Project

Ecology of plant-hummingbird interactions along an elevational gradient

Scientific Progress Report

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Study site

Bosque del Tolomuco

Cerro de la Muerte

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INTRODUCTION

A primary aim of community ecology is to identify the processes that govern species assemblages across environmental gradients (McGill et al. 2006), allowing us to understand why biodiversity is non-randomly distributed on Earth. Mutualistic interactions such as those between plants and their animal pollinators are the major biodiversity component from which the integrity of ecosystems depends (Valiente-Banuet et al. 2015). The vast majority of flowering plant species, especially in tropical regions, only produce seeds and subsequently fruits if pollinators transfer pollen grains from the anthers to the stigmas of their flowers, in a mutually beneficial relationship. Without this service, many interconnected species and ecosystem functioning would simply collapse. The interdependence of plant and pollinators can be assessed using a network approach, which is a powerful tool to analyze the complexity of ecological systems (Ings et al. 2009), especially in highly diversified tropical regions.

Mountain regions provide pronounced environmental gradients across relatively small spatial scales and have proved to be a suitable model system to investigate patterns and determinants of species diversity and community structure (Körner 2000, Sanders and Rahbek 2012). Although some studies have investigated the variation in plant–pollinator interaction networks across elevational gradients (Ramos-Jiliberto et al. 2010, Benadi et al. 2013, Maglianesi et al. 2015), such studies are still scarce, particularly in the tropics. In the Neotropics, hummingbirds (Trochilidae) are considered to be effective pollinators (Castellanos et al. 2003). They have been classified into two distinct groups: hermits and non-hermits, which differ mainly in their elevational distribution and their level of specialization on floral resources, i.e., the proportion of floral resources available in the community that is used by species (Stiles 1978). Hermit hummingbirds mostly occur in wet lowland forests and are specialized on specific floral resources (Snow and Snow 1972). Non-hermit hummingbirds split in eight clades which may be found along a wide range of elevations and are in overall less specialized than hermits (Feinsinger and Colwell 1978).

To study the processes that determine biodiversity across time and space including mutualistic interactions, we will use a hierarchical cross-scale approach that integrates network ecology, statistical modeling and experimentation. More specifically, we will: (1) evaluate the patterns of species and functional β-diversity in hummingbirds and their food plants along an elevation gradient in Costa Rica; (2) evaluate the ecological and evolutionary drivers of plant-hummingbird interactions along this gradient to test theoretical predictions about network structure; (3) quantify how and why interaction β-diversity (i.e., the combination of changes in both species composition and interacting partners) changes across elevations. Addressing this integrative set of objectives will yield a new perspective on one of the most fundamental questions in ecology and evolution; that is, what mechanisms drive species diversity and mutualistic interactions in ecological communities. A particular strength of our work lies in that we will collect a unique and extensive dataset along four elevational bands in Costa Rica that will serve as an important resource for the broader scientific community to test and develop new theory in community ecology and evolution.

METHODS

Study site and sampling design

Field data collection was conducted at 12 study sites in four elevation bands ranging from 700 m a.s.l. to 3.100 m a.s.l. in central-southern Costa Rica on the Pacific slope of the Talamanca mountains (Fig. 1). The Tolomuco Forest is located at kilometer 18 of the inter-American highway in the canton of Pérez Zeledón. It is a 22-ha property that offers accessible trails for hiking through the forest and cabins equipped to stay. It also offers its visitors a peaceful environment surrounded by nature to relax and enjoy. Bird watching is their specialty, it is possible to observe around 241 bird species, due to its good location and its diversity of habitats, such as garden areas, forest edges, open areas and the forest itself. The name of this forest alludes to the mammal *Eira barbara* from the family Mustelidae which is commonly known as tolomuco.

To monitor species abundance patterns, flowering phenology and hummingbird flower visitation, we will use a combination of a transect and time-lapse cameras (described below). The transect will be 1.5 km long (spanning no more than 200 m of elevation) × 10 m wide. Sampling will be done once per month with approximately even time spacing between sample periods; extreme weather will be avoided. Four kinds of data will be taken on each transect: hummingbird (and flower piercers) counts, interaction observations, flower abundance and flower morphology.

Data collection in the field transect

(a) Hummingbird counts: any hummingbird heard or seen at a distance of 20 m from the observer will be recorded at the species level using binoculars and a local bird guide.

(b) Interaction observations: any plant species with flowers visited by a hummingbird will be noted.

(c) Flower abundance: any plant with flowers fitting the traditional ornithophilous syndrome (Faegri and van der Pijl 1979) within a distance of ~5 meters of the transect will be counted and identified to species level. Characteristics of a flower with the ornithophilous syndrome include brightly colored flowers (purple, red, orange or yellow) with medium to long corollas. Because hummingbird-pollinated plant species do not always fit into this syndrome (Ollerton et al. 2009), we will also consider plant species with flowers fitting other pollination syndromes (e.g., bat- or insect-pollinated flowers) that are likely to be visited by hummingbirds as well. For each plant either all flowers will be counted or in the case of bushes, total flowers on 3 representative branches will be counted and used to extrapolate the number of flowers on the plant. Each species will be collected once and pressed in order to archive our work and/or verify identification with an expert.

(d) Flower morphology: flower corolla length (the distance from the flower opening to the back of corolla) will be measured on at least three plant individuals. Wherever possible, we will estimate the effective corolla distance by cutting open flowers and measuring the corolla length extending back to the flower nectaries.

Time-lapse cameras

To record the interactions between plant and hummingbird species in the understory, we will use the time-lapse camera strategy that was developed by Weinstein (2015) and has dramatically increased our ability to collect data. Time-lapse cameras, which take a picture every second, will be placed at individual flowering plants along the above described transect to capture visitation by hummingbirds. We will place 6 cameras on the flowering plants found along the transect roughly proportional to their abundance. The cameras turn on at dawn and record an image every second for 3 days, resulting in a dataset of millions of images. These images are efficiently processed using Motion Meerkat (Weinstein 2015) which can be used to sort out images with hummingbirds which can be manually identified. This approach minimizes reliance on time-consuming human flower observations, greatly increasing data collection in time and space permitting a rigorous test of network theory. Thus, this project will generate a unique dataset on plant-hummingbird interactions which will be made available to the scientific community for theoretical and applied questions. Based on the cameras data, we will build an interaction matrix with plant species as rows, hummingbird species as columns and each cell filled with the observed frequency of pairwise interactions. This interaction matrix will be used to calculate network metrics such as specialization, modularity and nestedness.

Trait data

We will use the following hummingbird functional traits to calculate functional diversity: body mass (weight of a live individual), bill length (length of the bill from base to tip), tarsus length (length from the outer bend of the tibiotarsal articulation to the base of the toes), wing loading (the ratio of body mass to wing area), and wing aspect ratio (the quotient of twice the square of the wing length divided by wing area). High wing loading represents a high body mass to wing area ratio and a high aspect ratio denotes narrow wings. While some species in the studied community are sexually dimorphic, the standard deviation of a trait value within a species including measures of both sexes is much lower than the standard deviation of a trait across males of different species (Graham et al. 2012). Intraspecific variation related to sex is, therefore, unlikely to influence our results.

RESULTS

After 11 months of data collection, we filmed a total of 131 individuals from 32 flowering plant species at Bosque del Tolomuco, from which 16 were visited by eight hummingbird species. The total number of plant-hummingbird interactions was 665, between 16 plant species and seven hummingbird species. The White-throated mountaingem (*Lampornis castaneoventris*) had the highest interaction frequency with 279 interactions, followed by the Stripe-tailed Hummingbird (*Eupherusa eximia*) with 181 interactions and the Green-hermit (*Phaethornis guy*) with 92 interactions (Table 1, Fig. 2, 3). The Green-crowned Brilliant (*Heliodoxa jacula*) and the Violet-headed Hummingbird (*Klais guimeti*) were the most uncommon species with only one or two observed interactions (Fig. 4).

The most visited plant species were *Cavendishia confertiflora* (Ericaceae) with 161 visits, *Palicourea lasiorrachis* (Rubiaceae) with 104 visits, and *Razisea spicata* (Acanthaceae) with 95 visits (Table 1; Fig. 5).

Table 1. Number of interactions between plant and hummingbird species at Bosque del Tolomuco, Costa Rica.

	Elvira chionura	Eupherusa eximia	Heliodoxa jacula	Klais guimeti	Lampornis castaneoventris	Phaethornis guy	Selasphorus scintilla	TOTAL
Alloplectus tetragonus	0	7	0	0	0	16	0	23
Besleria solanoides	0	3	0	0	12	0	0	15
Cavendishia confertiflora	0	0	0	0	158	3	0	161
Columnea polyantha	0	0	0	0	0	28	0	28
Hillia triflora	0	4	0	1	1	1	0	7
Macrocarpaea valerii	0	23	0	0	56	0	0	79
Malvaviscus achanioides	0	0	0	0	0	3	0	3
Malvaviscus concinnus	0	1	0	0	0	7	0	8
Palicourea angustifolia	1	0	0	0	25	0	4	30
Palicourea lasiorrachis	80	0	0	0	0	0	24	104
Pitcairnia brittoniana	1	65	2	0	0	0	0	68
Psammisia ramiflora	0	0	0	0	7	7	0	14
Psychotria chiriquensis	0	1	0	0	20	0	0	21
Razisea spicata	0	69	0	0	0	26	0	95
Sobralia amabilis	0	4	0	0	0	1	0	5
Symbolanthus pulcherrimus	0	4	0	0	0	0	0	4
TOTAL	82	181	2	1	279	92	28	**665**

We had a total of 2.786 flower counts within the transect, corresponding to 43 plant species, where the most abundant species were *Miconia tonduzii* (Melastomataceae), followed by *Palicourea angustifolia* and *P. lasiorrhachis* (Rubiaceae) with 1049, 274 and 249 flowers, respectively (Table 2).

Tabla 2. Flower abundance of plant species observed within the transect at Bosque del Tolomuco, Costa Rica.

Order	Family	Plant Species	N° flowers
Asparagales	Orchidaceae	*Epidendrum sotoanum*	5
Asparagales	Orchidaceae	*Epidendrum lacruste*	2
Asparagales	Orchidaceae	*Maxillaria porrecte*	2
Asparagales	Orchidaceae	*Miltoniopsis warscewiczii*	8
Asparagales	Orchidaceae	*Sobralia amabilis*	1
Asterales	Campanulaceae	*Burmeistera vulgaris*	1
Commelinales	Commelinaceae	*Dichorisandra amabilis*	7
Commelinales	Commelinaceae	*Tradescantia zanonia*	9
Ericales	Ericaceae	*Cavendishia confertiflora*	42
Ericales	Ericaceae	*Psammisia ramiflora*	83
Gentianales	Gentianaceae	*Macrocarpaea valerii*	110
Gentianales	Gentianaceae	*Symbolanthus pulcherrimus*	59
Gentianales	Rubiaceae	*Coussarea caroliana*	32
Gentianales	Rubiaceae	*Hillia triflora*	8
Gentianales	Rubiaceae	*Hoffmannia pittieri*	1
Gentianales	Rubiaceae	*Palicourea angustifolia*	274
Gentianales	Rubiaceae	*Palicourea lasiorrhachis*	249
Gentianales	Rubiaceae	*Palicourea padifolia*	128
Gentianales	Rubiaceae	*Psychotria aubletiana*	30
Gentianales	Rubiaceae	*Psychotria chiriquensis*	40
Gentianales	Rubiaceae	*Hoffmannia psychotriiflora*	8
Lamiales	Acanthaceae	*Justicia angustibracteata*	3
Lamiales	Acanthaceae	*Razisea spicata*	31
Lamiales	Gesneriaceae	*Alloplectus tetragonus*	8
Lamiales	Gesneriaceae	*Besleria solanoides*	70
Lamiales	Gesneriaceae	*Columnea consanguinea*	1
Lamiales	Gesneriaceae	*Columnea magnifica*	2
Lamiales	Gesneriaceae	*Columnea polyantha*	25
Lamiales	Gesneriaceae	*Drymonia turrialvae*	2
Lamiales	Lamiaceae	*Scutellaria hookeri*	5
Malpighiales	Violaceae	*Viola scandens*	159
Malvales	Malvaceae	*Malvaviscus achanioides*	2
Myrtales	Melastomataceae	*Conostegia montana*	109
Myrtales	Melastomataceae	*Leandra melanodesma*	8
Myrtales	Melastomataceae	*Miconia pittieri*	11
Myrtales	Melastomataceae	*Miconia tonduzii*	1049
Myrtales	Melastomataceae	*Ossaea micrantha*	10

Poales	Bromeliaceae	*Guzmania nicaraguensis*	1
Poales	Bromeliaceae	*Pitcairnia brittoniana*	162
Poales	Bromeliaceae	*Tillandsia excelsa*	13
Poales	Bromeliaceae	*Vriesea lyman-smithii*	2
Zingiberales	Heliconiaceae	*Heliconia gracilis*	3
Zingiberales	Maranthaceae	*Calathea brenesii*	11
TOTAL			**2.786**

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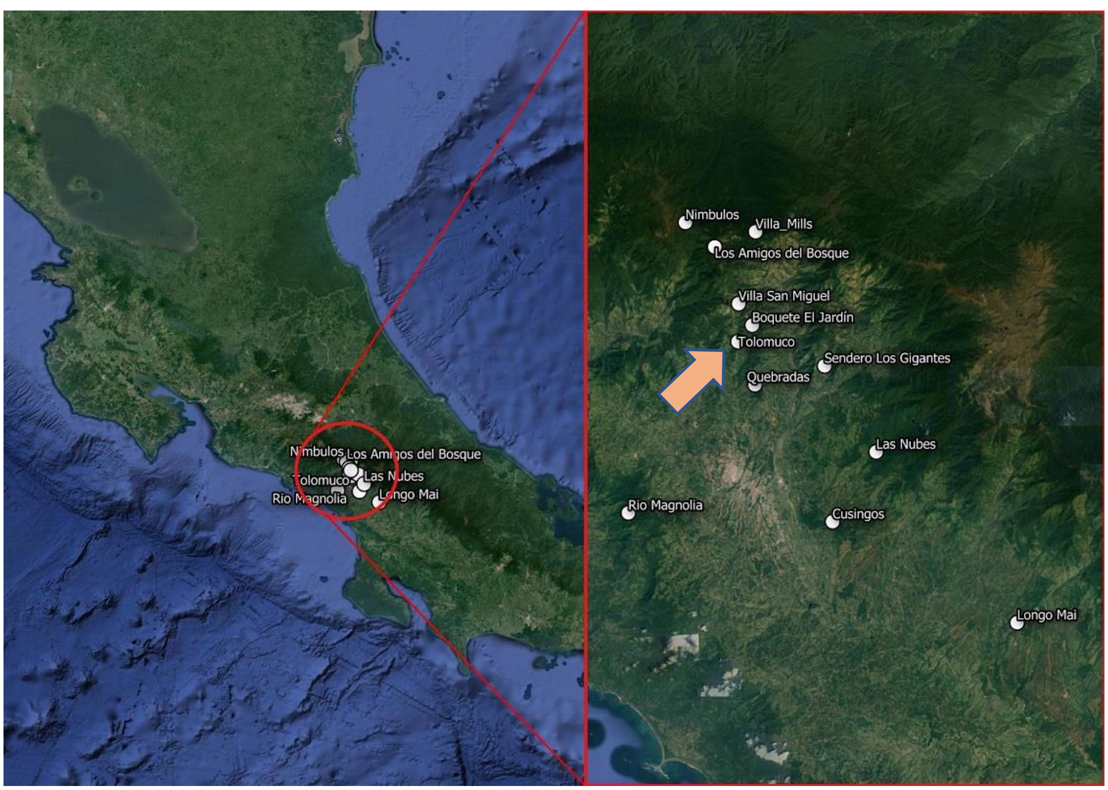

Figure 1. Area of the project including the 12 study sites across an elevational gradient.

Figure 2. The Stripe-tailed Hummingbird (*Eupherusa eximia*) visiting *Pitcairnia brittoniana* (Bromeliaceae) at Bosque del Tolomuco. Photo: EPHI project.

Figure 3. The Green-hermit (*Phaethornis guy*) visiting *Columnea polyantha* (Gesneriaceae) at Bosque del Tolomuco. Photo: EPHI project.

Figure 4. The Green-crowned Brilliant (*Heliodoxa jacula*) and the Violet-headed Hummingbird (*Klais guimeti*) observed in the Bosque del Tolomuco. Photos: Alejandro Castro Jiménez.

Figure 5. Plant species fitting the ornithophilous syndrome that were visited by hummingbirds in Bosque del Tolomuco: *Cavendishia confertiflora* (Ericaceae) and *Razisea spicata* (Acanthaceae).