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ASSEMBLAGE OF NECTARIVOROUS BIRDS AND THEIR FLORAL RESOURCES IN AN ELFIN FOREST OF THE CENTRAL ANDES OF PERU

ENSAMBLE DE AVES NECTARÍVORAS Y SUS RECURSOS FLORALES EN UN BOSQUE ACHAPARRADO DE LOS ANDES CENTRALES PERUANOS

Oscar Gonzalez[1], Camilo Díaz[2] and Bernie Britto[3]

Abstract

Nectarivorous birds (hummingbirds, flowerpiercers, and conebills) and their floral resources in an elfin forest of the central Andes of Peru (Unchog, Carpish Mountains) are described. This forest is well-known for its concentration of endemic species, mainly birds. We recorded the nectarivorous birds, vascular plants and the interactions among them between 2011-2014. The birds were recorded by direct observations and mist nets. Plants were evaluated with Gentry plots and occasional collection. A total of 26 nectarivorous bird species have been reported in this forest, however from our observations we detected from this assemblage 17 bird species that feed in plants' nectar. A total of 27 plant species were visited by the birds. The nectarivorous birds were hummingbirds (Trochilidae, 12 species), flowerpiercers (Thraupidae, 4 species) and a conebill (Thraupidae: 1 specie). The plants were from 16 families and 14 orders. One species of hummingbird, *Metallura theresiae*, is endemic to Peru. On plants, *Greigia macbrideana*, *Puya pseudoeryngioides*, *Centropogon isabellinus*, *Miconia alpina* and *Brachyotum lutescens* are endemic to Peru. We comment on the species reported in previous expeditions and in the current checklists. Since this forest is important for its large number of endemic species, we comment on its current threats and the importance of accounting for ecological interactions to conserve montane forests.

Key words: montane forests, flowerpiercers, hummingbirds, ecological interactions, Huánuco.

Resumen

Se describen las aves nectarívoras (colibríes, pinchaflores y picoconos) y sus recursos florales en un bosque achaparrado de los Andes centrales peruanos (Unchog, Cordillera Carpish). Este bosque es bien conocido por su concentración de especies endémicas, principalmente aves. Registramos a las aves nectarívoras, plantas vasculares y sus interacciones entre el 2011 al 2014. Las aves fueron registradas por observaciones directas y redes de neblina. Las plantas fueron evaluadas con parcelas de Gentry y colecta ocasional. Un total de 26 especies nectarívoras han sido reportadas en este bosque, sin embargo, en nuestras observaciones detectamos 17 especies de aves que se alimentan del néctar de las plantas. Un total de 27 especies de plantas fueron visitadas por las aves. Las aves nectarívoras fueron colibríes (Trochilidae, 12 especies), pinchaflores (Thraupidae, 4 especies) y un picocono (Thraupidae: 1 especie). Las plantas fueron de 16 familias y 14 órdenes. Una especie de colibrí, *Metallura theresiae*, es endémica del Perú. Sobre plantas, *Greigia macbrideana*, *Puya pseudoeryngioides*, *Centropogon isabellinus*, *Miconia alpina* y *Brachyotum lutescens* son endémicas del Perú. Comentamos sobre las especies reportadas en expediciones previas y en listas actuales. Puesto que este bosque es importante por su gran número de especies endémicas, comentamos acerca de las amenazas actuales y en la importancia de considerar las interacciones ecológicas para la conservación de los bosques montanos.

Palabras clave: bosques montanos, colibríes, Huánuco, interacciones ecológicas, pinchaflores.

Introduction

The "montane forest" is dominated by woody vegetation (trees, lianas and bushes) over 1 000 m elevation where the Amazon forest meets the Andes up to 3 200 or 3 800 m (Terborgh, 1985; Stotz *et al*., 1996). It is possible to find different vegetation zones that have their own flora and physiognomy; the soil and amount of precipitation also vary (Richards, 1996). The elfin forest is at the upper top of the montane forest gradient in the Andes ("Bosques pluviales montanos", sensu León *et al*., 2006), right before the tree-line (Brack & Mendiola, 2000). This ecosystem includes a community of trees with small leaves and shrubs usually no more than 10 m tall, loaded with epiphytes, mosses and lichens in a permanent cloud base. They grow in soil with quartzite, sandstones and granites, and are also stunted by fire, drought stress and wind pruning (Terborgh, 1971; Stotz *et al.*, 1996; Ashton, 2003). There are elfin forests in other mountain chains besides the Andes (e.g. Puerto Rico; Nevling, 1971); even though the climatic conditions and physiognomy of plants are similar, the species composition is very different. For a discussion in terminology see Stadtmuller (1987). Prance (1989), quoted by Stotz *et al.* (1996), mentioned that the plant composition is similar to the upper montane forest, with many of the same plant genera but different species of Ericaceae, Brunelliaceae, Clusiaceae, Compositae, Aquifoliaceae, Melastomataceae, Rhamnaceae, Escalloniaceae and Cunoniaceae. Terborgh (1971) included Orchidaceae as predominant. In the treeline of the Andes, trees of the genus *Polylepis* (Rosaceae) are expected (Ashton, 2003), but there are areas with few individuals. This may be because of intensified logging after the Spanish conquest in the XVI century (Gareca *et al.*, 2013).

Up to 24% of all terrestrial biodiversity of the planet is estimated to live in the montane forest of tropical America (Birdlife International & Conservation International, 2005). In Peru, this forest lies in the domain of an Endemic Bird Area known as the Peruvian high Andes, which is of special conservation concern given its high biological importance and current levels of threat; many bird populations are restricted to small forest patches (Terborgh, 1971; Patterson *et al.*, 1998; Stattersfield *et al.*, 1998). The high diversity of species is a result of the topography and habitat heterogeneity, as occurs in Amotape-Huancabamba zone (Mutke *et al.*, 2014). Stotz *et al.* (1996) report that the elfin forest of the central Andes harbors 34 bird species that use it as primary habitat, and 15 of them are restricted to this kind of forest. These habitat-restricted species that dwell at the top of the mountains are important for the design of nature reserves (Young, 2007). Fjeldsa *et al.* (1999) found that endemic birds in the tropical Andes are correlated with a history of stable climate; however Young & León (2007) mention that the treeline near the top of the Andean mountains is a dynamic ecosystem that may promote speciation and a unique community.

Nectarivorous birds have long been recognized as important components of high elevation forests in tropical America (Wolf *et al.*, 1976; Renjifo *et al.*, 1997; Blake & Loiselle, 2000). For example, Terborgh (1977) while studying bird diversity along an altitudinal gradient in Vilcabamba in Peru, found that nectarivorous birds (hummingbirds and flowerpiercers) accounted for nearly 50% of the netted individuals near timberline. While in the high Andes forest of Cuzco, Ramirez *et al.* (2007) and Lloyd (2008) found nectarivorous to be the most abundant guild of birds. Similarly, in the elfin forest of Yanachaga National Park (~ 90 km south-east of Carpish Mountains), Gonzalez (2008) found *Diglossa* and *Metallura* were the most abundant birds in the community. The importance of nectarivorous birds such as hummingbirds as pollinators is well known (Bawa, 1990; Kessler & Kromer, 2000). In the high Andean forest of Bolivia, where the weather is humid and cold, birds were the main pollinators, especially for *Puya* spp. and other bromeliads (Kromer *et al.*, 2006). Hummingbirds are the most abundant family of nectarivorous birds and also with most restricted distribution in the tropical Andes (Herzog & Kattan, 2011).

Here we describe the community of nectarivorous birds and the plants they visit with observations of bird and plant surveys across 4 years (2011-2014) in the elfin forest of Unchog in the cordillera Carpish of Huánuco, Peru. We focused on nectarivorous birds and their plant resources, comparing the expected assemblage of bird-plant interactions of the available literature with our results. The surveys were conducted as part of a dissertation project on bird-flowering plant networks (Gonzalez, 2015). We also discuss the previous records of nectarivorous birds in the area and the ecological significance of the plants in the elfin forest ecosystem.

Materials and Methods

Study Area

The Carpish Mountains represent montane forest in central Peru which is rich in endemic species of plants and animals. The Carpish Mountains are in the Department of Huánuco, accessible from the main highway ("carretera central") connecting the cities of Huánuco and Tingo María. Botanical expeditions in this area have occurred since the 18th century with the Spanish explorers Ruiz and Pavon (Beltran & Salinas, 2010); later expeditions occurred in the 1930's and 1940's (Weberbauer, 1945; Goodspeed & Stork, 1955). Ferreyra (1950) described the vegetation and was the first to propose that Carpish be designated a national park, due to its high level of endemic species. As Beltran & Salinas (2010) explain, a single classification for the vegetation system is not possible, so these botanists and the ornithologists Parker & O'Neill (1976) differentiated the following vegetation zones: premontane forest (1 600 – 2 300 m), montane forest (2 300-2 800 m), elfin forest (2 800 – 3 600 m) and puna grassland (over 3 600 m).

The Carpish Mountains was not a protected area at the end of this study. The area has been disturbed by cattle grazing and fire (Franke *et al.*, 2005) and the main central highway allowed human colonization that caused severe deforestation (Dourojeanni *et al.*, 2010). Part of the landscape below 2 000 m was already modified in the 1950's and 1970's (Goodspeed & Stork, 1955; Tallman, 1974), but original vegetation is still present in higher and inaccessible areas, which function as a natural refuge (Sylvester *et al.*, 2014). There remain important portions of elfin forest at the treeline that harbor endemic bird species (Wege & Long, 1995). An assessment of the montane forest in Peru lists this area as a priority for conservation (CDC-UNALM & TNC, 2006).

There have been ornithological studies in Carpish early in the past century (Zimmer, 1930), besides inventories and a description of mixed species flocks (Vuilleumier, 1970). Carpish has been the object of interest for Louisiana State University through several field expeditions (Tallman, 1974; Parker & O'Neill, 1976). They discovered new species of endemic birds there (Blake & Hocking, 1974; Lowery & Tallman, 1976). Carpish has been a preferred place for birdwatching in Peru (Valqui, 2004) because of the high richness of endemic birds, however tourism has not been frequent due to past problems (years 1980 – 2000) with security in the area. Terrorist groups and drug-dealers have dominated here (Fjeldsa *et al*., 2005), something that hinders the visit of birdwatchers and researchers (Puhakka *et al*., 2011). Despite this social problem, Peruvian researchers have completed inventories of plants (Salinas, 2005) and amphibians (Rodríguez, 2007) in the lower areas.

Unchog (3 800 m, 09°42'32.3" S, 076°09'39.1" W), where we did our surveys, is communal land of the Comunidad Campesina Cochabamba of Huánuco. There were three elfin forest patches with continuous vegetative cover (Unchog, Magma and Simeompampa), with ~8 ha each and no more than 2 km apart from each other (Figure 1). The predominant trees are several species of the *Weinmannia* genus, which is common in the Andes above 2 000 m (Rapp *et al*., 2012). Between these elfin forest patches, there were native shrubs and pastures.

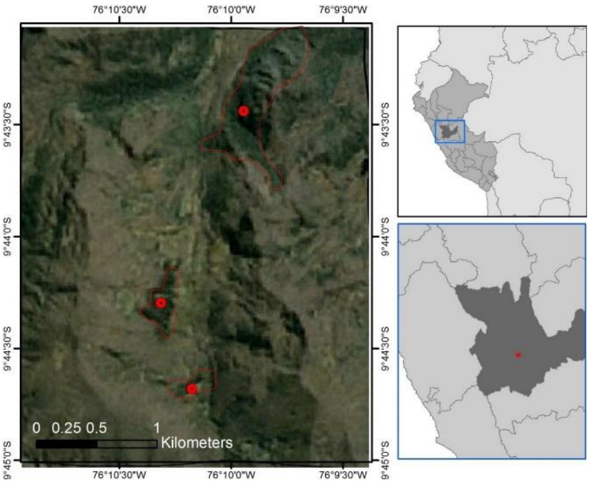


Figure 1. Location of the elfin forest of Unchog in Peru. The forest patches sampled are marked in red.

Data collection

Unchog forest was visited during different periods from May 2011 to August 2014, over a total of 134 days; 17 days within May-July of 2011, 24 days within February, July-November of 2012, 41 days in January-July, September, November of 2013 and 52 days in January and May-August of 2014. For more details in sampling effort, see Gonzalez & Loiselle (2016). This forest has a dry and rainy season, and some bird species are more prone to be present or plants blossoming depending on the season. We clumped our observations of both seasons during the entire research time to increase the chance to see all birds and plants of this network. Oscar Gonzalez identified nectarivorous birds (hummingbirds, flowerpiercers and conebills) walking along the forest edges and inside forests mainly in the morning with binoculars. In addition, mist-nets in different areas of the three forests patches were used (2 399 net-hours) and we recorded songs with a Marantz PMD-620 voice recorder and a Sennheiser shotgun microphone. This methodology of bird evaluation followed the protocol of Bibby *et al.* (2000), mist nets were preferred over point counts as a better method for detection due to the cryptic behavior of small birds in the cloud forest (Martin *et al*., 2017). We recorded all birds captured in mist nets but for the aim of this study, we are reporting just the nectarivorous. Passerine birds were banded with unique color band codes. Identification follows Schulenberg *et al*. (2007). The names for the birds were taken from the South American Classification Committee list for Peru (Remsen *et al*., 2016) and Avibase (Avibase, 2003).

We compared our observations to bird lists from previous expeditions to the area, which were primarily conducted by Louisiana State University, Field Museum of Natural History, American Museum of Natural History and Museo de Historia Natural of the Universidad Nacional Mayor de San Marcos. O. Gonzalez visited the bird collections of these institutions. These expeditions did intense collection of birds in the Unchog area mainly in the summer season (May-August) to survey Carpish mountains. We also used eBird records (eBird, 2015) to document observations of birds in Unchog forest up to July 2014. The eBird data are records of bird species presence taken by professional and amateur birdwatchers (Sullivan *et al*., 2014), displayed in bird checklists of specific locations evaluated in different ways. We focused the location as "Unchog" in our search.

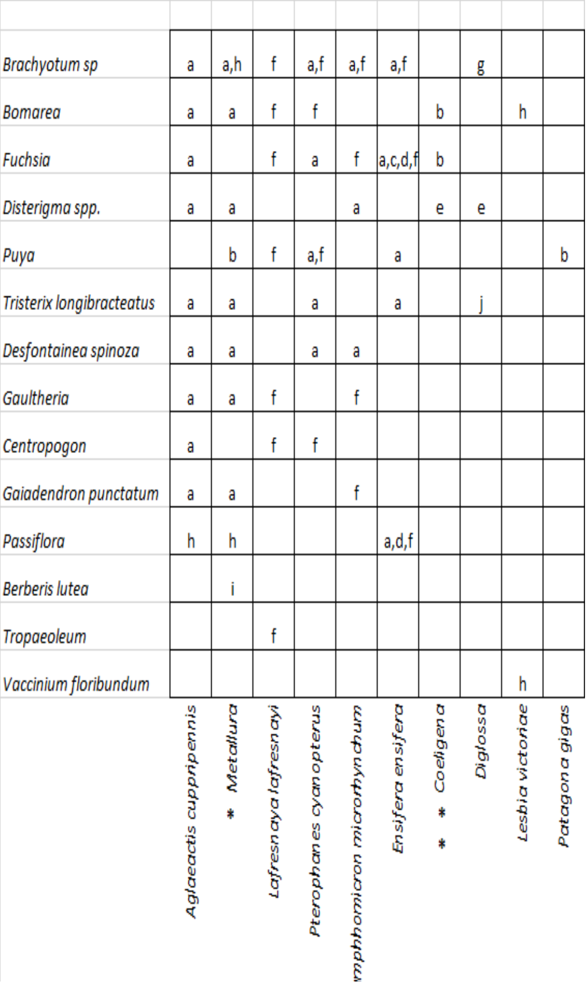
The survey of flowering plants visited by birds was done by setting up two Gentry plots (Gentry, 1982) which were five transects of 100 x 2 m inside the forest patches and occasional collecting by Bernie Britto and Camilo Díaz. This occasional collecting consisted of recording the plants that were not seen inside the plots but were into our study area. Plant identification was done by specimens collected and by photographs. The vouchered plant samples were deposited to the herbarium of the Universidad Peruana Cayetano Heredia and the specimens were compared with others in the herbarium of the Museum of Natural History of the Universidad Nacional Mayor de San Marcos. As authorities for plant names we used the works of Mabberley (1987), Brako & Zarucchi (1993) and The International Plant Names Index (IPNI, n.y.).

For the visualization of the assemblage of nectarivorous birds and their visited plants, we collected the available records on bird-plant visitation of Andean elfin forests from the literature, looking for the species or genera that we recorded in Unchog. Then we ordered the assemblage in a two x two matrix; by species that have most of the interactions at the top left in a nested structure (Jordano *et al*., 2009). We called this the theoretical network. Then we ordered our observations on the nectarivorous birds visiting flowers of the plants in the same way, but here we had a qualitative matrix, measured by how many times a bird species visited a plant species. Then we applied the function visweb of the bipartite package in the software program R (Dormann *et al.*, 2008), which is useful to visualize interaction networks in a grid with different colors or tones that represent the strength of the interaction. This quantitative assemblage was called the observed network. We compared the theoretical network with the observed network with parameters for qualitative networks, using the function networklevel in bipartite (Dormann *et al*., 2008). In order to do this, we converted the quantitative network in a qualitative network for our observed assemblage. Connectance and nestedness were chosen as reliable indicators to compare qualitative networks (Jordano *et al*. 2009). Connectance measures the proportion of interactions, by dividing the total number of species interactions by the total size of the matrix (Birds x plants). Nestedness measures the order of interactions in the matrix, being zero a random distribution and 100 perfect nestedness; here we used the indicator NODF (Dormann *et al.*, 2008).

Results

We gathered information on interactions of ten nectarivorous bird taxa with 14 plant taxa from nine sources (Figure 2). The assemblage of birds and plants that we observed interacting by nectar in the elfin forest of Unchog were 44 species (Figure 3). The qualitative data is available in Figshare (Gonzalez, 2016). Connectance in the theoretical network was 0.3, nestedness (NODF) 68.26; while in the observed network, the connectance was 0.385 and nestedness 54.93.

We found a total of 27 plant taxa that were used by birds as nectar sources. The plants belonged to 14 orders, 16 families and 24 genera. None of the plants or bird species were exotic. Two of the genera (*Disterigma* and *Rubus*) had multiple species that were identified but we could not confirm whether all of them were visited by the birds (Table 1). The data in eBird (2015) record a total of 26 nectarivorous birds between 2011 and 2014. We evidenced that 17 of them visited flowers of nectar-producing plants. Twelve of these birds belong to the order Apodiformes, family Trochilidae (hummingbirds) and 5 to the order Passeriformes, family Thraupidae (4 flowerpiercers, 1 conebill). The flowerpiercers are considered nectar-robbers (not true pollinators) and the conebill, an occasional nectarivorous bird.



	Aglaeactis cuppripennis	* *Metallura*	*Lafresnaya lafresnayi*	*Pterophanes cyanopterus*	*mphbomicron microrhynchum*	*Ensifera ensifera*	** *Coeligena*	*Diglossa*	*Lesbia victoriae*	*Patagona gigas*
Brachyotum sp	a	a,h	f	a,f	a,f	a,f		g		
Bomarea	a	a	f	f			b		h	
Fuchsia	a		f	a	f	a,c,d,f	b			
Disterigma spp.	a	a			a		e	e		
Puya		b	f	a,f		a				b
Tristerix longibracteatus	a	a		a		a		j		
Desfontainea spinoza	a	a		a	a					
Gaultheria	a	a	f		f					
Centropogon	a		f	f						
Gaiadendron punctatum	a	a			f					
Passiflora	h	h				a,d,f				
Berberis lutea		i								
Tropaeoleum			f							
Vaccinium floribundum									h	

a = Gutierrez & Rojas (2001), b = Schuchmann (1999), c = Berry (1985), d = Abrahamczyk *et al.* (2014), e = Navarro *et al.* (2008), f = Gutierrez-Zamora (2008), g= Stiles *et al.* (1992), h = Córdova & Fajardo (2018), i = Hesse (2010).

* The species is *tyrianthina* in all cases except for *M. odomae* in Hesse (2010).

** Could be *Coeligena torquata* or *C. violifer*.

Figure 2. Theoretical Bird-flower visitation network in the elfin forest. Plants are in the vertical side and birds in the horizontal side, in a nested order by interaction strength. The letter in each filled square is the reference for that interaction. White squares mean no interaction.

On plants, *Greigia macbrideana*, *Puya pseudoeryngioides*, *Centropogon isabellinus*, *Miconia alpina* and *Brachyotum lutescens* are endemic to Peru (León *et al*., 2006). A bird species of conservation concern is the hummingbird *Metallura theresiae*, endemic from Peru (Schulenberg *et al*., 2007). Three of

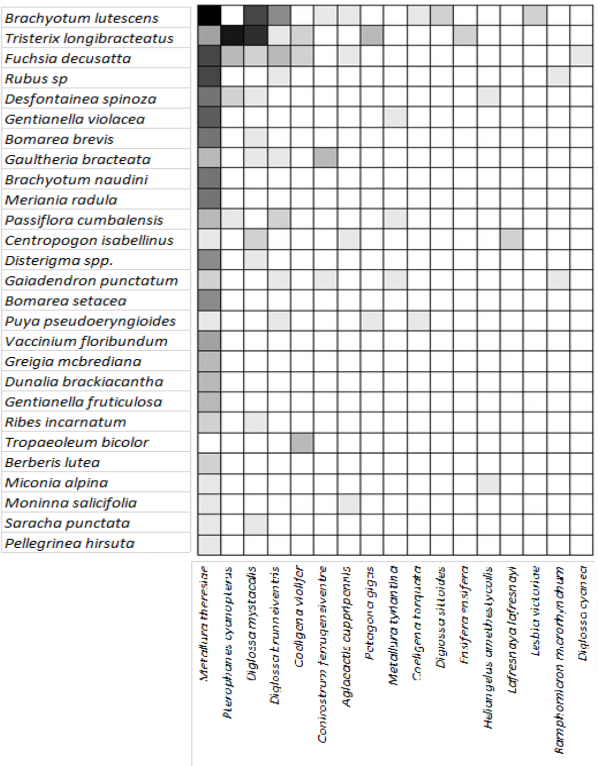


Figure 3. Observed Bird-flower visitation network in the elfin forest. Plants are on the vertical side and birds in the horizontal side, in a nested order by interaction strength. Each filled square represent an interaction, the darker the square, the stronger the interaction is. White squares mean no interaction. The maximum number of interactions was 45, minimum zero.

the bird species found (*Metallura theresiae, Pterophanes cyanopterus* and *Conirostrum ferrugineiventre*) are considered typical of the elfin forest by Parker *et al*. (1996).

Discussion

Network properties of the nectarivorous assemblage

The assemblages, or networks of nectarivorous birds and their resources provide an important framework to study ecological principles such as diversity, distribution, adaptation and energy flow (Rojas-Nossa, 2013; Bennett *et al*., 2014; Abrahamczyk & Kessler, 2015; Gonzalez & Loiselle, 2016). The information gathered from nine sources on nectarivorous birds that visited plants in the Andes gave us a limited view of the real interactions in the elfin forest, because there were fewer taxa than in the observed network. The connectance of the observed network was higher, but the nestedness lower. This could indicate that the assemblage of plants and nectarivorous birds could be more fragile than expected because nestedness is considered an indicator of resistance of communities to perturbations (Bascompte *et al.*, 2003). However, we have the limitation that this theoretical network is a compilation of data from different areas, even though from tropical Andean forests, the endemism of plants and animals is high (Stattersfield *et al*., 1998) and the preferences of birds on specific plants might switch. Then, it is important to analyze in some detail the members of the assemblage.

Nectarivorous Birds

We recorded the nectarivorous bird species that were reported by Tallman (1974) and Parker & O'Neill (1976), who did intensive search for birds in the Carpish area; but not all of the species in the eBird record (2015) were seen in Unchog forest or interacting with plants (Table 2). The species of this potential network that we did not record in the interactions were *Colibri thalassinus, Colibri coruscans, Chalcostigma ruficeps, Chalcostigma stanleyi, Metallura phoebe, Agaleactis castelnaudii, Amazilia chionogaster, Conirostrum cinereum* and *Conirostrum sitticolor*. However, during our field study (2011-2014) almost all the records for eBird (2015) were in the dry season; there were no records in February, April and September.

It is highly likely that the contributing people for the eBird records went outside the limits of the elfin forest to see these species, because the tourists who come to this birding hotspot do not just birdwatch in the elfin forest. They get in the montane scrub of the Huallaga valley that borders with the elfin forest and they can also go beyond this forest to the cloud forest limit; it is possible to see bird species there that do not frequent the core of the elfin forest (Valqui, 2004). The White-tufted Sumbean *Agaleactis castelnaudii* was recorded in eBird's record of Unchog by three people (eBird, 2015), two of them said that they saw them in the montane scrub outside the elfin forest (F. Schmidt, G. Schoezler, personal communication to O. Gonzalez). *A. castelnaudii* with White-bellied hummingbird *Amazilia chionogaster* and Sparkling Violetear *Colibri coruscans* are usually seen in the neighboring habitat too (O. Gonzalez, personal observation). The altitudinal limit of *A. chionogaster* is 3 500 m, and Green violetear *Colibri thalassinus* is 3 300 m. These are located below our observation areas. *A. chionogaster* was seen just once at the beginning of the study and was not seen visiting any flower. *C. thalassinus* is known to make altitudinal migrations in Central America (Levey & Stiles, 1992). Black Metaltail *Metallura phoebe* usually does not overlap with other species of *Metallura* (Schulenberg *et al*., 2007), but it could be confused with *M. theresiae* which seems black from a distance. The data on eBird can be a good reference to look for distributions (Sullivan *et al*., 2014), however it is necessary to recheck the data for possible mistakes before using it for comparison in a specific region (Gonzalez & Wethington, 2014). We registered Purple-backed Thornbill *Ramphomicron microrhynchum* as well as Parker & O'Neill (1976); but this species was not in the eBird's checklist (eBird, 2015) within the temporal and spatial range surveyed. The inclusion of a conebill as a nectarivorous bird might seem odd, but Moynihan (1963) mentioned that the species of this group are partly nectarivorous.

The tree line of Manu National Park, in the southern Peruvian Andes, has a very similar landscape to Unchog. Lloyd *et al*. (2012) found out a distinctive community of plants and birds, different from puna grasslands and the cloud forest. Bird pollinators that are expected in tree line zones include a dozen hummingbirds such as Great Sapphirewing *Pterophanes cyanopterus,* Sword-billed Hummingbird *Ensifera ensifera* and species of the genus *Coeligena, Eriocnemis* and *Heliangelus*, the last two restricted to the elfin forest. We did not observe *Eriocnemis* in this study.

The Coppery Metaltail *Metallura theresiae* was the most dominant flower visitor in this ecosystem, so it could be the most effective pollinator (Willmer, 2011). In other tree line ecosystems in the central Andes, the small hummingbirds Tyrian Metaltail *Metallura tyrianthina* and Amethyst-throated Sunangel *Heliangelus amethysticollis* are dominant (Gonzalez, 2008; Lloyd *et al*., 2012; Toloza-Moreno *et al*., 2014) but in Unchog, *M. theresiae* has taken over the tree line and these other hummingbirds stay in lower elevations. The diversification of *Metallura* hummingbirds was recent (Garcia-Moreno *et al*., 1999), hummingbirds have their beta-diversity associated with elevation (Weinstein *et al*., 2014). *M. tyrianthina* is subordinate (Does not compete, it is not dominant) to *M. theresiae* and other sister species when it is present at higher elevations (Heindl & Schuchmann, 1998).

Hummingbirds of the genus *Coeligena* visits several species of plants in Andean forests, Schuchmann (1999) reported them visiting *Bomarea*, but we did not observe *Coeligena* feeding on *Bomarea*. The other plants reported by Schuchmann were not in our study area. Schuchmann (1999) also did not report *Tristerix* as food for *Pterophanes cyanopterus* as we observed. Gutiérrez & Rojas (2001) in the paramos of Colombia, found that there is a strong dependence of several small billed hummingbirds with *Brachyotum*. They also found dependence of *Pterophanes* with *Puya*; but not with *Tristerix* which was also present there. *Metallura odomae*, sister taxa of *Metallura theresiae* in high elevation montane forest in the north of Peru feeds mainly in *Brachyotum* and in *Berberis* (Hesse, 2010). Small-billed hummingbirds rely on *Brachyotum*, its importance in the network is explained in Gonzalez & Loiselle (2016). Schuchmann (1999) mentions that the Shining Sunbeam *Aglaeactis cupripennis* does local migrations, *Heliangelus* prefers shrubs in the ecotone between paramo and forest and *Coeligena* forages in the forest itself or forest edges.

The Moustached flowerpiercer *Diglossa mystacalis* has a large range that is not limited to the elfin forest (Parker & O'Neill 1976); Black-throated Flowerpiercer *Diglossa brunneiventris* is common in disturbed areas and non-forested habitat (Becker *et al.*, 2008; Vaicenbacher *et al*., 2014). Masked Flowerpiercer *Diglossa cyanea* travels with mixed species flocks in cloud forests (Guevara *et al*., 2011; Arbelaez-Cortes & Marin-Gomez, 2012) and was uncommon.

Flowering plants visited by birds

The ornithophilus plants expected in the elfin forest according to Schuchman (1999) could be woody, vines and shrubs. Those are members of the genus *Bomarea, Fuchsia, Lobelia, Passiflora, Brachyotum, Befaria* or *Datura.* We did not find visitors for *Lobelia, Befaria* or *Datura*.

As Stiles (1985) described, in high elevation ecosystems like this elfin forest, the birds pollinate mainly shrubs. The Melastomataceae *Brachyotum, Meriania* and *Miconia* were cataloged as hummingbird-pollinated by Varassin *et al*. (2008). The shrub *Brachyotum* spp. is an important source of nectar of several nectarivorous species in this region; first descriptions on the flowers of this genus noted that hummingbirds pollinate it (Renner, 1989a). However, Stiles *et al*. (1992) suggested that these plants are adapted to pollination by the *Diglossa* flowerpiercers. The plant more connected was *Brachyotum lutescens* which is an endemic species of Peru only found in this region and maybe in critical situation (León, 2006). As for the shrub *Hypericum*, common here and in the northern Andes paramo (Caceres *et al*., 2014), the shrub *Brachyotum* may be a foundational species; they are the first in colonizing a non-woody area and start forest regeneration (Guenter *et al*., 2009). Furthermore, *Brachyotum* facilitates movement among forest patches as nectarivorous birds that move between patches may forage on *Brachyotum* which is common in the non-forested matrix. Similar to Gutiérrez & Rojas (2001), who studied a tree line zone between montane forest and paramo, *Brachyotum* (*B. lutescens* and *B. naudini*) is most visited by hummingbirds and then other plants identified in this study: *Fuchsia, Passiflora* and *Tristerix.*

Ollerton *et al*. (2009) identified the plants that have birds as pollinators in the elfin forest of Urubamba (Cuzco). Plants that have a common genus in Unchog forest are: *Bomarea, Fuchsia, Gaultheria, Passiflora, Puya,* and *Rubus.* Wolf *et. al*. (1976) reported that *Centropogon* and *Fuchsia* are common plants used by hummingbirds in the high altitude forest of Central America. Cronk & Ojeda (2008) and Willmer (2011) identified *Fuchsi*a and *Passiflora* as typical bird-pollinated flowers. Botanists such as Weberling (1989) and Gentry (1993) recognize that *Fuchsia* plants are adapted for the visitation by hummingbirds. Gentry (1993) also confirmed that *Brachyotum* and *Tristerix* are characteristic for hummingbird pollination. In New Zealand, *Tristerix* is known to suffer the effect of pollination limitation in the seed set (Montgomery *et* *al*., 2001), even though is self-compatible. However, it has populations that are gynodioecious (hermaphrodite and female flowers) so that could be an evolutionary advantage in case there would not be pollinators (Arroyo & Raven, 1975; Atsatt & Rundel, 1982; Robertson *et al*., 1999). In one hermaphroditic species of *Fuchsia*, its nectar production is assumed related to the evolution of the pollination traits of the flower (Atsatt & Rundel, 1982). The presence of *Ensifera ensifera* in the montane forest limit with the paramo in Colombia is associated with the presence of blossoming peaks of *Fuchsia* and *Passiflora* (Gutiérrez & Rojas, 2001). However, specialization in pollination networks can be misleading (Schemske, 1983). In Unchog *Ensifera*, was seen occasionally and not visiting *Passiflora* but *Tristerix*. Furthermore, *Metallura theresiae* visited *Passiflora* flowers illegitimately (Gonzalez & Loiselle, 2016). Benevides *et al*. (2013) stated that *Passiflora* is a very important resource for several pollinators, but this plant was scarce in the elfin forest and did not receive many visitors.

It is known that *Puya* is a very important source for hummingbirds in the high Andes (Woods & Ramsay, 2001; Salinas *et al*., 2007; Hornung-Leoni *et al*., 2013). Schuchmann (1999) states that *Patagona gigas* is highly dependent on *Puya*. Besides this hummingbird species, we observed *Coeligena torquata*, *Metallura theresiae* and *Diglossa brunneiventris* visiting *Puya*, but the dependence on them was weak.

The blackberry *Rubus* had more than one species in the network but the shape of the flowers was very similar in all species. *Berberis* and *Tropaeolum* are genera that are present also in the Chilean Andes, but the weather here is temperate and they are pollinated by insects (Arroyo *et al*., 1982). The shrub *Dunalia spinosa*, related to *D. brakiacantha* in a premontane habitat also in the Chilean Andes, has flowers rich in nectar and is visited by different birds (Torres-Mura & Hertel, 2006). In a study involving *Disterigma* in Colombia, small-billed hummingbirds were the most common visitors; with *Coeligena* and a *Diglossa* that robbed its nectar as seldom visitors (Navarro *et al*., 2008). In the sampling we detected *Cavendishia bracteata*, *Pernettya postratta* and *Fuchsia apetala*; the first two flowers were visited by hummingbirds in Colombia (Gutierrez-Zamora, 2008). *F. apetala* has large and orange flowers, but we did not see any bird visitor to this species. Plants with small flowers such as *Pernettya postrata* and *Gualtheria* spp. could be able to self-pollinate (Luteyn, 2002) and did not have a strong dependence with birds. Epiphytes, which are known to be important as nectar resource in montane forests (Kromer *et al*., 2006) were almost absent here because at high elevations close to the treeline, the abundance of epiphytes drops (Zotz *et al*., 2014).

Factors that affect the assemblage

It is important to consider the bird composition of this assemblage might be affected by local movements or migrations, nectarivorous birds have been recorded to have local migrations in another montane forest such as in Manu (Merkord, 2010) or Costa Rica (Levey & Stiles, 1992; Boyle *et al*., 2011). On local movements of the birds in Unchog, it was observed that only one *Diglossa mystacalis* of 69 banded flowerpiercers (*D. mystacalis* and *D. brunneivent*ris) switched between forest patches in 8 months. We do not have information on movements of the hummingbirds here. It is known that hummingbirds fly long distances following floral resources (Levey & Stiles, 1992; Hobson *et al*., 2003; Gutierrez *et al*., 2004) and usually move between fragments of montane forest and high montane scrub habitats at high elevations (Toloza-Moreno *et al*., 2014). Even *Metallura theresiae* is observed all year round and nesting at different times of the year in the elfin forest (O. Gonzalez, personal observation) we cannot discard the possibility that this hummingbird moves to lower elevations. Hobson *et al*. (2003) proved with isotopes that hummingbirds move along an elevational gradient in a montane forest, among them *Metallura baroni*, an endemic. However, *Metallura theresiae* is at the core of the network observed here (Gonzalez & Loiselle, 2016) and appears to be constant throughout time and space (eBird, 2015).

About other vertebrates that are nectarivorous, bats are a possibility in our study area. Even though we did not observe bats visiting flowers, it is probable that nectarivorous bats of genus *Anoura*, observed in the upper montane forest of Yanachaga-Chemillen National Park (90 km southeast) reach the elevation of the elfin forest (Vivar, 2006); and pollinate *Macrocarpaea* flowers (Renner, 1989b); this tree has populations limiting the elfin forest. There are records in the Kosnipata valley in Cusco (1 600 m. elevation) of *Rubus* pollen transported by bats (Maguina *et al*., 2012) and of *Passiflora* pollen in a montane forest in Ecuador (Muchhala & Jarrin-V, 2002). Insects visited some plants that birds also visit; in the dry season of 2014 a total of 29 % of the flower visitors of *Gentianella violacea* were insects (O. Gonzalez, unpublished data).

Unchog forest is a place of high endemism of the tropical Andes, shown by this assemblage of nectarivorous birds and their resources, as well as several other birds and plants. This endemism in elfin forests leads to its importance for conservation efforts (Herzog & Kattan, 2011; Tejedor-Garavito *et al*., 2014). Unfortunately, the elfin forest is highly fragmented; and habitat loss by deforestation due to logging, livestock grazing or clearance for agriculture could hasten loss of pollinators and pollinator services. Detailed research is needed on the individual responses of plants to deforestation (Renner, 1998). The conservation of the tree line ecosystems, where there are remnants of elfin forests and enclosed watersheds are the resources for nectarivorous birds and also for several endemics, should be a priority for conservation (Ramirez-Villegas *et al*., 2014).

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Table 1. Identity and characteristics of the plants visited by nectarivorous birds at Unchog forest. Frequency in flowers /ha. Very rare(VR) = Less than 40, Rare (R) = Between 40-100, Frequent (F) = Between101 – 1 000, Common (C) = More than1 000. Life form: T = tree, V = vine, S = Shrub, H = Herb. Conservation status is based in Leon *et al*. (2006): CR = Critical; EN = Endangered; VU = Vulnerable; NE = Not evaluated; X = endemic without categorization. Pollination syndrome: O = Ornithophilus, E = Entomophilus, C = Chiropterophilus.

Taxa	**Frequency**	**Life form**	**Conservation Status**	**Pollination syndrome**
ASTERALES				
Campanulaceae				
Centropogon isabellinus E. Wimm	F	S	X	O
BRASSICALES				
Tropaeolaceae				
Tropaeolum bicolor Ruiz & Pav.	VR	V		O
ERICALES				
Ericaceae				
Disterigma spp.*	F	S		E
Gaultheria bracteata G. Don	C	S		
Pellegrinia hirsuta (Ruiz & Pav. Ex G. Don) Sleumer	VR	S	NE	O
Vaccinium floribundum H.B.K.	C	H		E
FABALES				
Polygalaceae				
Monnina salicifolia Ruiz & Pav.	VR	T		E
GENTIANALES				
Gentianaceae				
Gentianella fruticulosa (Dombey ex Weddell) Fabris ex J. Pringle	C	H	EN	O
Gentianella violacea (D. Don ex G. Don) Fabris	C	H	VU	O
GENTIANALES				
Loganiaceae				
Desfontainia spinosa Ruiz & Pav.	C	S		O
LILIALES				
Alstroemeriaceae				
Bomarea brevis (Herb.) Baker	C	H		O
Bomarea setacea (Ruiz & Pav.) Herb.	C	H		O
MYRTALES				
Melastomataceae				
Brachyotum lutescens (Ruiz & Pav.) Triana	C	S	CR	O
Brachyotum naudinii Triana	C	S		O
Meriania radula (Benth.) Triana, 1872	VR	T		E
Miconia alpina Cogn.	VR	T	X	E
MYRTALES				
Onagraceae				
Fuchsia decussata Ruiz & Pav.	C	V		O
POALES				
Bromeliaceae				
Greigia macbrideana L.B. Sm.	VR	H	EN	E
Puya pseudoeryngioides H. Luther	C	H	CR	O
RANUNCUNALES				
Berberidaceae				
Berberis lutea Ruiz & Pav.	VR	T		E
ROSALES				
Rosaceae				
Rubus sp.**	C	S		C
SANTALALES				
Loranthaceae				
Gaiadendron punctatum G. Don.	VR	S		E
Tristerix longebracteatus (Desr.) Barlow & Wiens	C	S		O
SAXIFRAGALES				
Grossulariaceae				
Ribes incarnatum Wedd.	R	V		E
SOLANALES				
Solanaceae				

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Taxa	**Frequency**	**Life form**	**Conservation Status**	**Pollination syndrome**
Dunalia brachyacantha Miers	R	S		O
Saracha punctata Ruiz & Pav.	VR	T		E
VIOLALES				
Passifloraceae				
Passiflora cumbalensis (H. Karst.) Harms	F	V		O

* *Disterigma* species could be *alaternoides* (H.B.K) Niedenzu 1889, *microphyllum* (G.Don) Luteyn or *pernettyoides* (Griseb. ex Wedd.) Nied.

** *Rubus* species could be *bogotensis* H.B.K OGM-107, *erythrocladus* C. Martius, *roseus* (Poiret, 1804), *weberbaueri* (Focke, 1910).

Table 2. Identity and characteristics of the nectarivorous bird assemblage. The frequency criteria is based on data of individuals captured in 100 net-hours: No data (ND), Very rare (VR) = Less than 2, Rare (R) = Between 3 to 5, Frequent (F) = Between 6 to 11, Common (C) = more than 12. Conservation status: E = Endemic for Peru, I= Elfin forest indicators (Parker *et al.* (1996). Record: x = This study, e = eBird.

Taxa	**Frequency**	**Conservation status**	**Record**
APODIFORMES			
Trochilidae			
Colibri thalassinus (Swainson, 1827)	ND		e
Colibri coruscans (Gould, 1846)	ND		e
Heliangelus amethysticollis (d'Orbigny & Lafresnaye 1838)	R		x, e
Lesbia victoriae (Bourcier & Mulsant, 1846)	VR		x,e
Ramphomicron microrhynchum (Boissonneau, 1840)	VR		x
Chalcostigma ruficeps (Gould, 1846)	ND		e
Chalcostigma stanleyi (Bourcier, 1851)	ND		e
Metallura tyrianthina (Loddiges, 1832)	R		x,e
Metallura theresiae (Simon, 1902)	C	E, I	x,e
Metallura phoebe (Lesson & Delattre, 1839)	ND		e
Aglaeactis cupripennis (Bourcier 1843)	VR		x,e
Aglaeactis castelnaudii (Bourcier & Mulsant, 1848)	ND		e
Coeligena torquata (Boissonneau 1840)	VR		
Coeligena violifer (Gould, 1846)	F		x,e
Lafresnaya lafresnayi (Boussonneau 1840)	VR		x,e
Ensifera ensifera (Boissonneau 1840)	R		x,e
Pterophanes cyanopterus (Fraser, 1840)	F	I	x,e
Patagona gigas (Vieillot, 1824)	R		x,e
Amazilia chionogaster (von Tschudi, 1846)	ND		e
PASSERIFORMES			
Thraupidae			
Conirostrum cinereum (d'Orbigny & Lafresnaye 1838)	ND		e
Conirostrum sitticolor (Lafresnaye, 1840)	ND		e
Conirostrum ferrugineiventre (Sclater, PL, 1855)	VR	I	x,e
Diglossa mystacalis (Lafresnaye, 1846)	C		x,e
Diglossa brunneiventris (Lafresnaye, 1846)	C		x,e
Diglossa sittoides (d'Orbigny & Lafresnaye 1838)	VR		x,e
Diglossa cyanea (Lafresnaye 1840)	VR		x,e

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