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Artificial bat roosts did not accelerate forest regeneration in abandoned pastures in southern 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 Cavelier, 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

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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 rainforest (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 m^2 (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

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