All study areas are in Submontane Wet Tropical Forest and are located in the same watershed (Sarapiquí Basin) with similar soil and elevation condi-

tions (35–235 m asl) and are separated by a maximum of 6 km (Guariguata *et al.* 1997). Annual rainfall in the region is around 4000 mm and mean temperature is around 25°C (McDade *et al.* 1994). Study areas included mature (LS, TR and RM; Table 1) to secondary forests (BJ and SC; Table 1).

BAT ROOST SAMPLING.—Leaf tents, or bat-constructed roosts in leaves, are used by bats as sleeping roosts during daylight and as feeding roosts at night (Rodriguez-Herrera *et al.* 2007). We searched for a specific type of bat roost, namely bifid tents, constructed from leaves of several understory palm species and palm-like Cyclanthaceae that are usually 1–1.5 m above the soil. These tents are formed by bats making elongated 'J' or 'V' cuts along both sides of the midrib on leaves with bifurcated tips and folding them down along the midrib. Neotropical tent-roosting bats may use up to 77 species of plants to construct tents in at least eight types of architectures (Rodriguez-Herrera *et al.* 2007). We chose to focus on this specific type of tent (bifid) because: (1) they are more abundant and conspicuous in the forest understory of the study sites than other tent types; (2) by concentrating sampling within a single type of tent we excluded, or at least reduced, any possible effect of tent type on the bat-generated seed rain; and (3) these tents are mostly constructed and used by *A. watsoni* bats, although they may be used by other bat species such as *Artibeus cinereus*, *Mesophylla macconnelli*, *Rhinophylla pumilio*, and *Uroderma bilobatum* (Rodriguez-Herrera *et al.* 2007).

Our sampling design consisted of walking through the forest sites looking for as many tents as we could find, ensuring that each sampled leaf tent was at least 100 m apart from other tents. For all leaf tents found, 1 m² of soil surface immediately beneath the tent was scanned for seeds using a wooden frame to delimit the search area. If no seeds were found in a first scan, we recorded a seedless tent that was excluded from further analysis. We excluded seedless tents, as these tents may be used by bats for purposes other than feeding roosts, such as protection against rainfall, regulation of body temperature, protection against predators and parasites, or in sexual selection (Rodriguez-Herrera *et al.* 2007). When seeds were

TABLE 1.   *Number of leaf tents with seeds and seedless tents at each forest site sampled also showing median values and range of number of seeds and seed species > 8 mm found under leaf tents at the Sarapiqui Basin, Costa Rica.*

Site	Geographical position	Forest type	Tents with seeds	Seedless tents	No. seeds (median; range)	No. seed species (median; range)
La Selva (LS)	15°25′52″ N 84°00′10″ W	Mature, large reserve	30	30	433 (5; 1–88)	17 (2; 1–5)
La Tirimbina (TR)	10°23′58″ N 84°08′06″ W	Mature, large reserve	12	26	58 (6.5; 1–10)	13 (2.5; 1–4)
El Bejuco (BJ)	10°27′13″ N 84°03′48″ W	Secondary, small patch	8	10	31 (3.5; 1–7)	7 (1.5; 1–4)
Socorro (SC)	10°25′48″ N 84°05′35″ W	Secondary, small patch	8	3	41 (3.5; 1–12)	12 (2.5; 1–5)
Ramirez (RM)	15°26′41″ N 84°04′57″ W	Mature, small patch	53	14	247 (3; 1–36)	29 (1; 1–5)

found, the leaf litter was first carefully removed and all seeds > 8 mm in length were collected. This cutoff criterion was based on the ability to identify collected seeds without germination treatments. Seeds smaller than this threshold are more likely to be rapidly buried and were often covered by fungus or were too deteriorated to be reliably assigned to species or morphospecies. No buried seeds were collected to avoid including seeds before tent construction by the bats. For each leaf tent with seeds underneath, we also scanned for seeds (using the same cutoff criterion) in four additional quadrats (control quadrats) of the same area (1 m^2) established in the four cardinal directions about 5 m away from the tent quadrats. This procedure was necessary to: (1) compare the bat-generated seed rain with the seed rain sampled in the same forest site but away from the tent influence; (2) exclude from tent quadrats any seed species also found in at least one of the nearby control quadrats, thus distinguishing and eliminating seeds that could be present in tent quadrats due to contagious seed rain of fruiting trees in the vicinity. The four tent quadrats were pooled for all subsequent analyses and compared against tent quadrats with seeds. This experimental design was suitable for testing our hypothesis because we could compare the effect of bat tents on seed rain while controlling for local tree species composition. However, resources for construction of tents (understory palms and Cyclanthaceae) are more abundant in mature forest sites than in disturbed areas (Capers *et al*. 2005); thus, number of seeds and species in tent and nontent quadrats were standardized to a quadrat basis (1 m^2) for statistical comparisons. All leaf tents were visited once between April and June 2007, before the peak fruiting period for the flora of this region (August–October). All seeds collected were identified to the finest taxonomic level possible by comparison with herbarium specimens of fruits at LS and consultations with a plant taxonomist (Orlando Vargas from La Selva staff). Species were also classified according to their preferred habitat (mature forest vs. successional forest) and life form based on the descriptions available in the 'Flora Digital de La Selva' data base available online (http://sura.ots.ac.cr/local/florula3/en/index.htm).

BAT SEED DISPERSAL AND SEEDLING RECRUITMENT.—To assess the potential contribution of bat-generated seed rain for the seedling community in both mature and secondary forests, we used data on woody seedling recruitment previously collected in 1 ha forest monitoring plots in four secondary and two mature forest sites within the study region. In each plot, we surveyed all tree seedlings ≥ 20 cm tall and < 1 cm dbh within 1000 1 × 2 m^2 quadrats (total area = 0.2 ha). Seedling survey data from 2006 were then scored for all seed species found beneath bat tents and control quadrats (excepting lianas). Thus, we could assess the correlation between species-specific abundance of seeds under bat roosts and respective seedling abundance in both mature and secondary forest plots. Because we did not follow the seed fate under bat roosts, these data provided a reasonable proxy for estimating the importance of *A. watsoni* dispersal for seedling regeneration.

STATISTICAL ANALYSIS.—We used log-likelihood ratio tests (*G* tests) to account for differences in the proportion of leaf tents with seeds between large, undisturbed and small, disturbed habitats. We generated a species accumulation curve based on 1000 randomizations using the program EstimateS 7.5.2 (Colwell 2005) to assess the completeness of our sampling effort. EstimateS was also used to calculate the Chao–Jaccard similarity index between tent and control plots based on 1000 randomizations. We chose this particular index of similarity because it fits well for small samples with many rare species (Chao *et al*. 2005). To determine whether forest patch size affects the abundance and species richness of the bat-generated seed rain we used generalized linear models with a log-link function for a Poisson distribution of data (McCullagh & Nelder 1989). Forest patch size (large vs. small reserves), treatment (tent vs. control quadrats) and their interaction were used as factors in the model. Pearson's correlation analyses on log(*x*+1) transformed data (to improve normality) on both seeds and seedlings abundance were used to assess the correlation between species-specific abundance of seeds in both tent and control quadrats and the respective abundance of seedlings registered in mature and secondary forest plots. All statistical analyses were performed using JMP version 7.

RESULTS

SEEDS DISPERSED BY BATS.—We found 194 leaf tents, from which 103 tents had seeds > 8 mm underneath. The percentage of seedless tents varied from 20 to 68 percent among forest sites and was higher in the large reserves (*G* = 17.0, df = 1, *P* < 0.0001; Table 1). A total of 1030 seeds from 46 species were found in all tent quadrats pooled. After excluding seeds potentially originating from neighbor fruiting trees and those species dispersed by abiotic means, a total of 810 seeds from 43 species were included in the analyses. These animal-dispersed seed species comprised trees, palms, and lianas associated with different habitats and forest successional stages (Table S1).

All seeds found under bat roosts showed signs of manipulation, such as tooth marks and total or partial removal of pulp/arils from seeds. Thirteen of 43 seed species (30.2%) had a total of ten or more seeds and accounted for 89.3 percent of all seeds sampled in all tent quadrats. *Spondias radlkoferi* accounted for 50.5 percent of all seeds collected (*N* = 410) under leaf tents, followed by *Calophyllum brasiliense* with 9.7 percent (*N* = 79) of all seeds. Only these more abundant seed species occurred in ten or more leaf tents (Table S1). Remaining seed species (69.8%; *N* = 30) occurred at low abundances (≤ 10 seeds found across all tents) and most seed species (90.4%; *N* = 38) were found in fewer than ten tent quadrats. Twenty species (45%) were found in only one leaf tent.

The large number of rare seed species affected species-accumulation curve that showed a nonasymptotic pattern, suggesting that more extensive sampling would yield a significant increase in the number of plant species dispersed by leaf-roosting bats (Fig. 1). In control quadrats sampled away from leaf tent influence we found only 268 seeds from 34 seed species, averaging 0.65 ± 1.5 and 0.18 ± 0.23 species/m^2. In contrast, the average density of seeds and species under bat roosts were almost ten times greater than in control quadrats averaging 7.86 ± 12.5 and 1.78 ± 1.18 species/m^2, respectively. Tent quadrats shared only 25 seed species with
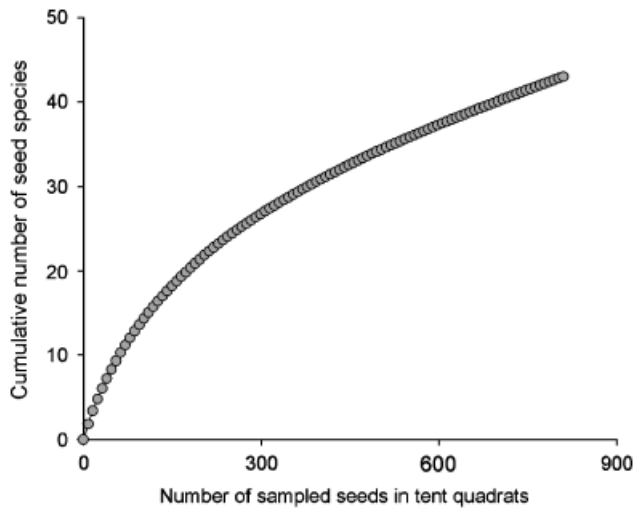
FIGURE 1. Mean species accumulation curve for number of seed species found under leaf tents based on 1000 randomizations of the data set (Sobs) in the Sarapiquí Basin, Costa Rica.

control quadrats, representing 58 percent of total species found under bat tents (Chao–Jaccard estimator = 0.754).

HABITAT TYPE EFFECTS AND INFLUENCE ON SEEDLING RECRUITMENT.—The generalized linear model suggests that tent influence had a significant direct effect on density of both seeds and species (all P values < 0.0001; Table S2) whereas forest habitat had no direct effect (all P values > 0.6; Table S2). We sampled fewer large seeds underneath bat roosts in small, disturbed than in large, undisturbed forest habitats (χ^2 = 4.16, df = 1, P = 0.04; Fig. 2A) but virtually the same number of species under leaf tents in both types of habitat (χ^2 = 0.92, df = 1, P = 0.33; Fig. 2B). The distribution of leaf tents according to the abundance of seeds found underneath was strongly right-skewed in both large reserves and small forest patches; high densities of seeds under bat roosts were infrequent (Fig. 2A, B). Furthermore, the seedling community may be partially influenced by dispersal patterns of tent-roosting bats. Species-specific abundance of seed species (excluding lianas) found beneath leaf tents was positively correlated with the respective abundance of recruited seedlings in both mature and secondary forests (Fig. 3A, B). In contrast, no significant associations were found between species-specific abundance of seeds in control quadrats and the respective abundance of seedlings in any type of forest (Fig. 3C, D).

DISCUSSION

Our results demonstrate that Neotropical fruit bats play a more important role in dispersing large seeds than previously thought. In our study area, tent-roosting bats disperse at least 43 species of several plant families with differing habitat preferences and life forms, suggesting that these bats have a broad dietary habit including fruits from mature forest and successional tree species. Bat dispersal may significantly shape the seed rain of both large, undisturbed and small, disturbed forest patches, as comparisons between bat-generated and nearby nontent samples showed strong differences in seed abundance, species richness, and species composition. Further, the positive correlations between species-specific abundance of bat-dispersed seeds and regenerating seedlings in both mature and secondary-forest plots indicate that bats can influence seedling community composition. Habitat disturbance, however, may affect this dispersal system as we detected a significant decrease in the abundance of bat-generated seed rain in small forest patches.

Considering the contribution of other larger fruit bats (both tent and nontent roosting) to community-wide seed dispersal, the importance of Neotropical frugivorous bats for the dispersal of large-seeded plants could potentially be even greater. This study focused on only a single type of leaf tent primarily used by *A. watsoni*, one of the smallest fruit bats that occur in the study area (*ca* 11 g) that use mainly lower-canopy and understory strata. However, this kind of leaf tent may also be used by larger fruit bats such as *Artibeus jamaicensis* (Rodriguez-Herrera *et al.* 2007). This may explain why several plant genera with seeds > 2 cm were frequently found under leaf tents. Small *A. watsoni* and other larger *Artibeus* (*e.g.*, *A. jamaicensis* and
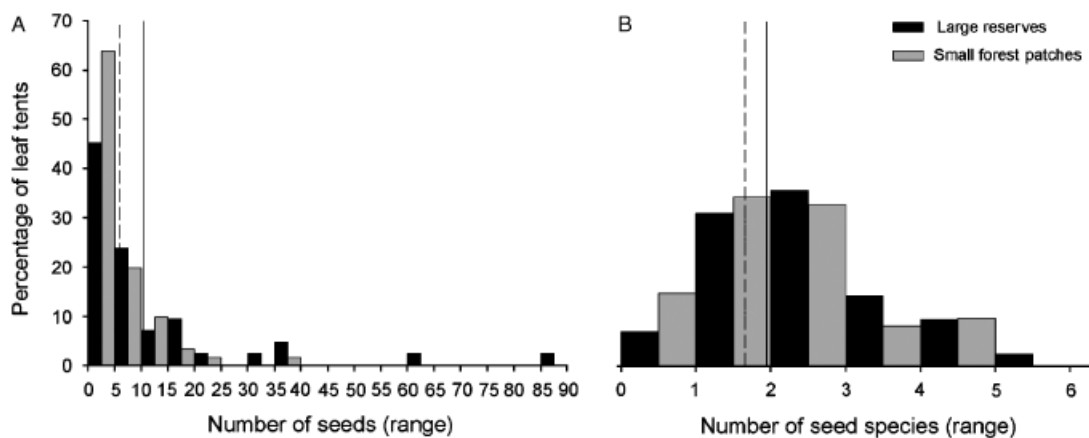

FIGURE 2. Distribution of leaf tents according to abundance of seeds (A) and number of seed species (B) at the Sarapiquí Basin, Costa Rica. Also shown, mean values for large reserves (solid line) and small forest patches (dashed line).
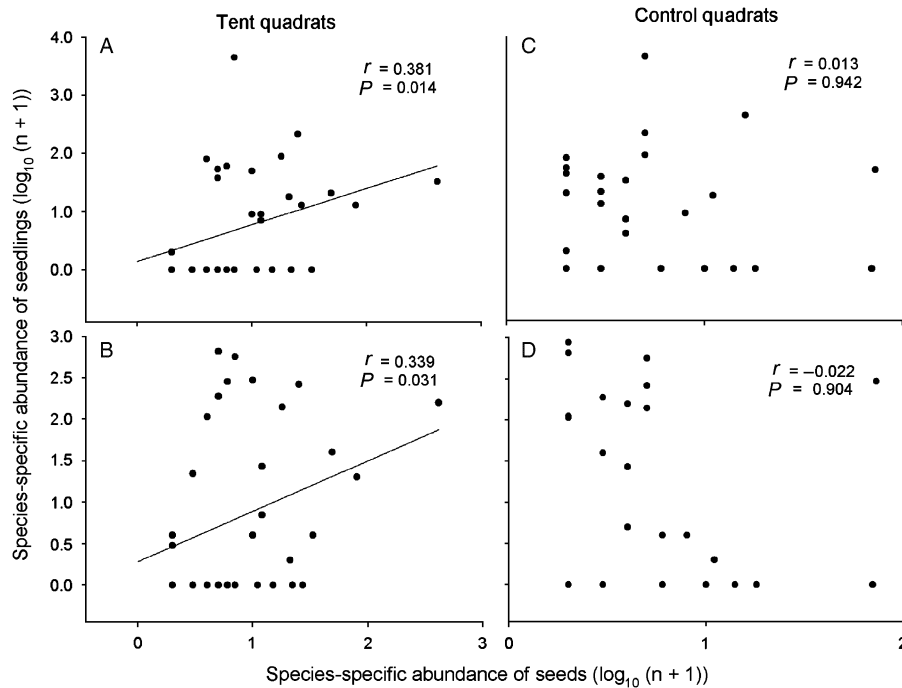
FIGURE 3. Pearson's correlations between species-specific abundance of seed species found in both tent quadrats (A, B) and nontent quadrats (C, D) and respective abundance of seedlings in both mature and secondary forest at the Sarapiqui Basin, Costa Rica. Each dot corresponds to a single tree species.

Artibeus lituratus) are closely related phylogenetically and have similar dietary habits (Giannini & Kalko 2004); hence, it is not surprising that they may occupy the same leaf tents. Species belonging to genera *Spondias*, *Calophyllum*, *Otoba*, and *Quararibea* (Table S1) are among the largest seeds of the regional flora and, excepting *Spondias*, all mentioned species are associated with mature forest habitats and upper-canopy layer (McDade *et al.* 1994). Moreover, some of the recorded plant species (*e.g.*, *Virola* spp., *Simarouba glauca*, and *Protium* spp.) are thought to be mainly dispersed by large birds (*e.g.*, toucans and guans) but were frequently found under bat roosts, supporting the assertion that even distantly related taxa such as bats and birds may compete for resource (Palmeirim *et al.* 1989). These findings strongly contradict the argument that Neotropical furgivorous bats, due to morphological and ecological constrains, are irrelevant to the dispersal of large-seeded tree species from mature forest, a role played in Old World tropical forests by larger Pteropodid bats (flying-foxes; Muscarella & Fleming 2007).

The elevated seed rain under bat tents in comparison with adjacent nontent quadrats raises questions regarding the benefits of dispersal by leaf-roosting bats, as clusters of seeds may be more susceptible to natural enemies and/or intraspecific competition (Janzen 1970). However, 69 percent of all seed species found underneath leaf-tent roosts had fewer than ten seeds across all leaf tent, and half of the species were represented by a single seed (Table S1). Absolute numbers of seeds per tent quadrat ranged widely (1–88 seeds), but high densities of seeds were infrequent (Table 1; Fig. 2). Furthermore, secondary seed dispersal by rodents may significantly scatter seeds over the forest floor (Vander Wall 2002). Analogous to the clumped dispersal patterns created by monkeys or

tapirs, seed dispersal by tent-roosting bats may increase seedling establishment at the population level for seeds deposited far away from cospecific adults (Romo *et al.* 2004, Queenborough *et al.* 2007). Moreover, dispersal by tent-making bats in secondary forests may promote colonization and seedling establishment of mature forest species, such as *C. brasiliense*, *Welfia* spp., and *Protium* spp., which are not present as fruiting trees in secondary forest in our study sites (Norden *et al.* 2009). Tent and nontent quadrats shared only 25 seed species, and only three of 46 seed species were excluded from our samples due to possible contagious seed rain from neighbor trees. Thus, tent-making bats may significantly enhance the density and diversity of allochtonous seed rain at the local scale (Martinez-Ramos & Soto-Castro 1993).

Although we did not account for the eventual fate of bat-dispersed seeds, we found significant correlations between the species-specific abundance of seeds dispersed by bats and the abundance of respective seedlings in both mature and secondary forests (Fig. 3). If differential seedling abundance within our study areas is simply due to species differences in local fruit availability (and therefore higher local rates of frugivory, dispersal, and recruitment), we would also expect to find a significant correlation between species-specific abundance of seeds and seedlings in adjacent nontent samples. Our results therefore suggest that tent-making bats may influence the local seed rain and therefore the abundance of seedlings of the tree species they feed on and disperse. This influence may still persist even though other vertebrate species such as monkeys and birds also serve as dispersal agents for these seed species.

Dispersal of large seeds by bats can assume critical importance for plant dynamics in defaunated forest fragments and large tracts

of forests from where large frugivores have been depleted or extirpated due to hunting or loss of habitat (Wright *et al.* 2007b). Mature forest tree species developed larger seeds than their early-successional counterparts as an adaptation for germination and establishment in shaded environments, and are considered to depend on disappearing large frugivores for successful seed dispersal (Terborgh & Nuñez-Iturri 2006). Therefore, bats are an important component of the remnant fauna that may help to maintain tree diversity and promote forest regeneration in disturbed landscapes (Wright *et al.* 2007b). Our results highlight the need for further study of Neotropical frugivorous bats and their role in the dispersal of large seeds in tropical forest ecosystems.

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

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

TABLE S1. *List of seed species found under* Artibeus watsoni *feeding tent roosts and adjacent non-tent quadrats.*

TABLE S2. *Results of the generalized linear models fitted to number of seeds and seed species/m^2.*

FIGURE S1. The Sarapiquí basin in Northeastern Costa Rica.

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