

Artificial bat roosts did not accelerate forest regeneration in abandoned pastures in southern Costa Rica



J. Leighton Reid^{a,*}, Ellen K. Holste^b, Rakan A. Zahawi^c

^a Department of Environmental Studies, University of California, 1156 High St, Santa Cruz, CA 95064, USA

^b Department of Forestry, Ecology, Evolutionary Biology, and Behavior Program, Michigan State University, 480 Wilson Road, Room 126 Natural Resources, East Lansing, MI 48824, USA

^c Organization for Tropical Studies, Apartado 73-8257, San Vito de Coto Brus, Costa Rica

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ABSTRACT

Artificial roosts have been proposed as a tool for augmenting bat populations and catalyzing tropical forest regeneration. In the best case scenario, roosts would attract seed-carrying bats (Family Phyllostomidae) into degraded pastures and form nucleating patches of native vegetation. We tested this scenario by monitoring 48 artificial roosts in pastures and adjacent forest fragments in southern Costa Rica over 2 years. Half of the pasture roosts were exposed to direct sunlight and half were affixed to 4-m living stakes of *Erythrina poeppigiana* (Walp.) O.F. Cook that provided shade. After 2 years, 94% of roosts in forest and 40% of roosts in pasture had been used by bats at least once – primarily for nocturnal feeding. Maximum daily temperature inside of roosts was the best microclimatic predictor of bat visitation. We identified at least five species of bats that visited roosts, including two frugivores (*Carollia* and *Glossophaga* spp.). Bat-mediated seed dispersal increased with the number of frugivorous bat detections at roosts, but seedling recruitment did not increase with either bat detections or seed abundance over a 2-year period. Given that bats rarely used roosts in pastures, and bat visitation did not increase seedling recruitment, our data suggest that artificial bat roosts did not accelerate forest regeneration in abandoned, premontane pastures in southern Costa Rica. This method could be refined by investigating alternative roost designs, barriers to seedling recruitment below roosts, improvement of roost microclimatic conditions in pastures, and ability of bats to detect roosts in different habitats.

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1. Introduction

Tropical deforestation exacerbates climate change, undermines rural livelihoods, and disarticulates the most diverse terrestrial communities on the planet (Chhatre and Agrawal, 2009; Myers et al., 2000; Pan et al., 2011). Some 27 million hectares of tropical forest were cleared between 2000 and 2005, two-thirds of which were in Latin America (Hansen et al., 2008). The impacts of this forest loss can be partially mitigated through ecological restoration – the process of assisting the recovery of degraded ecosystems to their historic trajectories (SER, 2004; Lamb et al., 2005; Rey Benayas et al., 2009). Many degraded lands will regenerate naturally (Chazdon, 2003; Letcher and Chazdon, 2009), but when succession is arrested or time is of the essence, active intervention may be necessary to overcome barriers to recovery (Holl and Aide, 2011; Martínez-Garza and Howe, 2003).

Cattle pastures are ubiquitous throughout the tropics and frequently represent an endpoint in the process of land conversion

following deforestation. As grazed hillsides become eroded and rural farmers seek opportunities in cities, these lands are often sold or abandoned (Rey Benayas et al., 2007). As such, pastures have become a focus in the literature on tropical forest restoration (Holl and Kappelle, 1999). Natural regeneration in pastures is limited by a suite of factors including sparse seed banks and seed rain, high seed predation, and poor germination, survival, and growth (Aide and Cavellier, 1994; Cubiña and Aide, 2001; Holl, 1999; Nepstad et al., 1996). Of these, seed rain is often considered a primary limitation because other barriers to establishment come into play only when seeds are present. Because the majority of Neotropical trees have seeds dispersed by animals (Howe and Smallwood, 1982), a challenge for practitioners is to increase animal visitation to areas with reduced habitat resources, stressful microclimate, and increased predation risk.

Standard restoration practice in tropical pastures is to plant trees. Tree planting is an effective strategy because it ameliorates multiple barriers to natural regeneration including seed limitation (Cole et al., 2010; Lindell et al., 2013) and seedling survival and growth (Cole et al., 2011). Establishing tree plantations, however, is expensive and can result in significant legacy effects, such as

* Corresponding author. Tel.: +1 831 459 1665; fax: +1 831 459 4015.

E-mail address: jlreid@ucsc.edu (J.L. Reid).

altered nutrient cycling and tree species composition compared to natural secondary forests (Celentano et al., 2011). As a result, many researchers are now exploring more low-cost, light-handed interventions to catalyze forest regeneration. These have included: bird perches (Aide and Cavelier, 1994; Holl, 1998a; Miriti, 1998; Zanini and Ganade, 2005), essential oils of bat-dispersed fruits (Bianconi et al., 2012), giant stakes (Zahawi, 2008), artificial bat roosts (Kelm et al., 2008), and applied nucleation (Holl et al., 2011).

Among these novel applications, artificial bat roosts are particularly promising. Neotropical fruit bats (family Phyllostomidae) are among the most important seed dispersers in fragmented and early successional ecosystems (Fleming, 1988; Galindo-González et al., 2000; Arteaga et al., 2006; Muscarella and Fleming, 2007; Mello et al., 2008), but deforestation and forest degradation threaten many populations (Fenton et al., 1992; Schultze et al., 2000; Hutson et al., 2001). Bats in deforested landscapes may be limited by shortages of food or suitable roosts, excessive pesticides, or persecution by humans (Mickleburgh et al., 2002; Evelyn and Stiles, 2003; RELCOM, 2009). Frugivorous Phyllostomids in Costa Rica use a variety of roost types including caves, hollow trees, vine tangles, human infrastructures, and foliage (Foster and Timm, 1976; Fleming, 1988; Fenton et al., 2000). The premise of the artificial roost strategy is that by provisioning suitable roosts for frugivorous bats, restoration practitioners may attract bats and overcome seed rain barriers in degraded pastures. In the only existing study on this method, researchers installed simulated tree cavities in forest fragments in northern Costa Rica (Kelm et al., 2008). Within a few weeks, up to 10 species of bats colonized the roosts in large numbers (up to ~200 individuals per roost). These bats included several frugivores (*Carollia* and *Glossophaga* spp.), and seed rain around the roosts increased significantly compared to seed rain far from the roosts. It is still unknown whether artificial roosts outside of forest fragments will attract bats, or whether increases in seed rain actually translate to increased seedling establishment; a variety of studies demonstrate that seedling recruitment should not be taken for granted (reviewed in Reid and Holl, 2012).

The purpose of this experiment was to test whether artificial bat roosts can be used to accelerate forest regeneration in tropical pastures. To do so, we monitored bat activity, seed rain, soil nutrients, and seedling establishment at 48 artificial roosts in abandoned pastures and forests in southern Costa Rica over 2 years. Our experiment was designed to evaluate (1) whether bats will use artificial roosts in pastures; (2) whether bat activity in roosts increases seed rain and plant-available soil nutrients (N, P); and (3) whether increases in seed rain translate to greater seedling recruitment. We predicted that bats would prefer roosts with greater vegetation cover due to improved microclimate and that bat activity in roosts would increase seed rain and soil nutrients via guano deposition (Duchamp et al., 2010) but not seedling recruitment due to low seed germination and survival in pastures (Holl, 1999).

2. Methods

2.1. Study area

This study was conducted in the countryside surrounding the Las Cruces Biological Station (LCBS; 8°47'7"N, 82°57'32"W; rainfall ≈ 4 m year⁻¹; elevation 1100–1200 m) in Coto Brus County, Costa Rica. Mean annual temperature is approximately 21 °C, and there is a distinct dry season from December to March. The area around LCBS was primarily covered by tropical premontane rain-forest (Holdridge et al., 1971) until the 1950s, when government-sponsored immigration led to a population influx and development of the region (Edelman and Seligson, 1994). Farm land was

primarily used for coffee production until low prices in the 1990s caused many farmers to convert their lands to pasture (Rickert, 2005). Currently the landscape is a diverse mix of agricultural fields and forest patches.

Soils in our study area vary but are generally characterized by mild acidity, low phosphorus, high organic matter, and aluminum saturation levels below those considered toxic (Holl et al., 2011; Landon, 1984; Uehara and Gillman, 1981). Pasture vegetation is generally dominated by a mix of native and non-native grasses but also includes many ruderal herbs. The regional bat community includes at least 59 species, of which 23 are primarily frugivorous (LCBS, 2012).

2.2. Experimental design

We installed 48 artificial roosts at five sites in June–July 2009 (three sites) and July–September 2010 (two sites). In each site, we installed six roosts in degraded pastures and three to six in adjacent forest fragments (based on availability of space). Roosts were randomly assigned to one of three treatments: forest, giant stake, or post (Fig. 1). Forest roosts were affixed to tree trunks. Pasture roosts were either affixed to wooden or galvanized steel posts exposed to direct sunlight (Post treatment) or to giant stakes of *Erythrina poeppigiana* (Walp.) O.F. Cook (Giant stake treatment; Fabaceae). Giant stakes are large (4 m long) limbs cut from trees that are planted bare and resprout quickly (Zahawi, 2008). We used giant stakes to assess whether increased canopy cover from resprouting branches would ameliorate temperature extremes and increase bat visitation to roosts. We planted stakes 50 cm deep and allowed them to grow for 3 months before affixing roosts. Stakes that died within the first year were replaced. Within a year, most giant stakes sprouted a canopy with a mean area of 2.7 ± 1.7 m² (SE).

Each roost was paired with a control plot that did not have a roost. Controls were situated 10 m away from roosts in a random compass direction. At each roost and control, we measured seed rain, soil nutrients, and seedling recruitment. Spacing between roosts and controls reflects spatial constraints imposed by working at multiple study sites on small, private land holdings, and was adequate given observed differences in seed rain between occupied roosts and their paired controls.

2.3. Artificial roosts

Roosts consisted of emulated tree hollows constructed using a wooden frame, Fibrolit walls, and a 1.9-cm plastic screen on the ceiling (Fig. 1). Interior dimensions were 40 × 40 × 60 cm. Fibrolit is an inexpensive construction material made from wood fiber and concrete that is widely available in Latin America and is resistant to insects and water. Roosts were open on the bottom to provide access for bats. Roost interiors were dark, and temperatures varied by treatment (Table A1). We mounted the roosts on trees or poles 2–3 m above the ground in order for the entrance to be accessible above the level of exotic pasture grasses.

2.4. Roost monitoring

Roosts were monitored for bat activity twice per month over a period of 2 years. Seed traps (see Section 2.5) below roosts were checked for evidence of bat use (i.e., feces, insect parts, or masticated fruit), and roosts were inspected for colonization (i.e., day-roosting bats). We used motion-activated infrared video cameras and digital photographs to confirm visitation from seed trap evidence and to evaluate bat composition. Cameras were constructed and deployed following Frick et al. (2009). We identified bats with



Fig. 1. Artificial bat roosts and experimental treatments. (a) post treatment: bat roost affixed to a wooden post in a pasture; (b) giant stake treatment: roost affixed to a giant stake of *E. poeppigiana*; (c) giant stake after 2 years of growth with a canopy diameter > 4 m; and (d) forest treatment: roost affixed to a tree with an infrared video camera near the opening. Photos a, b, and d by J.L.R. Photo c by C. Ericson.

Table 1
Species composition of bats that used artificial roosts in forests and pastures.

Species	Diet	Number of roosts used ^a (colonized ^b)		Max individuals
		Forest	Pasture	
<i>Carollia</i> spp.	Fruit	1 (1)	1 (0)	2
<i>Desmodus rotundus</i>	Blood	2 (0)	0 (0)	–
<i>Glossophaga</i> spp.	Nectar, Fruit	1 (1)	2 (0)	5
<i>Micronycteris</i> spp.	Insects	2 (1)	0 (0)	6
<i>Mimon crenulatum</i>	Insects	1 (0)	0 (0)	2
Unidentified spp.		15 (3)	16 (0)	8

^a Use refers to evidence of bat visitation (e.g., feces or masticated fruit in a seed trap).

^b Colonization refers to observations of bats sleeping inside of roosts during the day.

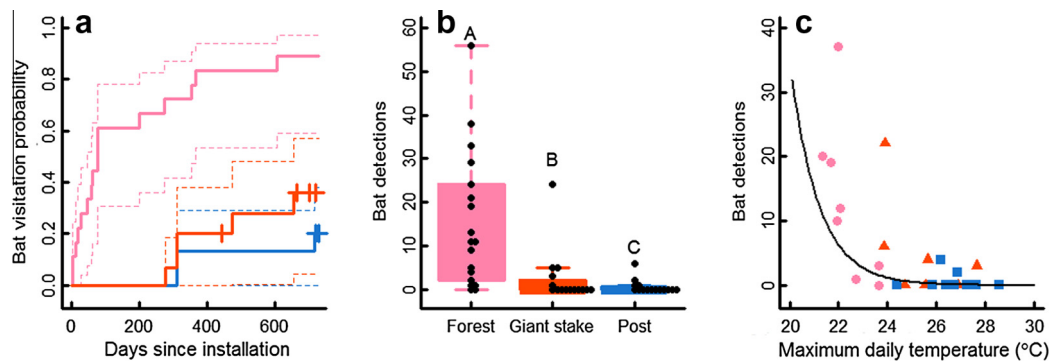


Fig. 2. Bat detections in artificial roosts during 2 years of monitoring in forest and pastures in southern Costa Rica. (a) Probability that a roost has been used (i.e., for nocturnal foraging) at least once over time. Treatments are denoted by shading: pink = forest, orange = giant stake; blue = post. Dotted lines represent 95% confidence intervals of Kaplan Meier survival probability. Cross hatches denote roosts that were not monitored for the entire 2-year period. (b) Total bat detections in each treatment. Each dot represents one artificial roost. Points are stacked to prevent overplotting. Boxes represent standard box plots. Letters denote statistically significant differences ($\alpha = 0.95$) from post hoc tests (Tukey's Honestly Significant Difference). (c) Bat detections as a function of maximum daily temperature inside roosts. Treatment is indicated by shape: circle = forest; triangle = giant stake; square = post. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Reid (2009) and an unpublished field key for Costa Rica (Timm, York, Rodríguez-H., and Laval).

Microclimate is an important determinant of roost selection by Microchiropteran bats (Boyles, 2007). To evaluate the relationship between roost microclimate and bat visitation, we measured roost temperature at 15 min intervals in 25 roosts at three sites over a 2-week period in July 2011 (HOBO Pendant[®] temperature logger, Onset Corporation, Cape Cod, MA). Data loggers were placed inside of the roosts near the ceiling to evaluate as closely as possible the microclimate experienced by roosting bats.

2.5. Seed rain

To assess the influence of bat visitation on seed rain, we collected seeds twice per month from each roost and paired control plot. Seed traps were made from fine gauge (0.5 × 0.5 mm) mosquito netting hung from a wire hoop (0.25 m²) on 50 cm wooden legs. The elevated seed trap design prevented seed deposition by terrestrial animals. A local reference collection was used to identify seeds (Cole et al., 2010). Only seeds that were likely to have been dispersed by bats were included in the analysis. Probable

Table 2
Diagnostic statistics for linear mixed-effects models of bat visitation to artificial roosts.

Response (num. detections)	Model fit (Adj. r^2 /p)	Parameter	Level	Estimate	SE	P
All bats	0.58/<0.001	Intercept	–	2.33	0.28	<0.001
		Treatment	Giant stake	–1.60	0.17	<0.001
			Post	–2.94	0.32	<0.001
Frugivores	0.38/<0.001	Intercept	–	0.80	0.47	0.0862
		Treatment	Giant stake	–1.69	0.36	<0.001
			Post	–1.94	0.40	<0.001
Insectivores	0.35/<0.001	Intercept	–	–0.05	1.26	0.971
		Treatment	Giant stake	–1.53	0.28	<0.001
			Post	–4.24	1.01	<0.001

Table 3
Pairwise comparisons of bat visitation to artificial roosts (Tukey's Honestly Significant Difference) in southern Costa Rica.

Response (num. detections)	Hypothesis	Estimate \pm SE	z	P
All bats	$M_{\text{stake}} - M_{\text{forest}} = 0$	-1.60 ± 0.17	–9.20	<0.001
	$M_{\text{post}} - M_{\text{forest}} = 0$	-2.94 ± 0.32	–9.11	<0.001
	$M_{\text{post}} - M_{\text{stake}} = 0$	-1.34 ± 0.36	–3.76	<0.001
Frugivores	$M_{\text{stake}} - M_{\text{forest}} = 0$	-1.69 ± 0.36	–4.74	<0.001
	$M_{\text{post}} - M_{\text{forest}} = 0$	-1.94 ± 0.40	–4.87	<0.001
	$M_{\text{post}} - M_{\text{stake}} = 0$	-0.25 ± 0.50	–0.50	0.868
Insectivores	$M_{\text{stake}} - M_{\text{forest}} = 0$	-1.53 ± 0.28	–5.47	<0.001
	$M_{\text{post}} - M_{\text{forest}} = 0$	-4.24 ± 1.01	–4.21	<0.001
	$M_{\text{post}} - M_{\text{stake}} = 0$	-2.71 ± 1.03	–2.62	0.020

bat-dispersed seeds were identified from a local database of >500 bat fecal samples (M. Penuelas et al. unpublished data) and an on-line database of bat/plant interactions (Geiselman et al., 2002). This method of inference conservatively predicts which seeds may have been dispersed by bats.

2.6. Soil nutrients

To assess the influence of bat guano deposition on soil nutrients (N, P), we collected three soil cores (10 cm depth, 2 cm diameter) below each roost and adjacent control at the outset of the study. We conducted follow-up sampling after the first and second years at one site with particularly high bat visitation. Cores were composited and homogenized to represent one sample per roost or control. Plant available nitrogen (N) was extracted with potassium chloride and analyzed colorimetrically with an ammonium salicylate and ammonium cyanurate colorimetric method to detect ammonium (Sinsabaugh et al., 2000) and vanadium (III), and sulfanilamide and N-(1-naphthyl)-ethylenediamine dihydrochloride (NED) to quantify nitrate (Doane and Horwath, 2003). Sum of inorganic N pools was calculated by summing nitrate and ammonium levels of each composited soil sample. Total N was measured by the dry combustion method with an Elemental Combustion CHNS-O analyzer (ECS 4010, Costech Analytical Technologies, Valencia, CA). Phosphorus (P) was extracted with a Mehlich III solution (Mehlich, 1984) and analyzed with an Optima 2100DV ICP Optical Emission Spectrometer (Perkin-Elmer, Shelton, CT) for total extractable P and colorimetrically with a continuous flow auto-analyzer (OI Analytical, College Station, TX) for plant-available P.

2.7. Seedling recruitment

To assess the overall effect of bat visitation on secondary succession, we measured tree seedling recruitment in a 2-m radius around roosts and controls during years 0, 1, and 2. During each rainy season (June–September), we counted all seedlings <1 m tall. Initial surveys were conducted within 3 months of roost

installation. Seedlings were identified by a local expert (F.O. Brenes) and from a regional reference collection (<http://www.ot-s.ac.cr/herbarium>). We did not mark individual seedlings, so some seedlings were counted in multiple years. This is accounted for in our definition of the response variable (see Section 2.8). Only seedlings likely to have been dispersed by bats were included in the analysis (see Section 2.5). We also estimated the percent cover of non-grass vegetation in each seedling plot with a ranking system: 0–5, 6–10, 11–25, 26–50, 51–75, 76–95, and 96–100%.

2.8. Data analysis

We used linear mixed-effects regression to evaluate the influence of treatments (forest, giant stake, post) on bat visitation. We chose a mixed-effect model because it allowed us to account for the non-Gaussian distribution of bat detections by specifying a Poisson family and log-link function. This framework also allowed us to include a random site effect. We produced separate models for frugivores, insectivores, and all bats combined. The model structure was $y = \beta_0 + \beta_1 x_1 + s_i + \varepsilon_i$ where y is the number of bat detections, β_0 is the y -intercept, β_1 is a vector of fixed-effect coefficients for each of the three treatments (x_1), s_i is the random effect for the i th site, and ε_i is the error term. For pairwise comparisons between treatments, we used a post hoc test (Tukey's Honestly Significant Difference).

We also performed a survival analysis to assess differences in the time until first roost visit by bats in each treatment. We used a Kaplan–Meier estimator of survival probability (Therneau, 2012) and log-rank tests to evaluate differences among treatments in use or colonization probability. We defined *use* as bat visitation to a roost (i.e., for nocturnal feeding) and *colonization* as bats sleeping in a roost during the day.

We used maximum likelihood model selection to evaluate the relationship between roost temperature and bat visitation (Burnham and Anderson, 1998). First, we built three linear mixed-effects models with different temperature calculations (daily mean, minimum, and maximum) as fixed factors to explain the number of bat detections over 2 years. We used a Poisson distribution, log-link function, and a random term for site. Then we calculated Akaike Information Criterion scores corrected for small sample sizes (AIC_c) and selected the best model based on the minimum AIC_c. We also compared models using microclimatic predictors to models using treatment and models using both microclimate and treatment.

We used a Wilcoxon paired sample test to compare differences in soil nutrients between roost and control plots within and across years.

To evaluate the relationship between frugivorous bat detections and seed rain abundance, we used linear mixed-effects regression. We defined a response variable (Δ seed abundance _{i}) as the difference in abundance of bat-dispersed seeds between the i th roost and the i th control over 2 years. Positive values represented an

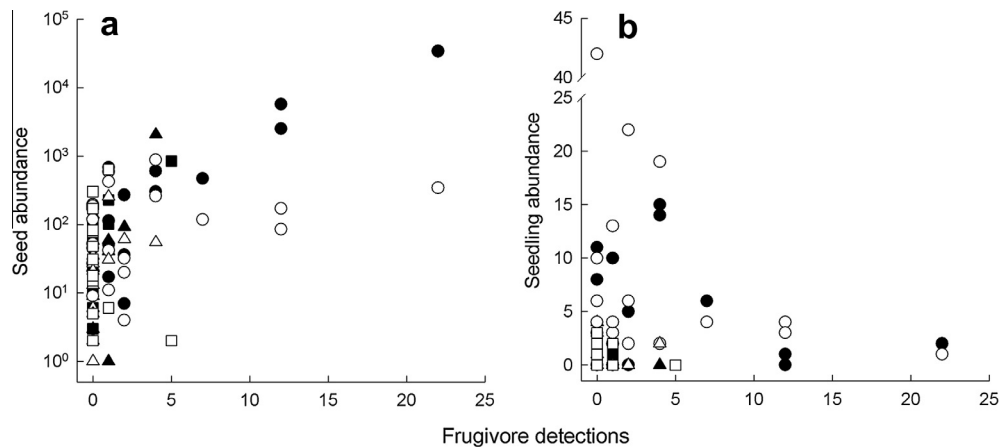


Fig. 3. Relationship between the number of frugivore detections and seed (a) and seedling abundance (b). Filled shapes represent artificial roosts, and hollow shapes represent controls. Treatment is indicated by shape: circle = forest; triangle = giant stake; square = post. Seed rain abundance is summed over the entire 2-year study period. Seedling abundance is from the second year of the experiment.

increase in seed rain compared to the control, and negative values represented a decrease. The response variable was strongly skewed by several high values but could not be log-normalized or modeled as a Poisson distribution because the data included negative numbers. Instead, we used a rank transformation to normalize the response variable.

We used a maximum likelihood hypothesis-testing approach to evaluate whether bat visitation and seed abundance influenced the rate of succession. As response variables, we used the difference in the change in tree seedling abundance (Δ tree seedling) and non-grass vegetation cover (Δ non-grass vegetation) between roosts and controls over 2 years, calculated as $y = (r_2 - r_0) - (c_2 - c_0)$ where y is the response variable (Δ tree seedling or Δ non-grass vegetation), and r_2 , r_0 , c_2 , and c_0 are the measured seedling abundance or non-grass vegetation cover for roosts (r) and controls (c) in years 0 and 2. Values greater than zero denote an increase below roost boxes relative to adjacent controls. For each variable, we constructed three models with the structure $y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + s_i + \varepsilon_i$ where β_1 is a vector of fixed effect coefficients for each of the three treatments (x_1), and β_2 is a fixed effect coefficient for seed abundance (model 1), ranked seed abundance (model 2), or frugivore detections (model 3). For each model, we used a Gaussian distribution and identity-link function. We evaluated the significance of each fixed factor by removing it from the model and comparing the simpler model to the more complex model based on AIC scores.

Model fit for each of the linear mixed effects regressions was assessed by inspecting plots of residuals and by regressing fitted values against observed values. We used the lme4 package (Bates et al., 2011) in R 2.15.0 (R Development Core Team, 2012) for these analyses.

3. Results

3.1. Use and colonization

During 2 years of monitoring we detected bat visitations in 26 out of 48 artificial roosts (54%). Seventeen out of 18 forest roosts (94%) were used at least once compared to 12 out of 30 roosts (40%) in pasture. Bats colonized at least three roosts as day roosts, and the remainder was either used as nocturnal feeding roosts or as day roosts for short periods of time (≤ 2 week). All 3 day roosts were in forests. At least five bat species used artificial roosts (Table 1; Fig. A1; Videos A1–A2), three of which colonized roosts permanently, and two of which only used roosts for nocturnal feeding.

Bats used roosts in forest sooner and with greater frequency than roosts in pasture (Fig. 2a–b). We found a strong treatment effect on bat visitation that was primarily driven by the difference between bat detections in forest versus pasture roosts (Table 2). Total bat detections and insectivore detections were greater in roosts affixed to giant stakes than in roosts affixed to posts, but frugivore detections were not statistically different between the two pasture treatments (Table 3). Additionally, time until first visitation was shorter in forest than in pasture ($X^2 = 28.4$, $P < 0.001$), but giant stakes and posts did not differ ($X^2 = 2.2$, $P = 0.142$).

Of three microclimatic predictors tested, maximum daily temperature was the best predictor of bat detection probability (Table A2). The number of roost visitations in both pasture and forest increased as maximum daily temperature in the roosts decreased, and the majority of bat detections (90.1%) were from roosts with maximum daily temperatures < 24 °C (Fig. 2c). A model using only maximum daily temperature to explain bat visits to 25 roosts over 2 years was better than models using treatment alone ($\Delta AIC_c = 7.0$) or treatment and maximum daily temperature ($\Delta AIC_c = 26.7$; Table A3).

3.2. Seed rain

Out of 76,563 seeds collected, 54,763 (71.5%) were from bat-dispersed species. Among bat-dispersed seeds, 84% were from shrubs, 16% were from trees, and less than 1% were from herbs, vines, and lianas (a species list is available from the corresponding author). Most seeds were from early-successional genera (94%), particularly *Piper* (78%), *Cecropia* (6%), and *Solanum* (6%), but *Clusia* (a genus that includes many mid-late successional trees) seeds were also common (6%). Seed rain abundance increased exponentially with greater frugivore detections (Fig. 3a). Ranked Δ seed rain abundance increased with the number of frugivore detections for shrub seeds (Adj. $R^2 = 0.30$), tree seeds (Adj. $R^2 = 0.22$), and all seeds combined (Adj. $R^2 = 0.38$, all $P < 0.001$; Table A4).

3.3. Soil nutrients

Nutrient concentrations did not differ significantly between roosts and adjacent controls over 2 years (Fig. A2). Both roosts and controls trended towards a decrease in nutrient levels over 2 years (all $P = 0.0625$) including total extractable P, total N, and the sum of inorganic N, indicating that variation across years was greater than between roosts and controls.

3.4. Seedling recruitment

We recorded 740 tree seedling detections. Sixty-nine percent of detections were mid-late successional species, 24% were early successional species, and 6% were non-native agricultural species. *Inga* was the most common genus of bat-dispersed seedling comprising 21% of detections, followed by *Allophylus* (17%), *Miconia* (14%), and *Calophyllum* (13%). Ninety-two percent of seedling detections were in forest, and 8% were in pasture (Giant stake = 3%; Post = 5%). Neither tree seedling abundance nor cover of non-grass vegetation (i.e., forbs and shrubs) increased with seed abundance, ranked seed abundance, or frugivore detections (Fig. 3b and Table A5).

4. Discussion

For artificial roosts to initiate nucleating succession in tropical pastures: (1) bats must use roosts in pasture; (2) bat visitation must increase seed rain; and (3) increased seed rain must translate to higher seedling recruitment. Our results corroborate previous observations that bats will find and use roosts quickly when they are located in forests and that bat visitation increases seed rain abundance (Kelm et al., 2008). However, bats in our study rarely visited roosts in pastures, and greater seed rain abundance did not lead to higher seedling recruitment over a 2-year period. As such, we conclude that artificial roosts did not accelerate forest succession in abandoned pastures in premontane southern Costa Rica.

4.1. Why did bats not visit roosts in degraded pasture?

There are at least three possible explanations for limited bat usage of roosts in degraded pasture. First, roost microclimate may have been unsuitable in pastures (Fig. 2c). Microclimate is an important determinant of roost use in bats (Boyles, 2007). Phyllostomid bats in Mexico, for example, preferentially roost in caves with temperature < 20 °C (Avila-Flores and Medellín, 2004). We observed that the most frequently-visited roosts were also the coolest roosts (max. daily temp. < 24 °C), both in pasture and in forest. Moreover, a model using only maximum daily roost temperature was a better predictor of bat detections than models using treatment or treatment and maximum daily roost temperature combined. This observation strongly suggests that microclimate is a driver of variance in artificial roost visitation.

Roosts may also have been difficult for bats to locate given that there are few resources (i.e., food, shelter) that would cause bats to spend significant amounts of time in degraded pastures. The sensory mechanisms for how bats locate suitable, uninhabited roosts are not well-understood. Noctule bats (*Nyctalus noctula*) and disc-winged bats (*Thyroptera tricolor*) use conspecific echolocation calls to locate suitable roosts (Ruczynski et al., 2007; Chaverri et al., 2013). This habit is not known in the Phyllostomidae, but two large Phyllostomid frugivores, *Artibeus jamaicensis* and *Artibeus lituratus*, appear to use auditory communication in defense against predators (August, 1979; Ryan et al., 1985). If Phyllostomid bats also use conspecific signals to find roosts, then time until roost detection could potentially be reduced by playing bat vocalizations from speakers. Similar strategies have worked well for other taxa, such as common murre (*Uria aalge*; Parker et al., 2007). Another technique for improving roost detection could involve olfactory attractants, such as odiferous fruit oils (Bianconi et al., 2012). Both of these concepts warrant further research.

Roosts in this study were modified for use in pastures from the design used by Kelm et al. (2008) in northern Costa Rica, and these modifications likely influenced how bats interacted with the roosts. Specifically, our roosts were smaller (96,000 cm³ vs.

> 565,704 cm³) and the opening had a different orientation that may have allowed in more light (open on the bottom vs. the side). Whereas several bat species in Kelm's study tended to sleep in roosts during the day, bats in our study generally used roosts for nocturnal feeding. Microchiropteran bats in several families preferentially select large, dark day roosts (Aguirre et al., 2003; Ferrara and Leberg, 2005; Usman, 1988). If our roosts were brighter than Kelm's, this could explain the observed difference in behavior. Colonized roosts in Kelm's study also had greater absolute numbers of day roosting bats, which could be explained by the greater size of the roosts in that study.

4.2. Why did increases in seed rain not translate to increased seedling recruitment?

The lack of relationship that we observed between seed rain and seedling recruitment in pastures suggests that secondary succession is limited by more than just seed dispersal. Seeds that arrive in degraded pastures have an extremely low probability of survival; as few as 0.1% of seeds in an experiment in montane Costa Rica survived over an 18-mo period (Holl, 2002). Seed mortality is attributable to predation, desiccation, and rot (Cole, 2009), and the few seedlings that establish are impeded by competition with pasture grasses (Holl et al., 2000) and sometimes intense herbivory (Nepstad et al., 1990). Therefore, restoration applications designed to increase forest regeneration must monitor not only seed dispersal but also seedling recruitment (Reid and Holl, 2012). Future studies could isolate the mechanisms that prevent seedling establishment below roosts by comparing the fate of seeds exposed to different groups of predators (Cole, 2009), manipulating above- and below-ground competition with ruderal vegetation (Holl, 1998b), or reducing nutrient stress by adding fertilizer (Carpenter et al., 2004).

Additionally, seeds dispersed below roosts in forest were likely maladapted for understory abiotic conditions. Most of the seeds recovered in this study were small seeds from early-successional trees and shrubs such as *Cecropia*, *Piper*, and *Solanum*. In contrast, the most abundant tree seedlings were of later-successional species such as *Inga* and *Allophylus*, which may have been dispersed by other animals such as monkeys or birds. These observations support isotopic evidence from northern Costa Rica that *Carollia* spp. bats more frequently disperse early-successional seeds to late-successional environments than vice versa (Voigt et al., 2012). If this is the case, then *Carollia*-dominated bat roosts are also unlikely to meaningfully contribute to seed diversification in secondary forests and tree plantations. Instead, future research should explore the influence of bat roosts in forest on adjacent pasture development, or alternative roost designs to attract a different frugivore assemblage. Planting broad-leaved palms and *Heliconia* spp., for example, could provide roosting habitat for tent-making bats, some of which are known to disperse large, late-successional tree seeds (Melo et al., 2009).

The duration of this study (2 years) may have been insufficient for detecting an influence of increased seed rain on seedling recruitment. Seedling recruitment in tropical forests has considerable interannual variability, with large cohorts becoming established in some years, and few individuals establishing in others (Connell and Green, 2000; Curran and Leighton, 2000). During the years of this study (2009–2012), seedling recruitment in other restoration sites in our study area that have been monitored continuously for 6 years were not abnormally low (Zahawi et al., 2013), which suggests that interannual variability in establishment was probably not an important factor. Nonetheless, we do not expect that a longer monitoring period would have revealed greater seedling recruitment below bat roosts in our pastures because: (1) seed rain below roosts in pastures was low due to a lack of

bat visitation in that habitat and (2) previous studies suggest that a very large input of seeds would be required to increase recruitment in pastures given extremely low survivorship (Holl, 2002).

4.3. What effect might insectivorous bats have on forest regeneration?

Our results and the results of a previous study show that in addition to frugivores, leaf-gleaning insectivorous Phyllostomids frequently use artificial roosts (Kelm et al., 2008). We observed that insectivore detections were greater in roosts affixed to giant stakes than in roosts with no shade in open pastures. Enclosure experiments in the Neotropics have shown that insectivorous Phyllostomids reduce arthropod abundance in agroforestry systems (Williams-Guillén et al., 2008) and reduce arthropods and herbivory on seedlings in tropical forests (Kalka et al., 2008). If insectivorous Phyllostomids colonize roosts in regenerating forests or tree plantations, they could improve seedling survival and growth by suppressing invertebrate herbivores.

4.4. Planting bat-dispersed trees and shrubs as an alternative to artificial roosts

An alternative strategy to accelerate succession inexpensively could be to plant patches of trees or shrubs that produce bat-preferred fruits. Fruiting plants attract bats via olfactory cues (Fleming, 1988; Thies et al., 1998; Mikich et al., 2003), and trees and shrubs improve germination sites by reducing grass competition (Holl, 2002). Planting bat-preferred trees and shrubs could therefore address limitations to both dispersal and survival. In premontane southern Costa Rica, such species might include *Piper*, *Ficus*, and *Calophyllum* species. This alternative strategy does not preclude the concurrent use of artificial roosts.

4.5. Conclusions

We have demonstrated experimentally that artificial bat roosts in southern Costa Rica did not accelerate forest regeneration in former pastures over a 2-year period because bats rarely used roosts in pastures and increased seed rain below roosts did not translate to greater seedling recruitment. The general approach of manipulating bat behavior to catalyze succession, however, merits further study. Potential areas for future research include alternative roost designs that take into account the gamut of Phyllostomid roosting habits; barriers to seedling establishment below roosts; effects of leaf-gleaning insectivores on herbivore suppression; improvement of microclimatic conditions in roosts in pasture environments; and the ability of bats to detect roosts in different habitats. Restoration practitioners may also find it useful to plant bat-preferred trees and shrubs.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.06.026>.

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