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Temporal variation in fungal communities associated with tropical hummingbirds and nectarivorous bats

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ABSTRACT

Species of yeasts and other microfungi carried by pollinators are of general ecological interest because some of these microbial species can grow in floral nectar and affect plant–pollinator interactions. It is, however, not well understood how the composition of fungal species found on pollinators varies over space or time. The spatial and temporal distribution patterns in the microfungi found on the bills of hummingbirds and in the mouths of nectarivorous bats was investigated along a gradient of deforestation within a Costa Rican countryside landscape. The community composition of microfungi found on hummingbirds' bills and bats' mouths underwent substantial compositional turnover over a 2-month period and between 2 yr. In contrast, fungal community composition was not significantly correlated with spatial distance, habitat type, species of hummingbirds, nor the forest dependency of the hummingbirds sampled for microfungi. These findings suggest that, in this landscape, fungal communities on a nectarivous vertebrate vector might be influenced primarily by temporal factors such as plant and flower phenology rather than spatial environmental heterogeneity.

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Introduction

Recent studies have shown that flower-visiting animals such as bees, beetles, ants and hummingbirds vector multiple species of microfungi from flower to flower as they forage for floral nectar (Brysch-Herzberg, 2004; Herrera et al., 2008, 2010; 2013; Belisle et al., 2012; Vannette et al., 2013; De Vega and Herrera, 2013). Once introduced into nectar, some of the fungi utilize the sugars and amino acids present in the nectar for growth (Vannette et al., 2013; Peay et al., 2012; Brysch-Herzberg, 2004; Herrera et al., 2008). These microbes are of general ecological interest because they have the potential to alter plant–pollinator interactions by changing the chemical properties of nectar (Herrera et al., 2008; Peay et al., 2012 De Vega and Herrera, 2013; Vannette et al., 2013) and, consequently, the attractiveness of flowers to pollinators (Herrera et al., 2013; Vannette et al., 2013). Recent research indicates that the effects of nectar-inhabiting microbes on

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plant–pollinator interactions depend on the identity of microbial species (Vannette et al., 2013; Good et al., 2014). If so, to improve our understanding of the implications of microbes in nectar, it is important to know how the community composition of fungi (and bacteria) found on pollinators may vary over space and time. However, few data are currently available to address this question.

In this paper, we report a survey of the community composition of fungal species found on the bills of hummingbirds and nectarivorous bats in Costa Rica. We hypothesized that the fungal communities would: (1) vary in species composition through time and (2) vary in both abundance and species composition through space across a gradient of deforestation in the countryside landscape. Our analysis for testing these hypotheses focused primarily on hummingbirds because we had more extensive data on hummingbirds than on bats.

Materials and methods

Study system

Hummingbird and microorganism sampling took place in and around the Las Cruces Biological Station (LCBS) in the Coto Brus Valley in southwestern Costa Rica (8° 47′ N, 82° 57′ W, 1 100 m above sea level). The LCBS encompasses ~280 ha of protected primary and mature secondary forest (Fig 1A). The climate of the region is characterized by a long rainy season (Stiles et al., 1989) and forests in the area are classified as premontane tropical wet forest (Holdridge, 1979). Over 60 % of the Coto Brus Valley, once forested, has been converted into cropland and pasture since the 1950s (Mendenhall et al., 2011; Sansonetti, 1995).

We sampled at 18 study sites within a 4 300 ha area (Fig 1). The study sites were classified into three types, as in Mendenhall et al. (2011): Las Cruces Forest Reserve (3 study sites), sun coffee plantations (6 study sites), and countryside forest elements (9 study sites). Sun coffee plantations had ~5–25 % seasonal canopy cover directly over the coffee shrubs, mostly consisting of nitrogen-fixing Poró trees (*Erythrina* spp.) and banana and plantain plants (*Musa* spp.). Countryside forest elements included clusters of trees of various sizes and qualities, live fences, hedgerows and riparian strips embedded in agricultural land, which were too complex in configuration to be considered isolated forest fragments (Mendenhall et al., 2011). Study sites were chosen to maximize spatial independence and avoid spatial clustering of a similar type (Fig 1A).

Hummingbird and bat sampling

Hummingbird bills were sampled for microfungi from Jan. 2, 2011 to Mar. 28, 2011 and from Jan. 7, 2012 to Feb. 28, 2012. In total we sampled 585 birds and bats in 2011 and 305 in 2012 (Table 1). Birds and bats were sampled by constant-effort mist netting. Mist-netting protocols consisted of twenty 12 × 2.5 m, ground-level mist nets with 32 mm mesh in a 3 to 5 ha plot haphazardly placed at each of the 18 study sites. After capture, hummingbirds and bats were fed sterile sugar water containing 50 % sucrose in Eppendorf tubes (Fig 1B), and the

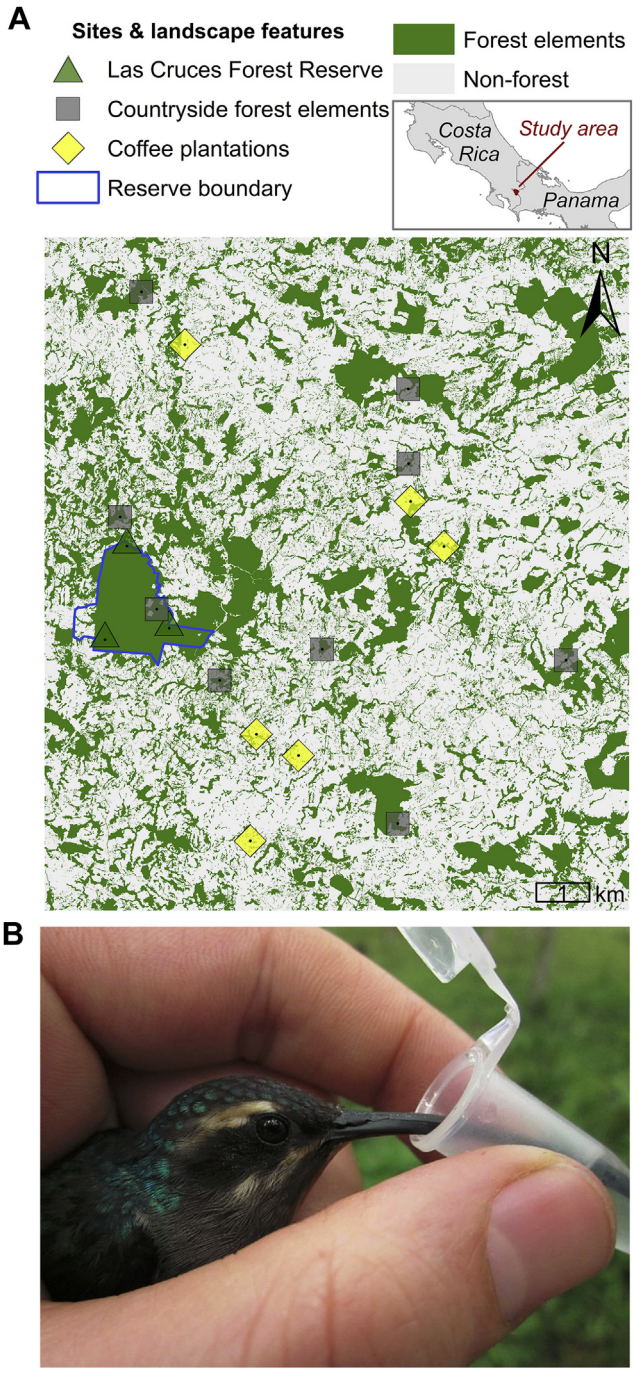

Fig 1 – (A) Map displaying study sites in Coto Brus, Costa Rica. The Organization for Tropical Studies Las Cruces Biological Station's Las Cruces Forest Reserve is outlined in blue. Each point represents one of 18 sites. (B) A Green Hermit being fed sterile sugar water (50 % sucrose) from an eppendorf tube.

remaining sucrose solution which had come into contact with birds' beaks and tongues was refrigerated for further analysis.

To minimize contamination, great care was taken to introduce only the hummingbirds' bills or the bats' tongue and the associated microbes into the sugar water, and the Eppendorf tubes closed immediately after inoculation. Even though some contamination may have been inevitable despite the care taken,

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