



Research Article

# The Manú Gradient as a study system for bird pollination

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## Abstract

## Background

This study establishes an altitudinal gradient, spanning from the highland Andes (2400 m) to lowland Amazon, as a productive region for the study of bird pollination in Southeastern Peru. The 'Manú Gradient' has a rich history of ornithological research, the published data and resources from which lay the groundwork for analyses of plant-bird interactions. In this preliminary expedition we documented 44 plants exhibiting aspects of the bird pollination syndrome, and made field observations of hummingbird visits at three sites spanning the Manú Gradient: 2800 m (Wayqecha), 1400 m (San Pedro), and 400 m (Pantiacolla). Some of the documented plant taxa are underrepresented in the bird pollination literature and could be promising avenues for future analyses of their pollination biology. The Manú Gradient is currently the focus of a concerted, international effort to describe and study the birds in the region; we propose that this region of Southeastern Peru is a productive and perhaps underestimated system to gain insight into the ecology and evolution of bird pollination.

## New information

Observations were made on 11, 19, and 14 putatively bird pollinated plant species found at the high-, mid- and low-elevation sites along the gradient, respectively. Hummingbirds visited 18 of these plant species, with some plant species being visited by multiple hummingbird species or the same hummingbird species on differing occasions. Morphometric data is presented for putatively bird-pollinated plants, along with bill measurements from hummingbirds captured at each of three sites. Voucher specimens from this study are deposited in the herbaria of the Universidad Nacional de Agraria de La Molina (MOL), Peru and the University of British Columbia (UBC), Canada. The specimens collected represent a 'snapshot' of the diversity of bird-pollinated flora as observed over 10 day sampling windows (per site) during the breeding season for hummingbirds of Manú.

## Keywords

Hummingbirds, elevational gradient, co-evolution, ornithophily, pollination ecology, Andes, Amazon, neotropics

## Introduction

Manú National Park is a UNESCO Biosphere Reserve nested within the most biodiverse region in the world: the tropical Andes (Myers et al. 2000). Manú Park, and its surrounding forests encompass a remarkable elevational gradient (hereafter the 'Manú Gradient') of over 3000 m, reaching from the lowland Amazon rainforest to the Puna grasslands of the high Andes. The Manú Gradient has a rich history of ornithological research (discussed in Walker et al. 2006), and over the last decade the Manú Gradient has been the focus of numerous ornithological studies as part of the Manú Bird Project (e.g. Merkord 2010, Jankowski et al. 2012a, Jankowski et al. 2012b, Londoño et al. 2014, Londoño et al. 2016, Dehling et al. 2014, Munoz 2016). Along the gradient, tree composition and forest structure have also been described (e.g. Jankowski et al. 2012b, Malhi et al. 2010, Hillyer and Silman 2010). The wide interest in the avian community of Manú make it an ideal system for studying hummingbird pollination: population structure, range limits, and locations of uncommon and understudied hummingbirds are described and published. For example, focused studies of the high elevation Shining Sunbeam (*Aglaeactis cupripennis*) have demonstrated the effectiveness of the Manú Gradient as a study system for bird pollination (Hazlehurst et al. 2016, Hazlehurst and Karubian 2016). Therefore, the objectives of this study were to, 1) document the occurrence of putatively bird pollinated plants with voucher specimens along the Manú Gradient, 2) describe the occurrence and diversity of hummingbirds using mist-net surveys, and 3) record hummingbird visitations to flowering plants.

## Materials and Methods

### Site Selection

We surveyed three field sites spanning an altitudinal gradient of 2400 m (400 m to 2800 m) in the southeastern Andes (Table 5): La Estación Biológica Wayqecha (Paucartambo Province, Cuzco Region, 2800 m), San Pedro (Paucartambo Province, Cuzco Region, 1400 m), and Pantiacolla (Manú Province, Madre de Dios Region, 400 m). This area is one of the most biologically rich regions in the world with an estimated species pool of nearly 1100 birds (Walker et al. 2006). To our knowledge, a comprehensive survey of the vascular plants of the region does not exist, although an increasing number of plant identification resources for this region are being made available by the Field Museum of Natural History (<http://fieldguides.fieldmuseum.org>). Wayqecha is characterized as high elevation cloud forest, with a mosaic of mature forest and areas with shorter trees and woody shrubs that transitions into puna grassland above treeline. San Pedro is predominately mid-montane humid rainforest, but also includes the lower extent of the montane cloud forest. Pantiacolla is situated at the interface between the Andean foothills and the lowland Amazon. Detailed environmental characteristics for these sites have been summarized in Malhi et al. (2016). Sampling was carried out between September 4, 2016 and October 13, 2016, falling within the avian montane breeding season. A distinct rainy season occurs from November through April and a dry season from May through August. Annual precipitation for higher elevations (2700-3000 m) ranges from 1700-2000 mm (Girardin et al. 2010) and is generally >2000 mm for lowland (100-400 m elevation) sites (Rapp and Silman 2012). Time constraints afforded less than two weeks ( $10.3 \pm 2.1$  days) for botanical and avian sampling at each site.

Table 1.

Putatively bird pollinated plants along the Manú Gradient.

| Plant Genus        | Specific epithet | Family       | Collection number(s) for plant specimens deposited in the herbaria of MOL and UBC | Corolla length (mm) | Corolla width (mm) | Nectar (% sugar, * = not recorded) | Corolla colour(s) | Hummingbird visited | Habitat notes                                        |
|--------------------|------------------|--------------|-----------------------------------------------------------------------------------|---------------------|--------------------|------------------------------------|-------------------|---------------------|------------------------------------------------------|
| <i>Besleria</i> L. | sp. 1            | Gesneriaceae | MMAB 1                                                                            | 8                   | 1                  | *                                  | red               |                     | Growing along trail's edge in relatively open canopy |

|                                 |                                                  |               |                |     |    |      |                                          |                                                                                            |                                                                                                                                                                         |
|---------------------------------|--------------------------------------------------|---------------|----------------|-----|----|------|------------------------------------------|--------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Heliconia</i> L.             | sp. 1                                            | Heliconiaceae | MMAB 10,<br>11 | 100 | 19 | *    | translucent<br>with pink                 |                                                                                            | Lowest point of<br>a bog with little<br>shade.<br>Pioneering<br><i>Cecropia</i> and<br><i>Schefflera</i> are<br>dominating<br>species. <i>Ruellia</i><br>also abundant. |
| <i>Centropogon</i>              | <i>granulosus</i> C.<br>Presl                    | Campanulaceae | MMAB 12,<br>13 | 40  | 15 | *    | yellow<br>within red<br>bract            |                                                                                            | Along ditches of<br>the Manu Road.<br>Typically at<br>points facing<br>South-East.<br>Relatively dry<br>forest edge.                                                    |
| <i>Centropogon</i>              | <i>granulosus</i> C.<br>Presl                    | Campanulaceae | MMAB 2,<br>3   | 35  | 15 | 25.5 | red and<br>yellow                        |                                                                                            | Vine growing<br>through dense<br>understory at<br>1-3 m.<br><i>Guadua</i><br>abundant.<br>Flowers at<br>breaks in the<br>canopy where<br>sunlight is more<br>abundant.  |
| <i>Sanchezia</i><br>Ruiz & Pav. | sp. 1                                            | Acanthaceae   | MMAB 20,<br>21 | 70  | 5  | *    | yellow<br>within red<br>bract            |                                                                                            | Along ditches of<br>the Manu Road.<br>Grows along<br>weedy species<br>including<br><i>Vernonia</i> ,<br><i>Calceolaria</i> , and<br><i>Gloxinia</i>                     |
| <i>Columnea</i>                 | <i>guttata</i> Poepp.<br>& Endl.                 | Gesneriaceae  | MMAB 22,<br>23 | 10  | 1  | 20   | yellow                                   |                                                                                            | Epiphytic.<br>Found readily in<br>the same<br>habitats as that<br>of <i>Columnea</i> sp.<br>1                                                                           |
| <i>Heliconia</i>                | <i>subulata</i> Ruiz<br>& Pav.                   | Heliconiaceae | MMAB 24,<br>44 | 40  | 10 | *    | bright<br>yellow in<br>dark red<br>bract |                                                                                            | Found in dense<br>stand of<br><i>Guadua</i> . Little<br>sunlight,<br>relatively dry.                                                                                    |
| <i>Guzmania</i>                 | <i>weberbaueri</i><br>Mez                        | Bromeliaceae  | MMAB 25,<br>26 | 37  | 7  | *    | yellow                                   | <i>Colibri thalassinus</i> ,<br><i>Doryfera ludoviae</i> ,<br><i>Heliodoxa leadbeateri</i> | Grows both as<br>an epiphyte and<br>from the<br>ground. Always<br>in high-moisture<br>environments<br>including bogs<br>but less<br>common near<br>river's edge.        |
| <i>Columnea</i>                 | cf.<br><i>inaequilatera</i><br>Poepp. &<br>Endl. | Gesneriaceae  | MMAB 27,<br>28 | 44  | 9  | 21.5 | red                                      |                                                                                            | Edge of fast-<br>flowing rocky<br>river with little<br>shade.                                                                                                           |

|                               |                                          |                 |                |     |    |      |                               |                                                                  |                                                                                                 |
|-------------------------------|------------------------------------------|-----------------|----------------|-----|----|------|-------------------------------|------------------------------------------------------------------|-------------------------------------------------------------------------------------------------|
| <i>Thrysacanthus</i><br>Moric | sp. 1                                    | Acanthaceae     | MMAB 29,<br>30 | 10  | 1  | 22.5 | red-purple                    |                                                                  | Along ditch of<br>the Manu Road.<br>East-facing, well<br>drained.                               |
| <i>Gurania</i>                | <i>eriantha</i><br>Poep. &<br>Endl.      | Cucurbitaceae   | MMAB 33        | *   | *  | *    | red                           |                                                                  | Along ditch of<br>the Manu Road.<br>Growing<br>through dense<br>vegetation,<br>flowers at edge. |
| <i>Drymonia</i>               | <i>semicordata</i><br>(Poep.)<br>Wiehler | Gesneriaceae    | MMAB 34,<br>35 | 10  | 2  | *    | yellow<br>within red<br>bract |                                                                  | Hanging over<br>edge of fast-<br>flowing rocky<br>river. Shaded by<br>various<br>Araceae.       |
| <i>Besleria</i> L.            | sp. 1                                    | Gesneriaceae    | MMAB 36,<br>37 | 20  | 8  | *    | bright red                    |                                                                  | Wet, dark, steep<br>rocky cliff. North<br>facing.                                               |
| <i>Drymonia</i>               | <i>urceolata</i><br>Wiehler              | Gesneriaceae    | MMAB 40,<br>39 | 20  | 5  | *    | red                           |                                                                  | Wet, dark, steep<br>rocky cliff. North<br>facing.                                               |
| <i>Erythrina</i> L.           | sp. 1                                    | Fabaceae        | MMAB 42,<br>41 | *   | *  | *    | orange-red                    |                                                                  | Flowers found<br>on ground at the<br>lowest point of a<br>bog with little<br>shade.             |
| <i>Passiflora</i>             | <i>coccinea</i> Aubl.                    | Passifloraceae  | MMAB 43,<br>38 | 120 | 60 | 22.5 | red                           | Unidentified                                                     | Growing from<br>0-12 m through<br>dense stand of<br>Guadua.                                     |
| <i>Centropogon</i>            | <i>congestus</i><br>Gleason              | Campanulaceae   | MMAB 45        | 32  | 10 | *    | pink-red                      |                                                                  | Dense stand of<br>Guadua.<br>Relatively humid<br>and little light.                              |
| <i>Oreocallis</i>             | <i>grandiflora</i><br>(Lam.) R. Br.      | Proteaceae      | MMAB 49,<br>48 | 46  | 12 | *    | red-purple                    | <i>Aglaeactis cupripenni</i> ,<br><i>Boissonneaua matthewsii</i> | Dominating tree<br>species in dry,<br>scrubby, elfin<br>forest.                                 |
| <i>Siphocampylus</i>          | <i>scandens</i><br>(Kunth) G.Don         | Campanulaceae   | MMAB 50,<br>51 | 47  | 8  | 16   | pink                          | <i>Adelomyia melanogenys</i>                                     | Along ditch of<br>the Manu Road.<br>Grows<br>indiscriminately<br>in sun or shade.               |
| <i>Siphocampylus</i>          | <i>orbignianus</i><br>A.DC.              | Campanulaceae   | MMAB 52,<br>53 | 54  | 17 | 12   | pink-red                      | <i>Coeligena</i> sp.                                             | Along ditch of<br>the Manu Road.<br>Grows<br>indiscriminately<br>in sun or shade.               |
| <i>Brachyotum</i>             | <i>rostratum</i><br>(Naudin)<br>Triana   | Melastomataceae | MMAB 54,<br>55 | 19  | 7  | 13   | red with<br>yellow tip        | <i>Aglaeactis cupripenni</i>                                     | Dry scrubby<br>elfin forest.<br>Dead ferns<br>make up dense<br>mat up to 1 m.                   |
| <i>Aetanthus</i>              | <i>nodosus</i><br>(Desr.) Engl.          | Loranthaceae    | MMAB 56,<br>57 | 70  | 5  | 14.5 | dark<br>purple                | <i>Coeligena</i> sp.                                             | Humid<br>transitional<br>forest at where<br>elfin forest<br>dimishes.                           |

|                                 |                                           |                  |                |     |    |      |                               |                                                                                     |                                                                                                                                 |
|---------------------------------|-------------------------------------------|------------------|----------------|-----|----|------|-------------------------------|-------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------|
| <i>Gaultheria</i><br>Kalm ex L. | sp. 1                                     | Ericaceae        | MMAB 58,<br>59 | 7   | 3  | *    | red with<br>yellow tip        | <i>Aglaeactis cupripenni</i> ,<br><i>Metallura tyrianthina</i>                      | Edge of pond<br>alongside other<br>Ericaceae<br>species.<br>Abundant light,<br>south facing.                                    |
| <i>Miconia</i> Ruiz &<br>Pavón  | sp. 1                                     | Melastomataceae  | MMAB 6,<br>7   | 15  | 13 | *    | pink                          | <i>Heliodoxa leadbeateri</i>                                                        | 3 m tree mostly<br>shaded by<br><i>Cecropia</i> and<br>other taller<br>species.                                                 |
| <i>Passiflora</i>               | <i>mixta</i> L.f.                         | Passifloraceae   | MMAB 60,<br>61 | 118 | 45 | *    | white-pink                    | <i>Ensifera ensifera</i>                                                            | Growing<br>through same<br>habitat as<br>Ericaceae gen.<br>sp. 1 and 2.<br>Flowers at<br>breaks in the<br>canopy.               |
| <i>Fuchsia</i> L.               | sp. 1                                     | Onagraceae       | MMAB 63,<br>62 | 65  | 45 | *    | bright pink                   |                                                                                     | Humid, dark<br>understory.<br>Habitat tends to<br>be rocky.                                                                     |
| <i>Desmodium</i><br>Desv.       | sp. 1                                     | Fabaceae         | MMAB 64,<br>65 | 20  | 19 | 16.5 | light red-<br>orange          | <i>Metallura</i> sp.                                                                | Rocky exposed<br>cliffside. Many<br>ferns. Dry.                                                                                 |
| <i>Siphonandra</i><br>Klotzsch  | sp. 1                                     | Ericaceae        | MMAB 66,<br>67 | 18  | 5  | *    | purple                        | <i>Aglaeactis cupripenni</i>                                                        | Edge of pond<br>alongside other<br>Ericaceae<br>species.<br>Abundant light,<br>south facing.                                    |
| <i>Bomarea</i> Mirb.            | sp. 1                                     | Alstroemeriaceae | MMAB 68,<br>69 | 18  | 7  | 18.5 | red with<br>white tip         |                                                                                     | Rocky cliff next<br>to slow-flowing<br>river. In dense<br>vegetation<br>including <i>Rubus</i><br>and <i>Asteraceae</i><br>spp. |
| <i>Drymonia</i>                 | <i>semicordata</i><br>(Poepp.)<br>Wiehler | Gesneriaceae     | MMAB 70,<br>71 | 40  | 17 | *    | yellow<br>within red<br>bract | <i>Glaucis hirsutus</i> ,<br><i>Heliodoxa aurescens</i> ,<br><i>Phaethornis</i> sp. | Ubiquitous<br>throughout<br>humid lowland<br>forest.                                                                            |
| <i>Pachystachys</i><br>Nees     | sp. 1                                     | Acanthaceae      | MMAB 72        | 60  | 8  | *    | red                           |                                                                                     | In the shade of<br>tall trees at<br>trail's edge.                                                                               |
| <i>Costus</i> L.                | sp. 3                                     | Costaceae        | MMAB 75,<br>74 | 30  | 5  | *    | yellow                        |                                                                                     | Relatively<br>common at<br>trail's edge,<br>even in low<br>light.                                                               |
| <i>Heliconia</i>                | <i>densiflora</i><br>Verl.                | Heliconiaceae    | MMAB 76,<br>77 | 47  | 7  | *    | orange<br>within red<br>bract |                                                                                     | High moisture<br>depression in<br>humid forest.<br>Medium shade.                                                                |
| <i>Costus</i> L.                | sp. 2                                     | Costaceae        | MMAB 78,<br>79 | 39  | 7  | *    | yellow<br>within red<br>bract |                                                                                     | Terra firma<br>approx 300 m<br>from Rio Madre<br>de Dios                                                                        |

|                             |                                               |                |                |                            |    |   |                                     |                        |                                                                            |
|-----------------------------|-----------------------------------------------|----------------|----------------|----------------------------|----|---|-------------------------------------|------------------------|----------------------------------------------------------------------------|
| <i>Columnea</i>             | aff. <i>schimpfii</i><br>Mansf.               | Gesneriaceae   | MMAB 8,<br>9   | 30                         | 5  | * | white                               |                        | Epiphytic. Can be found indiscriminately on any trees from at least 1-8 m. |
| <i>Besleria</i> L.          | sp. 4                                         | Gesneriaceae   | MMAB 80,<br>81 | 22                         | 8  | * | red                                 |                        | Terra firma approx 300 m from Rio Madre de Dios                            |
| <i>Heliconia</i>            | <i>schumanniana</i><br>Loes.                  | Heliconiaceae  | MMAB 82,<br>83 | 44                         | 5  | * | yellow<br>within red<br>bract       |                        | Abundant sunlight at clearing in forest.                                   |
| <i>Heliconia</i>            | <i>lingulata</i> Ruiz & Pav.                  | Heliconiaceae  | MMAB 84,<br>85 | 37                         | 4  | * | yellow<br>within<br>yellow<br>bract |                        | South-facing clay bank of the Alto Madre de Dios.                          |
| <i>Besleria</i> L.          | sp. 2                                         | Gesneriaceae   | MMAB 86,<br>87 | 19                         | 9  | * | orange                              | Unidentified           | Terra firma approx 300 m from Rio Madre de Dios                            |
| <i>Besleria</i> L.          | sp. 3                                         | Gesneriaceae   | MMAB 88,<br>89 | 15                         | 4  | * | orange                              | Unidentified           | Relatively exposed at trail's edge. Dense cluster of upto 20 individuals.  |
| <i>Heliconia</i>            | <i>metallica</i><br>Planch. & Linden ex Hook. | Heliconiaceae  | MMAB 90,<br>91 | 40                         | 4  | * | red                                 | <i>Phaethornis</i> sp. | High moisture depression in humid forest. Medium shade.                    |
| <i>Pentagonia</i><br>Benth. | sp. 1                                         | Rubiaceae      | MMAB 93,<br>92 | 31                         | 10 | * | yellow<br>within red<br>bract       | Unidentified           | High moisture depression in humid forest. Medium shade.                    |
| <i>Passiflora</i> L.        | sp. 1                                         | Passifloraceae | MMAB 94,<br>95 | 80mm long,<br>pre-anthesis | *  | * | red                                 |                        | Growing through dense understory including Melastomaceae.                  |
| <i>Pachystachys</i><br>Nees | sp. 2                                         | Acanthaceae    | MMAB 96,<br>97 | 50                         | 17 | * | red                                 | <i>Phaethornis</i> sp. | Relatively exposed at trail's edge.                                        |

Table 2.

Records of hummingbird-plant visitation along the Manú Gradient.

| Hummingbird Species                    | Plant visited                 | Plant Family  | Collection number | Site      |
|----------------------------------------|-------------------------------|---------------|-------------------|-----------|
| <i>Adelomyia melanogenys</i> Bonaparte | <i>Siphocampylus scandens</i> | Campanulaceae | MMAB 50           | San Pedro |
| <i>Aglaeactis cupripennis</i> Bourcier | <i>Gaultheria</i> sp. 1       | Ericaceae     | MMAB 58           | Wayqecha  |
| <i>Aglaeactis cupripennis</i>          | <i>Siphonandra</i> sp. 1      | Ericaceae     | MMAB 66           | Wayqecha  |

|                                              |                                  |                 |         |             |
|----------------------------------------------|----------------------------------|-----------------|---------|-------------|
| <i>Aglaeactis cupripennis</i>                | <i>Brachyotum rostratum</i>      | Melastomataceae | MMAB 54 | Wayqecha    |
| <i>Aglaeactis cupripennis</i>                | <i>Oreocallis grandiflora</i>    | Proteaceae      | MMAB 49 | Wayqecha    |
| <i>Boissonneaua matthewsii</i> Bourcier      | <i>Oreocallis grandiflora</i>    | Proteaceae      | MMAB 49 | Wayqecha    |
| <i>Coeligena</i> sp.                         | <i>Siphocampylus orbignianus</i> | Campanulaceae   | MMAB 52 | Wayqecha    |
| <i>Coeligena</i> sp.                         | <i>Aetanthus nodosus</i>         | Loranthaceae    | MMAB 56 | Wayqecha    |
| <i>Colibri thalassinus</i> Swainson          | <i>Guzmania weberbaueri</i>      | Bromeliaceae    | MMAB 25 | San Pedro   |
| <i>Doryfera ludovicae</i> Bourcier & Mulsant | <i>Guzmania weberbaueri</i>      | Bromeliaceae    | MMAB 25 | San Pedro   |
| <i>Ensifera ensifera</i> Lesson              | <i>Passiflora mixta</i>          | Passifloraceae  | MMAB 60 | Wayqecha    |
| <i>Glaucis hirsutus</i> Gmelin               | <i>Drymonia semicordata</i>      | Gesneriaceae    | MMAB 70 | Pantiacolla |
| <i>Heliodoxa aurescens</i> Gould             | <i>Drymonia semicordata</i>      | Gesneriaceae    | MMAB 70 | Pantiacolla |
| <i>Heliodoxa leadbeateri</i> Bourcier        | <i>Miconia</i> sp.1              | Melastomataceae | MMAB 6  | San Pedro   |
| <i>Heliodoxa leadbeateri</i>                 | <i>Guzmania weberbaueri</i>      | Bromeliaceae    | MMAB 25 | San Pedro   |
| <i>Metallura tyrianthina</i> Loddiges        | <i>Brachyotum rostratum</i>      | Melastomataceae | MMAB 54 | Wayqecha    |
| <i>Metallura</i> sp.                         | <i>Desmodium</i> sp. 1           | Fabaceae        | MMAB 64 | Wayqecha    |
| <i>Metallura tyrianthina</i>                 | <i>Gaultheria</i> sp. 1          | Ericaceae       | MMAB 58 | Wayqecha    |
| <i>Phaethornis</i> sp.                       | <i>Pachystachys</i> sp. 2        | Acanthaceae     | MMAB 96 | Pantiacolla |
| <i>Phaethornis</i> sp.                       | <i>Drymonia semicordata</i>      | Gesneriaceae    | MMAB 70 | Pantiacolla |
| <i>Phaethornis</i> sp.                       | <i>Heliconia metallica</i>       | Heliconiaceae   | MMAB 90 | Pantiacolla |
| Unidentified Trochilidae                     | <i>Besleria</i> sp. 2            | Gesneriaceae    | MMAB 86 | Pantiacolla |
| Unidentified Trochilidae                     | <i>Besleria</i> sp. 3            | Gesneriaceae    | MMAB 88 | Pantiacolla |
| Unidentified Trochilidae                     | <i>Passiflora coccinea</i>       | Passifloraceae  | MMAB 43 | San Pedro   |
| Unidentified Trochilidae                     | <i>Pentagonia</i> sp. 1          | Rubiaceae       | MMAB 93 | Pantiacolla |

Table 3.

Basic bill morphometrics from birds mist-netted along the Manú Gradient.

| Species                      | Sex<br>(F=Female,<br>M=Male,<br>U=Unknown) | Mean bill<br>length<br>(mm) | Bill<br>length<br>std dev<br>(mm) | Mean<br>bill width<br>(mm) | Bill<br>width<br>std dev<br>(mm) | Bill length<br>sample<br>size | Bill width<br>sample<br>size |
|------------------------------|--------------------------------------------|-----------------------------|-----------------------------------|----------------------------|----------------------------------|-------------------------------|------------------------------|
| <i>Adelomyia melanogenys</i> | F                                          | 14.55                       | 1.34                              | 2.7                        | 0                                | 2                             | 2                            |
| <i>Adelomyia melanogenys</i> | U                                          | 14.56                       | 1.10                              | 2.44                       | 0.18                             | 9                             | 9                            |

|                                                              |   |       |      |      |      |   |    |
|--------------------------------------------------------------|---|-------|------|------|------|---|----|
| <i>Aglaeactis cupripennis</i>                                | U | 18.06 | 1.05 | 2.64 | 0.11 | 5 | 5  |
| <i>Boissonneaua matthewsii</i><br>Bourcier                   | U | 18.4  | NA   | 2.9  | NA   | 1 | 1  |
| <i>Chalcostigma ruficeps</i> Gould                           | F | 11.5  | NA   | 2    | NA   | 1 | 1  |
| <i>Chalcostigma ruficeps</i>                                 | M | 11.9  | 1.27 | 2.2  | 0.14 | 2 | 2  |
| <i>Chlorostilbon mellisugus</i><br>Linnaeus                  | F | 20.5  | NA   | 2.7  | NA   | 1 | 1  |
| <i>Coeligena coeligena</i> Lesson                            | U | 29.47 | 3.30 | 2.65 | 0.21 | 9 | 10 |
| <i>Coeligena torquata</i><br>Boissonneau                     | M | 32.4  | 1.9  | 2.66 | 0.20 | 3 | 3  |
| <i>Coeligena torquata</i>                                    | F | 36.2  | NA   | 3    | NA   | 1 | 1  |
| <i>Coeligena violifer</i> Gould                              | U | 31.74 | 4.78 | 3.22 | 0.25 | 5 | 5  |
| <i>Coeligena violifer</i>                                    | M | 33.13 | 0.98 | 3.26 | 0.25 | 3 | 3  |
| <i>Coeligena violifer</i>                                    | F | 35.5  | 1.4  | 3.3  | 0.35 | 4 | 4  |
| <i>Colibri coruscans</i> Gould                               | U | 24.05 | 2.89 | 3.06 | 0.15 | 2 | 3  |
| <i>Colibri thalassinus</i>                                   | U | 21.46 | 1.72 | 3    | 0.17 | 3 | 3  |
| <i>Doryfera johannae</i> Bourcier                            | F | 26.2  | NA   | 3    | NA   | 1 | 1  |
| <i>Doryfera ludovicae</i>                                    | U | 27.62 | 7.90 | 2.75 | 0.14 | 7 | 8  |
| <i>Doryfera ludovicae</i>                                    | M | 30.8  | NA   | 2.6  | NA   | 1 | 1  |
| <i>Doryfera ludovicae</i>                                    | F | 31.2  | 1    | 2.5  | 0.26 | 3 | 3  |
| <i>Eutoxeres condamini</i><br>Bourcier                       | U | 24.23 | 1.52 | 3.87 | 0.68 | 8 | 7  |
| <i>Florisuga mellivora</i> Linnaeus                          | F | 18.1  | NA   | 2.6  | NA   | 1 | 1  |
| <i>Florisuga mellivora</i>                                   | M | 18.7  | 0.28 | 3.45 | 0.49 | 2 | 2  |
| <i>Glaucis hirsutus</i>                                      | M | 28.9  | NA   | 3.3  | NA   | 1 | 1  |
| <i>Glaucis hirsutus</i>                                      | U | 29.15 | 1.21 | 3.82 | 0.29 | 4 | 4  |
| <i>Helianzelus amethysticollis</i><br>d'Orbigny & Lafresnaye | M | 17.46 | 0.69 | 2.46 | 0.29 | 6 | 6  |
| <i>Helianzelus amethysticollis</i>                           | U | 18.5  | NA   | 2.5  | NA   | 1 | 1  |
| <i>Helianzelus amethysticollis</i>                           | F | 18.65 | 0.21 | 2.8  | 0.14 | 2 | 2  |
| <i>Heliodoxa leadbeateri</i>                                 | M | 20.56 | 0.99 | 2.95 | 0.05 | 6 | 6  |
| <i>Heliodoxa leadbeateri</i>                                 | U | 20.8  | NA   | 3.2  | NA   | 1 | 1  |
| <i>Heliodoxa leadbeateri</i>                                 | F | 22.27 | 0.82 | 3.2  | 0.16 | 4 | 4  |

|                                  |   |       |      |       |      |   |   |
|----------------------------------|---|-------|------|-------|------|---|---|
| <i>Ocreatus underwoodii</i>      | F | 15.6  | NA   | 2.5   | NA   | 1 | 1 |
| Lesson                           |   |       |      |       |      |   |   |
| <i>Ocreatus underwoodii</i>      | M | 15.8  | NA   | 2.2   | 0.84 | 1 | 2 |
| <i>Ocreatus underwoodii</i>      | U | 15.8  | NA   | NA    | NA   | 1 | 0 |
| <i>Phaethornis guy</i> Lesson    | F | 38.05 | 1.90 | 3.3   | 0.42 | 2 | 2 |
| <i>Phaethornis guy</i>           | U | 39.6  | NA   | 3     | NA   | 1 | 1 |
| <i>Phaethornis koepckeae</i>     | U | 34.5  | 2.09 | 3.725 | 0.17 | 4 | 4 |
| Weske & Terborgh                 |   |       |      |       |      |   |   |
| <i>Phaethornis superciliosus</i> | U | 35.43 | 2.19 | 3.65  | 0.58 | 6 | 6 |
| Linnaeus                         |   |       |      |       |      |   |   |
| <i>Thalurania furcata</i> Gmelin | F | 20.7  | 0.55 | 3.2   | 0.45 | 3 | 3 |
| <i>Thalurania furcata</i>        | M | 23.65 | 4.03 | 3.55  | 0.49 | 2 | 2 |
| <i>Thalurania furcata</i>        | U | 24.6  | 6.22 | 3.25  | 0.21 | 2 | 2 |
| <i>Threnetes leucurus</i>        | U | 28.52 | 0.99 | 3.675 | 0.22 | 4 | 4 |

**Table 4.**

Site information for putatively bird pollinated plants along the Manú Gradient

| Collection numbers | Site      | Latitude   | Longitude  | Altitude (m a.s.l.) | Date      |
|--------------------|-----------|------------|------------|---------------------|-----------|
| MMAB 1             | San Pedro | -13.056864 | -71.546146 | 1347                | 4-ix-2016 |
| MMAB 2, 3          | San Pedro | -13.057179 | -71.546566 | 1402                | 4-ix-2016 |
| MMAB 6, 7          | San Pedro | -13.057697 | -71.547385 | 1393                | 4-ix-2016 |
| MMAB 8, 9          | San Pedro | -13.057311 | -71.547086 | 1411                | 4-ix-2016 |
| MMAB 10, 11        | San Pedro | -13.058199 | -71.547978 | 1403                | 4-ix-2016 |
| MMAB 12, 13        | San Pedro | -13.057907 | -71.548086 | 1357                | 4-ix-2016 |
| MMAB 20, 21        | San Pedro | -13.054945 | -71.545872 | 1378                | 6-ix-2016 |
| MMAB 22, 23        | San Pedro | -13.056268 | -71.546039 | 1394                | 6-ix-2016 |
| MMAB 24, 44        | San Pedro | -13.05637  | -71.54609  | 1355                | 7-ix-2016 |
| MMAB 25, 26        | San Pedro | -13.058848 | -71.547884 | 1330                | 7-ix-2016 |
| MMAB 27, 28        | San Pedro | -13.059836 | -71.54739  | 1360                | 7-ix-2016 |
| MMAB 29, 30        | San Pedro | -13.058044 | -71.549996 | 1269                | 8-ix-2016 |
| MMAB 33            | San Pedro | -13.05773  | -71.548458 | 1439                | 8-ix-2016 |
| MMAB 34, 35        | San Pedro | -13.057514 | -71.543293 | 1324                | 8-ix-2016 |

|             |             |            |            |      |            |
|-------------|-------------|------------|------------|------|------------|
| MMAB 36, 37 | San Pedro   | -13.05634  | -71.541812 | 1547 | 9-ix-2016  |
| MMAB 40, 39 | San Pedro   | -13.054006 | -71.539007 | 1297 | 9-ix-2016  |
| MMAB 43, 38 | San Pedro   | -13.058459 | -71.548074 | 1363 | 10-ix-2016 |
| MMAB 42, 41 | San Pedro   | -13.058199 | -71.547978 | 1403 | 11-ix-2016 |
| MMAB 45     | San Pedro   | -13.191861 | -71.588599 | 1149 | 16-ix-2016 |
| MMAB 49, 48 | Wayqecha    | -13.173428 | -71.587187 | 2727 | 20-ix-2016 |
| MMAB 50, 51 | Wayqecha    | -13.17706  | -71.586071 | 2939 | 21-ix-2016 |
| MMAB 52, 53 | Wayqecha    | -13.179536 | -71.585172 | 2958 | 21-ix-2016 |
| MMAB 54, 55 | Wayqecha    | -13.180133 | -71.585235 | 2955 | 22-ix-2016 |
| MMAB 56, 57 | Wayqecha    | -13.174448 | -71.587465 | 2888 | 26-ix-2016 |
| MMAB 58, 59 | Wayqecha    | -13.176716 | -71.581308 | 2625 | 26-ix-2016 |
| MMAB 60, 61 | Wayqecha    | -13.174771 | -71.588345 | 2866 | 27-ix-2016 |
| MMAB 63, 62 | Wayqecha    | -13.174751 | -71.588335 | 2904 | 27-ix-2016 |
| MMAB 64, 65 | Wayqecha    | -13.191716 | -71.586709 | 2834 | 28-ix-2016 |
| MMAB 66, 67 | Wayqecha    | -13.18732  | -71.585754 | 2979 | 28-ix-2016 |
| MMAB 68, 69 | Wayqecha    | -13.173166 | -71.591911 | 2780 | 29-ix-2016 |
| MMAB 70, 71 | Pantiacolla | -12.656352 | -71.230691 | 398  | 6-x-2016   |
| MMAB 72     | Pantiacolla | -12.655418 | -71.229373 | 391  | 7-x-2016   |
| MMAB 75, 74 | Pantiacolla | -12.656351 | -71.230732 | 396  | 8-x-2016   |
| MMAB 76, 77 | Pantiacolla | -12.64719  | -71.240662 | 394  | 8-x-2016   |
| MMAB 78, 79 | Pantiacolla | -12.645874 | -71.234135 | 410  | 9-x-2016   |
| MMAB 80, 81 | Pantiacolla | -12.65622  | -71.231045 | 404  | 9-x-2016   |
| MMAB 82, 83 | Pantiacolla | -12.656216 | -71.230678 | 404  | 9-x-2016   |
| MMAB 84, 85 | Pantiacolla | -12.656545 | -71.231864 | 405  | 11-x-2016  |
| MMAB 86, 87 | Pantiacolla | -12.656431 | -71.231836 | 396  | 11-x-2016  |
| MMAB 88, 89 | Pantiacolla | -12.650034 | -71.225302 | 428  | 12-x-2016  |
| MMAB 90, 91 | Pantiacolla | -12.651347 | -71.22389  | 391  | 12-x-2016  |
| MMAB 93, 92 | Pantiacolla | -12.65138  | -71.223853 | 397  | 12-x-2016  |
| MMAB 94, 95 | Pantiacolla | -12.651421 | -71.223706 | 423  | 13-x-2016  |
| MMAB 96, 97 | Pantiacolla | -12.651113 | -71.223842 | 394  | 13-x-2016  |

Table 5.

Summary information and site descriptions for three sampling points along the Manú Gradient.

| Site (Latitude, Longitude)           | Period Collected and Netted | Altitudinal Range Sampled (m asl) | Number of Plants Species Collected | Number of Hummingbirds Netted | Number of Hummingbird Species Netted | Number of Bird Visits Recorded | General Site Description                                                                                                                                                                                                                                                |
|--------------------------------------|-----------------------------|-----------------------------------|------------------------------------|-------------------------------|--------------------------------------|--------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| San Pedro (-13.055387, -71.546832)   | 4-ix-2016 to 16-ix-2016     | 1149 - 1547                       | 19                                 | 76                            | 14                                   | 7                              | Montane cloud forest, <i>Cecropia</i> readily found in disturbed habitats. Dominant palm is <i>Wettinia</i> and canopy is generally composed of Clusiaceae, Rubiaceae, Melastomataceae and Lauraceae (Weng et al. 2004).                                                |
| Wayqecha (-13.1752615, -71.5884099)  | 20-ix-2016 to 03-x-2016     | 2625 - 2979                       | 11                                 | 65                            | 15                                   | 10                             | Highland cloud forest and puna grassland of mainly Asteraceae and Poaceae. <i>Oreocalis grandiflora</i> is a notable and abundant tree species. Araliaceae, Cunoniaceae, Chloranthaceae, Myrsinaceae, Sabiaceae, and Symplocaceae are readily found (Weng et al. 2004). |
| Pantiacolla (-12.656544, -71.231862) | 07-x-2016 to 13-x-2016      | 391 - 428                         | 14                                 | 31                            | 9                                    | 8                              | Lowland rainforest, includes both seasonally flooded and terra firme forests. Canopy dominated by Fabaceae, Malvaceae, Moraceae and Annonaceae (Weng et al. 2004, Weng et al. 2004)                                                                                     |

## Data Collection

Pre-cut singletrack trails were used to access sampling areas away from the Manú Road (main access road that runs along the southeastern border of Manú National Park). We sampled hummingbirds using standard (12 x 3 m, 34 mm mesh) mist-nets along trail systems only. Mist-netting sites were sampled during the primary breeding season (August–November) for two consecutive days from approximately 0600–1200 hrs during suitable weather conditions (i.e., no periods of extended heavy rain, high winds, or other situations that could compromise researcher or bird safety). Each site consisted of an array of ten to fifteen nets placed in forested and open habitat and spaced at intervals of 25–50

m. Ten sites were sampled at Wayqecha and San Pedro, and 8 sites were sampled at Pantiacolla. Hummingbird bill length was measured from the bill tip to the nares. Bill width was measured from the anterior edge of the nares. All captured hummingbirds were marked by cutting the terminal 1-2 cm of one rectrix to avoid resampling of individuals.

Both trails and the Manú Road were used to opportunistically collect plants. Plants were considered putatively bird pollinated if they met criteria adhering to typical bird pollination ‘syndromes’; namely, dilute nectar and long tubular flowers (Fenster et al. 2004), though we acknowledge the limitations of surveying by these criteria (Ollerton et al. 2009). Plants of interest were photographed, their location marked using a hand-held Garmin 64s global positioning system, and a description of the immediate habitat recorded. We then measured nectar concentration of mature flowers (Sper Scientific no. 66214-988), recorded corolla dimensions and colour (by visual inspection), and processed each plant using standard herbarium techniques Bridson and Forman 2000) (SERFOR collection permit no. 343-2016). All dried and pressed specimens are deposited at the herbaria of the Universidad Nacional Agraria La Molina (MOL), Peru and the University of British Columbia (UBC), Canada (SERFOR export permit no. 09125-2017).

## Results

We identified 44 putatively bird pollinated plants of interest belonging to 16 families (Table 1, Figs 1, 2, 3, 4, 5). Corolla length and width of sampled plants ranged from 8-120 mm ( $\bar{x} = 39.7 \pm 27.4$ ,  $n = 42$ ) and 1-60 mm ( $\bar{x} = 11.4 \pm 12.2$ ), respectively. We measured nectar concentration for 11 of these species. In each case, nectar concentrations fell within a typical bird pollination syndrome (Stiles 1978, Fenster et al. 2004), ranging from 12-25.5% (Table 1). Corolla colour and immediate habitat characteristics were recorded for each plant (Table 1, see also Table 5).

We recorded 23 hummingbird visitations to 18 plant taxa belonging to 12 plant families (Table 2). Bill length and width of sampled hummingbirds ranged from 11.5-39.6 mm ( $\bar{x} = 24.3 \pm 7.6$ ,  $n = 41$ ) and 2.5-3.0 mm ( $\bar{x} = 2.9 \pm 0.4$ ,  $n = 40$ ), respectively (Figs 6, 7, 8, Table 3).

Diversity of plants exhibiting the bird pollination syndrome does not differ across the gradient in the time frame sampled (Table 4).



Figure 1.

Diversity of putatively bird pollinated plants of the Manú Gradient. MMAB collection numbers listed in Table 1.

- a: MMAB 1 (*Besleria* sp. 1) [doi](#)
- b: MMAB 2, 3 (*Centropogon granulosus*) [doi](#)
- c: MMAB 6, 7 (*Miconia* sp. 1) [doi](#)
- d: MMAB 8, 9 (*Columnea* aff. *shimpfi*) [doi](#)
- e: MMAB 20, 21 (*Sanchezia* sp. 1) [doi](#)
- f: MMAB 22, 23 (*Columnea guttata*) [doi](#)



Figure 2.

Diversity of putatively bird pollinated plants of the Manú Gradient. MMAB collection numbers listed in Table 1.

- a: MMAB 24, 25 (*Heliconia subulata*) [doi](#)
- b: MMAB 26, 27 (*Guzmania weberbaueri*) [doi](#)
- c: MMAB 39, 40 (*Drymonia urceolata*) [doi](#)
- d: MMAB 45 (*Centropogon congestus*) [doi](#)
- e: MMAB 48, 49 (*Oreocallis grandiflora*) [doi](#)
- f: MMAB 50, 51 (*Siphocampylus scandens*) [doi](#)



Figure 3.

Diversity of putatively bird pollinated plants of the Manú Gradient. MMAB collection numbers listed in Table 1.

- a: MMAB 52, 53 (*Siphocampylus orbignianus*) [doi](#)
- b: MMAB 54, 55 (*Brachyotum rostratum*) [doi](#)
- c: MMAB 56, 57 (*Aetanthus nodosus*) [doi](#)
- d: MMAB 58, 59 (*Gaultheria* sp. 1) [doi](#)
- e: MMAB 60, 61 (*Passiflora mixta*) [doi](#)
- f: MMAB 62, 63 (*Fuchsia* sp. 1) [doi](#)



Figure 4.

Diversity of putatively bird pollinated plants of the Manú Gradient. MMAB collection numbers listed in Table 1.

- a: MMAB 64, 65 (*Desmodium* sp. 1) [doi](#)
- b: MMAB 66, 67 (*Siphonandra* sp. 2) [doi](#)
- c: MMAB 68, 69 (*Bomarea* sp. 1) [doi](#)
- d: MMAB 70, 71 (*Drymonia semicordata*) [doi](#)
- e: MMAB 74, 75 (*Costus* sp. 3) [doi](#)
- f: MMAB 76, 77 (*Heliconia densiflora*) [doi](#)



Figure 5.

Diversity of putatively bird pollinated plants of the Manú Gradient. MMAB collection numbers listed in Table 1.

- a: MMAB 78, 79 (*Costus* sp. 2) [doi](#)
- b: MMAB 80, 81 (*Besleria* sp.4) [doi](#)
- c: MMAB 82, 83 (*Heliconia schumanniana*) [doi](#)
- d: MMAB 84, 85 (*Heliconia lingulata*) [doi](#)
- e: MMAB 86, 87 (*Besleria* sp. 2) [doi](#)
- f: MMAB 92, 93 (*Pentagonia* sp. 1) [doi](#)

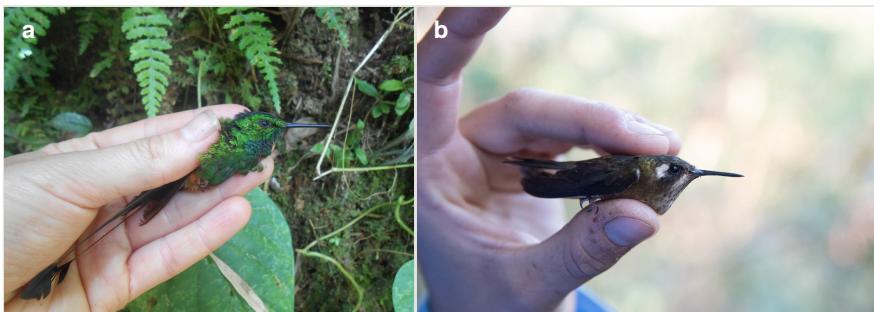


Figure 6.

Representative hummingbirds captured near San Pedro (Paucartambo Province, Cuzco Region, 1400 m). Photo "b" taken by Meredith Miles, Wake Forest University.

a: Booted Racket-tail (*Ocreatus underwoodii*) [doi](#)

b: Speckled Hummingbird (*Adelomyia melanogenys*) [doi](#)



Figure 7.

Representative hummingbirds captured near La Estación Biológica Wayqecha (Paucartambo Province, Cuzco Region, 2800 m).

a: Shining Sunbeam (*Aglaeactis cupripennis*) [doi](#)

b: Collared Inca (*Coeligena torquata*) [doi](#)



Figure 8.

Representative hummingbirds captured near Pantiacolla (Manú Province, Madre de Dios Region, 400 m).

a: Blue-fronted Lancebill (*Doryfera johannae*) [doi](#)

b: White-necked Jacobin (*Florisuga mellivora*) [doi](#)

## Discussion

Hummingbird pollination is common and well-established in Neotropical montane and lowland environments. Our observations and collected specimens exemplify that bird-plant interactions are readily observed along the Manú Gradient - an area that is relatively accessible has been subject to only a handful of studies on hummingbird pollination (*Oreocallis grandiflora*, Proteaceae; Hazlehurst et al. 2016, Hazlehurst and Karubian 2016).

Along the gradient, putatively bird pollinated plants were generally characterized by long corollas and were predominantly coloured red, yellow, orange, or some combination thereof. Previous documentation of bird pollination exists for each of the 16 families collected (Cronk and Ojeda 2008, Johnson and Nicolson 2008), but undocumented species-level bird pollination systems may arise from focusing on lesser-studied taxa (e.g. *Thyrsacanthus*, *Pentagonia*, *Pachystachys*). Many putatively bird pollinated plants contained too little nectar to effectively measure sugar concentration at the time of sampling. We suspect that early morning visitations by nectarivorous birds and insects (i.e., both pollinators and nectar robbers) influenced this outcome. Indeed, in some cases inspection of certain plants revealed that the flower had been recently robbed as indicated by punctures at the base of the corolla. In as little as bird pollination has been studied along the Manú Gradient, even less is known of the ecological and evolutionary dynamics of nectary robbery. As this survey was preliminary, time did not allow for multi-day sampling at one locale to isolate nectar. A focus on a specific plant taxon would allow familiarity for nectar phenology and hence, more effective collection of nectar.

We recorded 23 independent visits by hummingbirds to 19 different plant taxa over 33 days. These observations by no means represent a comprehensive list of the total diversity for hummingbirds (Walker et al. 2006), bird-pollinated plants, or the interactions between

these two groups. An estimate of total diversity will come only with an extended sampling effort at each site. Relatively few hummingbirds were captured or observed in the lowlands (Table 3) compared to the other two sites. It is likely that this resulted from differences in foraging behavior between hummingbird species, rather than local abundance. For example, in the lowlands, a higher proportion of hummingbirds (e.g. *Phaethornis*) exhibit traplining behaviour (i.e. repeated visits along a route of flowering locations) compared to territorial guarding of floral resources. In addition, because of the higher canopy, many of the trees, lianas, and epiphytes inhabit canopy heights that are logically difficult to sample.

The number of plants exhibiting bird pollination syndrome and number of bird visits observed are comparable between sites. That is, at a coarse scale we did not find any indication that elevation affects the absolute diversity of bird pollinated plant taxa (as expected by Cruden 1972), although the Manú Gradient would be an ideal location to test the hypothesis that bird and insect pollinated plants occupy distinct ecological niches. Between species, corolla length and width encompasses a great amount of variation, but hummingbird bill morphology varies less Tables 1, 3. This may speak to the adaptability of flowers relative to bills. It may be that because flowers serve a singular purpose (attraction and exclusion of pollinators and robbers, respectively), whereas bills have many uses (feeding, aggression, preening, balance), that bill evolution is relatively constrained. Bill morphology data will be used to inform phylogenetic tests of bill-flower shape evolution in future studies.

Evaluating the extent to which plants and their pollinators contribute to maintaining local biodiversity, and identifying keystone species within these systems (Ebenman and Jonsson 2005) will be important to maintaining ecological and cultural heritage in the Manú region (Ministerio del Ambiente (Ministry of Environment) 2017). This study provides a baseline for future work in pollination ecology along the Manú Gradient. Any one of the 44 plant species highlighted here warrants closer investigation, and we anticipate that further studies will help clarify the roles of hummingbirds as pollinators for the plant taxa described herein..

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