Project

Ecology of plant-hummingbird interactions along an elevational gradient

Scientific Progress Report

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Study site

Las Nubes Biological Reserve

York University

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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 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), 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 elevations 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 will be 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. Las Nubes Biological Reserve is one of these sites, which is located an hour East of the city of San Isidro El General with an area of 145 ha (9.388° N, -83.595° W). This Reserve is part of a project conducted by the Faculty of Environmental Studies (FES) at York University (Toronto, Canada), and supported by the Fisher Fund for Neotropical Conservation. Las Nubes Project supports the protection of the biological, ecological and social values of the Las Nubes Biological Reserve and adjacent area in southern Costa Rica. Since its creation in late 1990s, Las Nubes Project mission has been to contribute to community well-being in ways that are compatible and conducive to environmental conservation. The dry season at Las Nubes lasts from December to April and the wet season reaches a peak during October.

To monitor 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 seven months of data collection, we filmed a total of 29 flowering plant species at Las Nubes Biological Reserve, from which 17 were visited by eight hummingbird species. The total number of plant-hummingbird interactions was 769, where the Green Hermit (*Phaethornis guy*) had the highest interaction frequency with 411 interactions, followed by the Stripe-throated Hermit (*Phaethornis striigularis*) with 275 interactions (Table 1, Fig. 1,2 in Appendix). The most visited plant species were *Aechmea tonduzii* (Bromeliaceae) with 185 visits, *Heliconia beckneri* (Heliconiaceae) with 127 visits, and *Renealmia alpinia* (Zingiberaceae) and *Psammisia ramiflora* (Ericaceae) with 100 visits each (Table 1; Fig. 2,3 in Appendix).

Table 1. Number of interactions between plant and hummingbird species at Las Nubes Biological Reserve, Costa Rica.

	Amazilia tzacatl	*Colibri cyanotus*	*Doryfera ludovicae*	*Elvira chionura*	*Heliodoxa jacula*	*Phaethornis guy*	*Phaethornis striigularis*	*Thalurania colombica*	TOTAL
Aechmea tonduzii	0	0	0	1	0	43	140	1	185
Burmeinstera cyclostigmata	0	0	0	0	0	4	1	3	8
Calathea crotalifera	0	0	0	0	0	0	60	0	60
Cavendishia complectens	0	0	0	2	0	0	4	0	6
Centropogon granulosus	0	0	0	0	0	0	1	0	1
Elleanthus aurantiacus	5	0	0	1	0	0	5	0	11
Erythrina costaricensis	0	0	0	0	0	41	1	0	42
Heliconia beckneri	0	0	0	0	4	123	0	0	127
Malvaviscus concinnus	0	0	0	0	0	1	1	0	2
Malvaviscus sp	0	1	0	0	0	51	14	0	66
Maxillaria horichii	0	0	0	0	0	0	0	1	1
Poikilacanthus macranthus	0	0	0	0	0	4	1	0	5
Psammisia ramiflora	0	0	39	10	0	49	1	1	100
Psychotria poeppigiana	6	0	0	0	0	6	18	7	37
Razisea spicata	0	0	0	0	0	8	6	0	14
Renealmia alpinia	0	0	0	1	0	81	18	0	100
Scutellaria glabra	0	0	0	0	0	0	4	0	4
TOTAL	11	1	39	15	4	411	275	13	769

We recorded in average 1.967 flowers within the transect, corresponding to 46 plant species, where the most abundant species were *Leandra grandiflora* (Melastomataceae), *Ossaea cf brenesii* (Melastomataceae) and *Psammisia ramiflora* (Ericaceae) with 222, 217 and 211 flowers, respectively (Table 2). *Thalurania colombica* was observed in the transect feeding on *Elleanthus aurantiacus* (Orchidaceae) and *Palicourea padifolia* (Rubiaceae), whereas *Phaethornis guy*, *Florisuga mellivora*, *Elvira chionura* and *Amazilia tzacatl* were observed doing activities other than feeding, such as flying, perching or vocalizing (Fig. 4 in Appendix).

Tabla 2. Flower abundance of plant species observed within the transect in Las Nubes Biological Reserve, Costa Rica.

Plant species	**Number of flowers**
Aechmea tonduzii	1
Besleria solanoides	16
Besleria trichostegia	17
Blakea gracilis	8
Blakea litoralis	6
Burmeinstera cyclostigmata	7
Calathea crotalifera	172
Calathea guzmanioides	3
Cavendishia bracteata	1
Cavendishia complectens	7
Centropogon granulosus	15
Costus laevis	1
Drymonia turrialvae	3
Elleanthus aurantiacus	158
Elleanthus glaucophyllus	48
Epidendrum paraguastigma	136
Erythrina costaricensis	12
Guzmania donnell smithii	10
Guzmania nicaraguensis	15
Heliconia beckneri	4
Justicia aurea	20
Leandra grandiflora	222
Malvaviscus achainoides	1
Malvaviscus concinnus	14
Maxillaria horichii	90

Plant species	Number of flowers
Miconia loreyoides	11
Notopleura uliginosa	31
Ossaea cf brenesii	217
Palicourea alajuelensis	1
Palicourea albocaerulea	22
Palicourea padifolia	17
Phytolacca rivinoides	27
Pitcairnia brittoniana	7
Pleiostachya leiostachya	2
Poikilacanthus macranthus	90
Psammisia ramiflora	211
Psychotria buchtienii	29
Psychotria elata	4
Psychotria pilosa	194
Psychotria poeppigiana	18
Psychotria recordiana	9
Razisea spicata	13
Renealmia alpinia	4
Scutellaria glabra	18
Utricularia endresii	30
Vriesea viridiflora	1

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APPENDIX

Figure 1. The interaction between the Green Hermit (*Phaethornis guy*) and *Razisea spicata* (Acanthaceae) recorded at Las Nubes Biological Reserve. Photo: EPHI project.

Figure 2. The Stripe-throated Hermit (*Phaethornis striigularis*) visiting *Aechmea tonduzii* (Bromeliaceae) at Las Nubes Biological Reserve. Photo: EPHI project.

Figure 3. Plant species fitting the ornithophilous syndrome that were observed in Las Nubes Biological Reserve: *Renealmia alpinia* (Zingiberaceae), *Palicourea padifolia* (Rubiaceae) and *Justicia aurea* (Acanthaceae). Photos: María Alejandra Maglianesi.

Figure 4. The White-necked Jacobin (*Florisuga mellivora*) and the Rufous-tailed Hummingbird (*Amazilia tzacatl*) observed within the transect at Las Nubes Biological Reserve. Photos: Alejandro Castro Jiménez.