

Research Article

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Ecology and distribution of the “Critically Endangered” Blue-throated Hillstar *Oreotrochilus cyanolaemus*

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Summary

The Blue-throated Hillstar *Oreotrochilus cyanolaemus* is a recently described hummingbird endemic to the southern Andes of Ecuador. This “Critically Endangered” species faces multiple conservation problems; thus, acquiring basic ecological information is a key step for guiding sound and integral conservation actions. We performed a series of expeditions throughout the cordillera Chilla-Tioloma-Fierro Urco to gain new data about its ecology, abundance, breeding, and distribution. From November 2019 to March 2020, we surveyed a total of 161.6 km searching for *O. cyanolaemus*, and gathered data on encounter rates, microhabitats used, and flower resources used. From November 2020 to January 2021 we studied the breeding ecology of the species. Occurrence records of *O. cyanolaemus* were used to build a species distribution model, based on climatic variables and the normalised difference vegetation index (NDVI). We found that the species is relatively more abundant in the western and central portion of its distribution range. Males were found using more shrubby habitats than females, who used more open habitats. They visited flowers of 11 plant species, with *Chuquiraga jussieui* and *Puya* ssp. being the most frequently used flowers. Nests were found in caves and rocky walls, and only one out of three active nests was successful. The distribution model indicated that the species has a potential distribution range of 62.7 km². This manuscript is the first comprehensive evaluation of the ecological requirements of the species, and the information provided has important potential for use as a conservation guide for the species and its habitats.

Introduction

Charismatic or flagship species may become critical pillars for conservation efforts (Welton *et al.* 2010, Bennett *et al.* 2015). When charismatic species are also new to science, they may generate the essential momentum needed to raise awareness and funding for conserving their habitat. If properly planned, these actions may also contribute to preserving endangered ecosystems, which benefits less charismatic organisms and habitat specialists, making those charismatic species conservation umbrellas (*sensu* Roberge and Angelstam 2004).

The Blue-throated Hillstar *Oreotrochilus cyanolaemus* is a recently described hummingbird endemic to the southern Andes of Ecuador (Sornoza-Molina *et al.* 2018), which could serve as a conservation umbrella for some of the last tracks of paramo grasslands in the region. This hummingbird is only known from the cordillera Chilla-Tioloma-Fierro Urco, a small mountain range isolated from the rest of the Andes by a rim of dryer and lower valleys. It inhabits paramo grasslands, where it is largely confined to stands of shrubby habitats with an important presence of *Chuquiraga jussieui* (Asteraceae) plants. Yet, the data available to date are insufficient for a proper assessment of its demography, natural history, and ecological requirements. This dearth of information has precluded planning and implementing sound and integral conservation actions.

The estimated geographical range of *O. cyanolaemus* is roughly smaller than 100 km², and its population has been broadly estimated at 250–750 individuals (Sornoza-Molina *et al.* 2018). The species is severely threatened by habitat loss and degradation caused by the transformation of paramo grasslands to cattle pastures, exotic tree plantations, and agricultural fields, and massive destruction by extensive fires during the dry season. Based on these threats, its small extent of occurrence, and its presumed small population size, Sornoza-Molina *et al.* (2018) proposed categorising it as “Critically Endangered”. This suggestion was backed up in the national Red Data List (Freile *et al.* 2019) and the global Red Data List (BirdLife International 2022). However, basic natural history knowledge is still needed for better assessing its distribution and ecological requirements, population size, and trends.

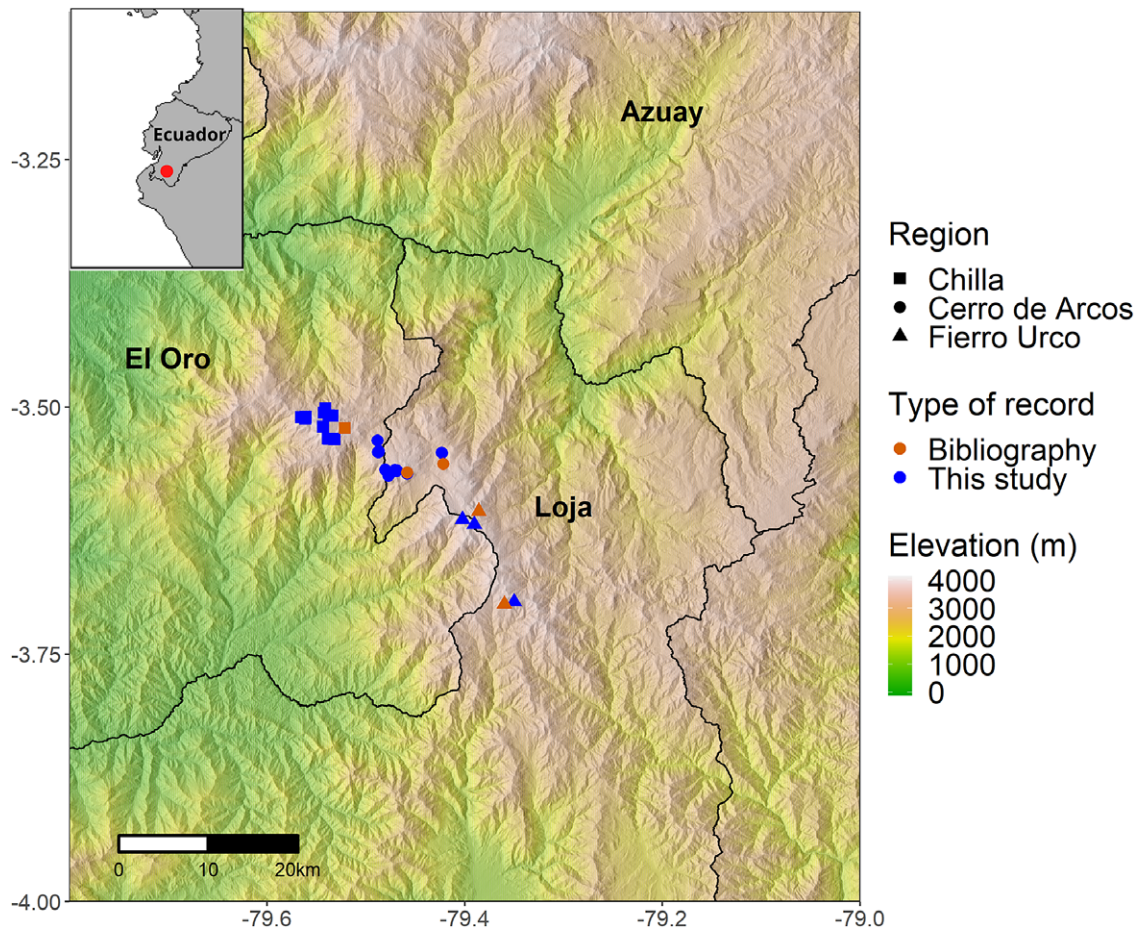


Figure 1. Study area and occurrences of *Oreotrochilus cyanolaemus* in three different regions in the cordillera Chilla-Tioloma-Fierro Urco. Occurrence records are overlaid on a digital elevation map. Symbols represent different regions within the cordillera, and colours depict if the occurrence records were obtained from published literature or from fieldwork carried out during this study.

Here, we significantly increase knowledge of the ecology, demography, and reproduction of *O. cyanolaemus*. We analyse encounter rates at three different regions, characterise the habitat use of males and females, as well as their preferred nectar sources, report on breeding ecology and reproduction success rates, and re-assess the potential distribution of the species. This information will be useful in designing and implementing specific conservation-oriented actions, and in moving forward towards more extensive monitoring efforts on population trends, reproduction success, phenology of resources, and habitat requirements.

Methods

Study site

The cordillera Chilla-Tioloma-Fierro Urco is a small mountain range separated from the main Andean chain by the low and dry valleys of the rivers León and Jubones to the north and east, and Catamayo-Puyango to the south (Sornoza-Molina *et al.* 2018). It is located within the provinces of Loja and El Oro, in southern Ecuador (Figure 1). This area is primarily covered by paramo grassland, with minor additional vegetation types including montane forests and shrublands. Plantations of the exotic *Pinus patula* tree and cattle pastures are also widespread throughout the study site. The climate is generally dry, with a marked drier and windier

period in June–August, and a wetter period in January–April (Oñate-Valdivieso *et al.* 2018).

Our study was conducted over two periods. In the first period, from November 2019 to March 2020, we performed bird surveys and gathered data on the ecology of the species. During the second period, from November 2020 to January 2021, we studied its breeding ecology.

Bird surveys and encounter rates

Previous knowledge about the preferred habitat and distribution of the species (Sornoza-Molina *et al.* 2018, Molina *et al.* 2021) was used to guide a series of expeditions throughout the cordillera Chilla-Tioloma-Fierro Urco, at elevations above 2,800 m. For logistical reasons, we divided the study area into three sections: west (hereafter called Chilla), centre (hereafter called Cerro de Arcos, a local name, in the Tioloma cordillera), and east (hereafter called Fierro Urco) (Figure 1). We visited sites with extensive coverage of paramo grasslands, patches of shrubby vegetation including *C. jussieui*, and areas with rocky outcrops considered potential nesting sites for the species. Given COVID-19 restrictions to mobility policies in Ecuador, sampling effort was irregular across the study period. In total, we were able to sample the region for 25 days: 9 at Chilla, 10 at Cerro de Arcos, and 6 at Fierro Urco. During each sampling day, two researchers walked over all available habitat types in the vicinity, keeping track of the distance covered

using a handheld GPS unit, and recording the number of individuals observed or heard. The total distance covered was 161.6 km (65.06 km at Chilla, 51.21 km at Cerro de Arcos, and 45.33 km at Fierro Urco), with a daily mean of 6.4 km (range = 2.66–17.9). Encounter rates per sampling day were obtained as the number of individuals recorded per km.

Ecological observations and habitat characterisation

We obtained behavioural data of each observed individual for as long as the bird was in view during our walks and recorded the following activities: foraging for nectar, foraging for arthropods, perching, and interactions with other hummingbirds. We classified the foraging methods as hovering or clinging (i.e. the bird grabbed the flower with its feet) in the case of nectar foraging, and sallying or hover gleaning when the bird was foraging for invertebrates. We also noted the plant species where the activity occurred. Based on plumage characteristics, each observed individual was classified as male or female (Sornoza-Molina *et al.* 2018). *O. cyanoaemus* acquires sexual dimorphism at the nestling stage (Molina *et al.* 2021), a characteristic that aided our classification; however, we could not visually age the observed individuals.

We also gathered detailed information about the microhabitat around each observed individual when the site was accessible to the researchers. This information was taken by placing a 20-m radius circular plot, centred on the first observation point of the focal individual. The microhabitat was characterised in terms of vegetation height, the number of shrubs, vertical heterogeneity of the vegetation, and coverage of different vegetation types, based on a protocol used in bird surveys (James and Shugart 1970). Vegetation height was obtained by estimating the mode of the height above the ground of the shrub layer within the plot. To measure the abundance of shrubs, we placed four 20-m transects directed north, south, east, and west from the centre of the plot. Next, we counted all the shrub stems that touched the extended arms of a person walking along each transect (the same person always took the data at a height above the ground of c.1.5 m). Using the same transects, the vertical heterogeneity of vegetation was measured by obtaining a vertical profile of the vegetation at sampling points located every 4 m along each transect. At each sampling point, we noted the presence/absence of vegetation in vertical sections of 0.5 m, starting at ground level and up to the tallest vertical section covered by vegetation. Then, the vertical heterogeneity of the vegetation was represented as a Shannon diversity index, based on the distribution of counts of sections covered with vegetation. Finally, coverage of different vegetation types within the plot was obtained by estimating the main vegetation type intersecting sections of 4 m along each transect of the four transects located inside the plot; vegetation types included were shrubs, trees, mosses, grasslands, rocks, and bare soil. A percentage of each vegetation type covering the plot was obtained by counting the number of sections occupied by each vegetation type in relation to the total number of sections sampled in a plot (20 sections).

Breeding ecology

From November 2020 to January 2021, we searched for nests of the species in caves and rocky walls in Chilla and Cerro de Arcos. When we found a nest, we revisited the site periodically to collect information about nesting success. In these searches, we also looked for old inactive nests, identified using previous knowledge about the species' nest (Molina *et al.* 2021). We gathered data about nest

location, height above the ground of nest, and if possible, nest morphology and materials (only in active nests). To inspect nests that were over 2 m above the ground we used climbing equipment.

Species distribution

We obtained occurrence localities from the literature (Sornoza-Molina *et al.* 2018), and from the surveys performed in this study. To model the species distribution (see below), we obtained 21 environmental variables of the study area, all downloaded from WorldClim, at a 30-second (~1 km²) resolution. These variables are related to different aspects of monthly temperature and precipitation between 1970 and 2000 (Fick and Hijmans 2017). We also acquired the normalised difference vegetation index (NDVI) from the MODIS terra satellite (Didan 2015), at a 250-m resolution, for every 16 days, starting from 1 January 2018 to 31 December 2020. This time frame covers the annual variability in NDVI related to variations of the local weather. The NDVI is correlated with above-ground primary productivity, and we used it here to capture differences in the vegetation across the study site. All the NDVI layers were averaged to obtain a mean NDVI per pixel. All the environmental variables were aligned and re-scaled at a resolution of 250 m per pixel, using the raster package (Hijmans and van Etten 2012) in R version 4.2.1 (R Core Team 2021).

Statistical analysis

Encounter rates

We compared encounter rates among Chilla, Cerro de Arcos, and Fierro Urco areas using a generalised linear model with a Poisson distribution of residuals and a log link (Zuur *et al.* 2009). The number of individuals encountered in each sampling day was used as response variable. To control for differences in sampling effort among days we used the distance covered each day as an offset. A post-hoc Tukey test was then used to test for pairwise differences between sampling areas.

Microhabitat and behaviour

We explored differences in the microhabitats used by individuals of different sexes. Significant variations in the coverage of vegetation types of microhabitats between sexes were evaluated with a chi-square test. We used single variate linear regression models to test for differences in the abundance of shrubs, the vertical heterogeneity of the vegetation, and vegetation height between microhabitats of males and females.

Differences in the species of flowers visited by males and females were determined with a chi-square test. To avoid non-independent observations of multiple foraging behaviours of a same individual, we only used the first foraging activity observed for the analysis (Hejl *et al.* 1990). Plant species were identified at a local herbarium, Herbario Azuay, at Universidad del Azuay. All visits to plant species with a single observation were grouped into a unique category named "Others".

Species distribution model

To obtain a more precise estimate of the distribution range and area occupied by *O. cyanoaemus* we created a species distribution model (SDM). The spatial extent of the model was limited by a 50-km buffer around the minimum convex polygon of all occurrence points of *O. cyanoaemus*. We excluded from this spatial extent areas with potentially suitable environmental conditions for the species (Sornoza-Molina *et al.* 2018), in which *O. cyanoaemus* has not been

recorded despite considerable survey effort invested and good quality information compiled out of the known range of the species (e.g. Cajas National Park, Astudillo *et al.* 2015; Podocarpus National Park, Ordóñez-Delgado *et al.* 2019). See Anderson and Raza (2010) for the rationale of excluding such areas. Within that polygon, we removed areas below 2,800 m elevation. The lowest elevation record for the species is 3,200 m; however, given the incomplete knowledge of the ecology of *O. cyanolaemus*, we decided to be conservative, and used a less restrictive threshold in our polygon. Occurrence records for *O. cyanolaemus* were processed to select records that were not within 1 km from each other, applying the function “thin” in the R package spThin (Aiello-Lammens *et al.* 2015), and chose the set of records that maximised the total number of occurrences. This filtering process reduced the potential autocorrelation of occurrence points (Aiello-Lammens *et al.* 2015). With no information about the home range of the species, the distance of 1 km for filtering the occurrences was chosen based on our field observations of foraging.

We used the machine-learning algorithm Maxent through the ENMeval package in R (Muscarella *et al.* 2014) to create the distribution model. Maxent is a machine-learning presence-only method that uses information of the environment at random background pixels, which are compared with the environment at pixels occupied by the focal species to produce a distribution model that maximises the entropy constrained by the known occurrences (Phillips and Dudík 2008). We generated 10,000 pseudo absences randomly created from the background polygon and created different models by changing the regularisation multipliers and feature classes. Regularisation multipliers penalise the complexity of the model, and we used values from 0.5 to 5 in steps of 0.5. Feature classes regulate the flexibility of the response to the predictor variables, and we used the following classes: L, LQ, H, LQH, LQHP: where L = linear, Q = quadratic, H = hinge, P = product. Model performance was assessed using the jackknife approach; this method uses all the occurrence records minus one in each interaction to train the model, and employs the withheld record for testing (Muscarella *et al.* 2014).

Model selection was based on Akaike’s Information Criterion corrected for small sample sizes (AICc), which favours the simplest models, and is robust to potential sampling bias in models with a low number of occurrence localities (Galante *et al.* 2018). Then, we evaluated model performance by calculating the area under the curve (AUC). These are methods that distinguish the ability of the model to discriminate between presence and background locations. Finally, we imposed a threshold to the continuous distribution model to create a map of presence/absence that allowed us to estimate the distribution range of the species. The threshold used was the 10 percentile value (i.e. 90% of the occurrence points contained within the predicted area), a somewhat conservative method but proper given the environmental complexity of the study area (Tinoco *et al.* 2009, Guevara *et al.* 2018).

Results

Relative abundance

Overall, we obtained 16 records of the species in Chilla, 19 in Cerro de Arcos, and 3 in Fierro Urco (Figure 1). Across the study area, the mean encounter rate was 0.35 (SE = 0.08) individuals/km. The encounter rate was higher in Cerro de Arcos and Chilla, compared with Fierro Urco (Figure 2, Table 1).

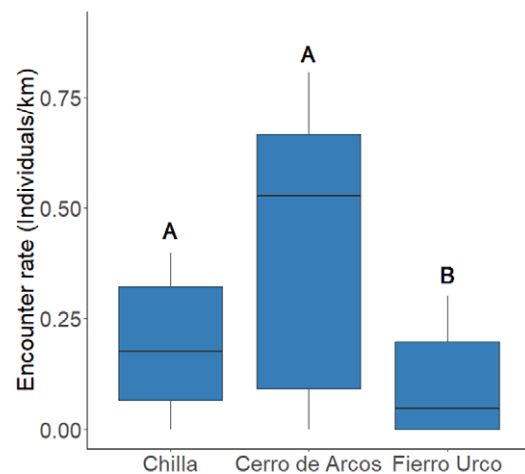


Figure 2. Mean and SE of encounter rates of *Oreotrochilus cyanolaemus* in different regions of its distribution. Different letters over the boxes indicate significant differences ($P < 0.05$) among regions tested with a post-hoc Tukey test.

Table 1. Results of a generalised linear model of encounter rates of *Oreotrochilus cyanolaemus* in different areas of the Chilla-Tiroloma-Fierro Urco mountain range, southern Ecuador. The intercept in the model corresponds to Cerro de Arcos.

	Estimate	SE	z value	P
Intercept	0.87	0.18	4.86	<0.01
Fierro Urco	-1.59	0.48	-3.29	<0.01
Chilla	-0.34	0.25	-1.34	0.18

Habitat characteristics

We obtained data for a total of 32 microhabitats (N males = 17, N females = 15). Males and females showed differences in the microhabitat used (Figure 3, Table 2). The microhabitat of males had a higher coverage of pastures, shrubs, and the ground bromeliad *Puya* species. (Bromeliaceae), while females used microhabitats with higher coverage of rocks ($\chi^2 = 142.15$, $df = 4$, $P < 0.01$) (Figure 3A). In terms of the vegetation structure, microhabitats of males had a higher abundance of shrubs (Figure 3B), and taller vegetation (Figure 3D); vertical complexity was similar between the microhabitats of males and females (Figure 3C).

Behaviour

We obtained 36 observations of nectar foraging, 21 for females, and 15 for males. *O. cyanolaemus* was found visiting flowers of 11 plant species: *C. jussieui* (Asteraceae), *Bomarea uncinifolia* (Alstroemeriaceae), *Puya hamata* (Bromeliaceae), *P. pygmaea* (Bromeliaceae), *Brachyotum* sp. (Melastomataceae), *Disterigma empetrifolium* (Ericaceae), *Macleania rupestris* (Ericaceae), *Castilleja fissifolia* (Orobanchaceae), *Clinopodium taxifolium* (Lamiaceae), *Oreocallis grandiflora* (Proteaceae), and *Ribes lehmannii* (Grossulariaceae). All those plants are native to the Ecuadorian paramo. The most frequently used resource was *C. jussieui* (16 visits); other important resources were *P. hamata* (eight visits) and *P. pygmaea* (four visits). All the other plant species were observed being used only once. There were some differences in resource use between females and males. In particular, males

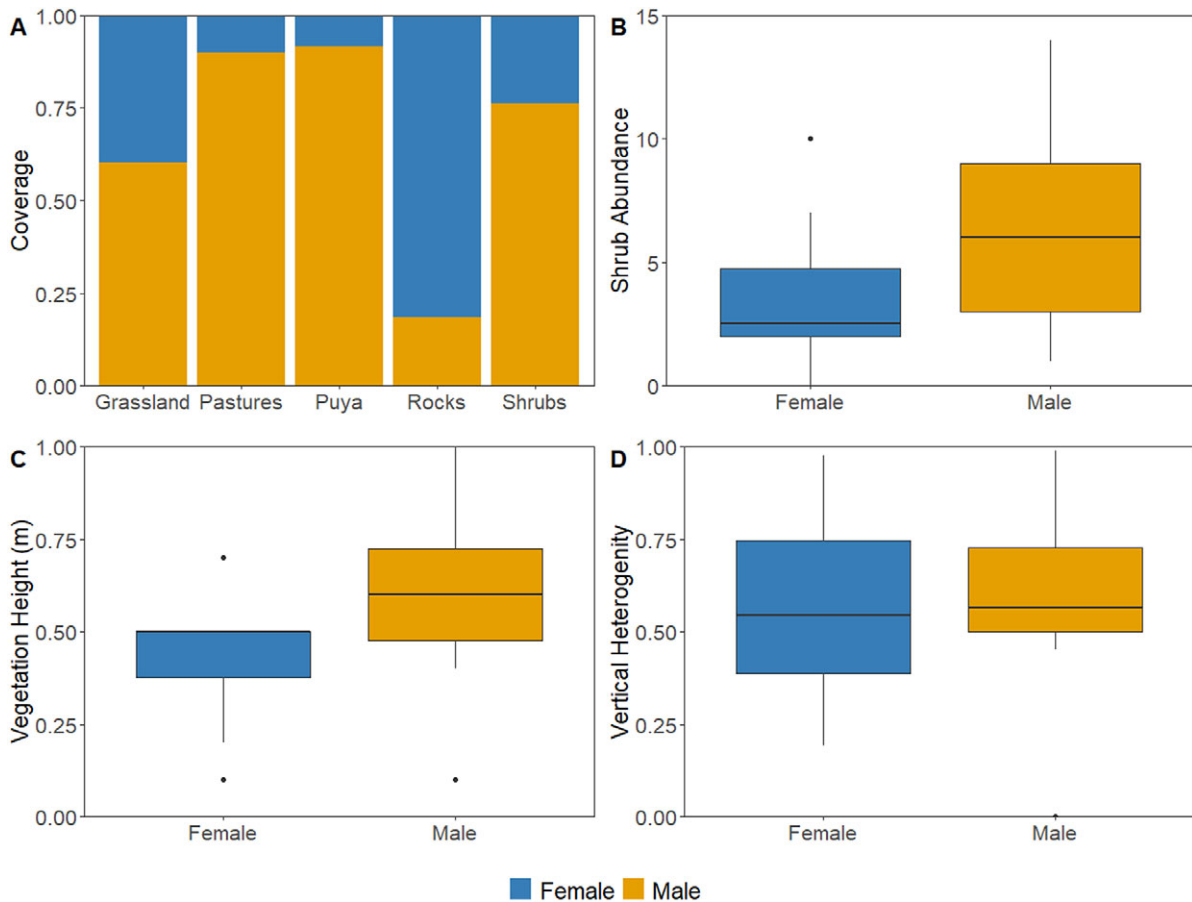


Figure 3. Microhabitat characteristics of female and male *Oreotrochilus cyanolaemus* individuals, measured inside 20-m radius circular plots, centred on the first observation point of focal individuals. (A) Frequency of the coverage of different vegetation types. (B) Abundance of shrubs. (C) Height of the vegetation. (D) Vertical heterogeneity measured by a Shannon diversity index.

Table 2. Results of linear regression models that test for differences in microhabitat characteristics used by females (intercept of the models) and males of *Oreotrochilus cyanolaemus* in different areas of the Chilla-Tioloma-Fierro Urco mountain range, southern Ecuador.

Microhabitat characteristic		Estimate	SE	<i>t</i> value	<i>P</i>
Number of shrubs	Intercept	1.4	0.23	6.1	<0.01
	Male	0.69	0.33	2.08	0.04
Vertical complexity	Intercept	0.69	0.11	6.53	<0.01
	Male	0.11	0.15	0.76	0.45
Vegetation height	Intercept	0.48	0.09	4.97	<0.01
	Male	0.32	0.14	2.29	0.02

showed a higher proportion of visits to *C. jussieui* (66.6% vs. 28.57%), while females showed a more diverse diet, with a similar proportion of visits to *C. jussieui*, *P. hamata*, and *P. pygmaea* (Figure 4). However, the proportion of visits to the different plant species did not differ statistically between sexes ($\chi^2 = 6.68$, $df = 3$, $P = 0.08$), probably because of the small sample size. In all foraging for nectar observations birds fed by clinging to the flower, except one that was hovering. We only obtained three observations of foraging for insects, and all were males that hovered gleaning from foliage. Perching sites were located at a mean height of 3.34 m ($N = 15$; range 1–4), and included rocks,

P. hamata, *C. jussieui*, *Gynoxys* sp. (Asteraceae), and the exotic tree *P. patula*.

Breeding

We found six nests, four in Chilla and two in Cerro de Arcos. Three of those nests were active and three were inactive old nests. Active nests were found between January and March. Four nests were placed in small ledges of rock walls, and two inside rocky caves (Table 3). The height above the ground of the nests ranged from 1.3 m to 8 m. The two nests found in Cerro de Arcos occupied the same

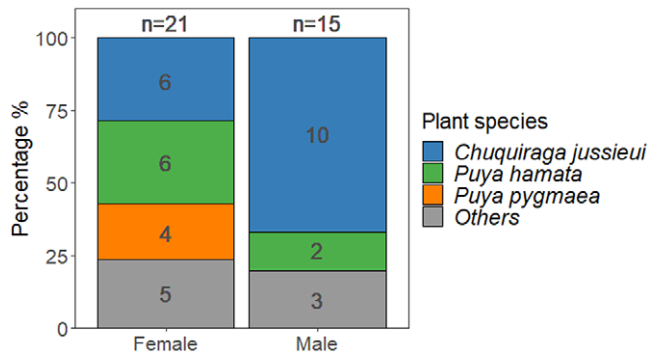


Figure 4. Proportions of visits to flowers of different plant species of male and female *Oreotrochilus cyanolaemus* individuals.

rock cave and were at c.1.5 m from each other. All nests were cup shaped, and were constructed with similar materials: an outer layer of mosses, small leaves, and twigs; an inner layer containing *Puya* downy fibres, and small black and white bird feathers (Figure 5). We were only able to measure one nest; it had an external diameter of 7 cm, internal diameter of 4 cm, depth of the nest chamber of 2 cm, and a height of 14 cm.

We observed three active nests that had either two eggs or two nestlings when found (Table 3). Only one was successful and produced two fledglings. The other two nests failed, one during the incubation period (indicated by egg remains) (Figure 5B), and in the second, fledglings were likely preyed upon (no remains found).

Distribution

Overall, we obtained 43 occurrence records of *O. cyanolaemus*, 38 gathered during our field work, and five compiled from the literature (Sornoza-Molina et al. 2018). All the occurrence records were at 3,250–3,800 m elevation, all within the Chilla-Tioloma-Fierro Urco range (Figure 1). However, only 19 records were used to model the species distribution after filtering out occurrences of sites closer than 1 km to each other. The best model was constructed with a regularisation penalty of 1.5 and a hinge feature class; this model had an AICc value of 327.53 (weighted AIC = 0.85) and an AUC value of 0.99. The SDM of *O. cyanolaemus* showed high suitability areas for the species exclusively in the Chilla-Tioloma-Fierro Urco mountain range, with a particular increase in suitability in its western and central region (Chilla and Cerro de Arcos) (Figure 6A). The final binary distribution model, depicting only

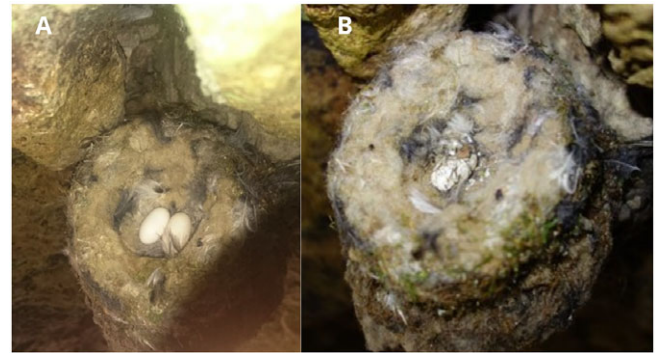


Figure 5. Nest of *Oreotrochilus cyanolaemus* containing two eggs when found on 19 January 2021 (A), and then on 21 January 2021 showing only egg remains (B).

areas with high suitability for the species (Figure 6B), indicated that *O. cyanolaemus* has a distribution range of 62.7 km².

Discussion

The successful and efficient conservation of a species is more likely accomplished if conservation actions are built upon sound science. Here we contribute basic information on the ecology and distribution of *O. cyanolaemus*, which can be used to guide conservation actions for this highly threatened species.

The differences in encounter rates among study areas indicated that *O. cyanolaemus* is more abundant in Cerro de Arcos and Chilla than in Fierro Urco. These differences could be related to low suitability of environmental conditions for the species in the eastern portion of its distribution. During our expeditions, we did not observe large shrubby patches, the main habitat for the species, in Fierro Urco. Thus, the populations of *O. cyanolaemus* are mainly concentrated in the western and central areas of the Chilla-Tioloma-Fierro Urco mountain range, with fewer individuals occupying Fierro Urco. It remains to be determined if the lack of shrubby habitats in Fierro Urco is natural or is the result of human disturbance. Such evaluation is critical to determine the potential value of that area for maintaining populations of the species. Yet, it is important to recall that our field surveys took place from November to March, leaving nearly six months unsampled. There could be potential seasonal movements of the species across its range that should be studied in the future.

Males and females used different microhabitats. Males occupied more shrubby microhabitats, with greater vegetation complexity

Table 3. Placement, contents, and fate of six nests of *Oreotrochilus cyanolaemus* found in Chilla-Tioloma-Fierro Urco mountain range, southern Ecuador.

Nest ID	Region	Encounter date	Nest placement	Condition of the nest when found	Height above the ground (m)	Outcome of the nest
1	Chilla	2 December 2019	Rock wall	Inactive	1.3	
2	Chilla	28 August 2020	Rock wall	Inactive	1.5	
3	Chilla	20 November 2020	Rock wall	Inactive	7	
4	Chilla	21 January 2021	Rock cave	Nest construction	5	Successful: two fledglings
5	Cerro de Arcos	19 January 2021	Rock cave	Two eggs found in the nest	5	Failed: eggs depredated
6	Cerro de Arcos	14 March 2021	Rock wall	Two fledglings	8	Failed: fledglings depredated

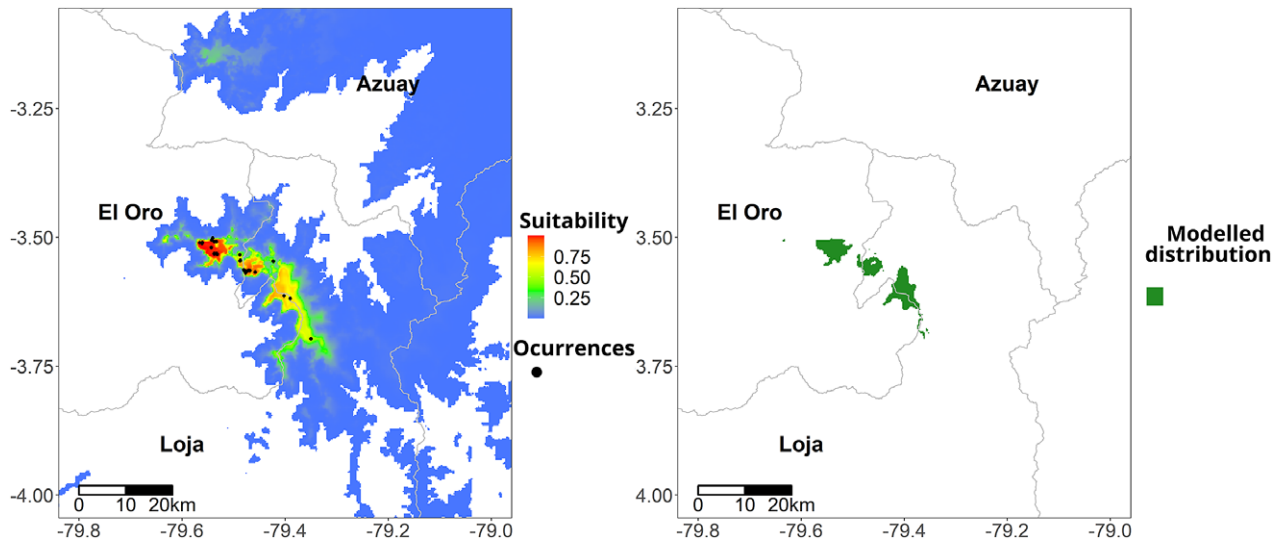


Figure 6. (A) Final model of suitable areas for *Oreotrochilus cyanolaemus* in south Ecuador. The predicted model was built using Maxent, with climatic variables and the normalised difference vegetation index (NDVI). (B) Binary map depicting the most suitable areas for the occurrence of *O. cyanolaemus*. This map was obtained after re-categorising the continuous suitability model using a threshold of 10 percentile value of pixels and it shows the estimated distribution range of the species.

compared with females, who used more open areas dominated by grasslands. Spatial segregation of habitats by sex is known in other species of *Oreotrochilus* (e.g. *O. chimborazo*, *O. estella*), in particular during the breeding period (Corley-Smith 1969, Carpenter 1976). However, habitat segregation by sex in *O. estella* is opposite to our findings, with females occupying shrubby habitats, and males using more open grasslands (Carpenter 1976). A more detailed study, exploring habitat use across time and breeding periods, and comparing between *Oreotrochilus* species, is needed to better understand this result.

The flowers of *C. jussieui*, *P. hamata*, and *P. pygmaea* were the most frequently used by *O. cyanolaemus*. *Chuquiraga* species are important resources for *Oreotrochilus* species, especially in the northern distribution of the genus (Corley-Smith 1969, Carpenter 1976, Ortiz-Crespo and Bleiweiss 1982). *C. jussieui* is a shrub with terminal flowers, which grows as monospecific patches or as part of shrubby patches. The high levels of dependency of *Oreotrochilus* on *Chuquiraga* apparently resulted from coevolutionary relationships between these two groups that have undergone a process of parallel adaptation to the harsh environmental relationships that dominate the high Andes (Abrahamczyk *et al.* 2017). We observed open flowers of *C. jussieui* throughout our study period, indicating that it can be a reliable food resource across the year. Nonetheless, phenological studies are needed to evaluate if there is seasonal variation in the phenology of *C. jussieui*, and if this variation could influence habitat use, movements, or reproduction of *O. cyanolaemus*.

Puya species have monocarpic arborescent rosettes with a terminal inflorescence (Varadarajan 1990, Jabaily and Sytsma 2013) that provide key nectar resources for many hummingbird species in the Andes (Hornung-Leoni *et al.* 2013, Restrepo-Chica and Bonilla-Gómez 2017). *P. hamata* has a tall inflorescence that can reach up to 4 m in height, and flowers that produce abundant nectar (Woods and Ramsay 2001). This species is well adapted to fires, with adults that can tolerate fires and seeds presenting high germination rates after paramo burning (García-Meneses and Ramsay 2014). This capacity to tolerate and even thrive after fires results in the development of *Puya* patches of different sizes within disturbed paramo grasslands (Miller and Silander 1991, Rivadeneira *et al.*

2020). Periodic paramo burning, used to stimulate regrowth of wild grasses for cattle ranching, is a common activity throughout the distribution range of *O. cyanolaemus*. Therefore, *P. hamata* might be a key resource for this hummingbird in human-altered areas. On the other hand, *P. pygmaea* presents a short, single inflorescence c.50 cm tall. We could not find ecological information about this species, but our observations indicate that it is present in low densities, scattered in rocky areas. It is worth noting that *Puya* plants have well-defined flowering phases in different seasons of a year (Restrepo-Chica and Bonilla-Gómez 2017, Varadarajan 1990), suggesting that the use of *Puya* species by *O. cyanolaemus* might be seasonal. This study was not designed to assess temporal variation in resource use of *O. cyanolaemus*, and we suggest it as a research priority to better assess key plant species needed for sustaining viable populations of *O. cyanolaemus*.

Clinging was the main foraging for nectar behaviour, as has been reported for other *Oreotrochilus* species (Carpenter 1976, Fjeldså and Krabbe 1990). Clinging for feeding saves energy, compared with hovering (Feinsinger and Colwell 1978), which can be advantageous for hummingbird species occupying high elevations in the Andes; reduced air density and low oxygen partial pressure impose significant metabolic constraints (Altshuler and Dudley 2003). The long tarsi and hallux claw of *Oreotrochilus* hummingbirds are advantageous for clinging to flowers (Carpenter 1976, Fjeldså and Krabbe 1990).

Only one of three active nests successfully produced two juveniles. The reproductive success of *Oreotrochilus* has been considered high as a result of low depredation pressure in the high Andes (Corley-Smith 1969). For instance, 16 out of 18 nests of *O. estella* were successful in the Andes of Peru (Carpenter 1976). In our study, the two nests that failed were likely attacked by predators (Table 3). Given the location of nests high in rocky walls, we suspect that avian predators were responsible. The Black-billed Shrike-Tyrant *Agriornis montanus* and the Great Thrush *Turdus fuscater* are nest predator species (Menezes and Marini 2017) that are common in our study area. In terms of nest placement and architecture, our nests were generally similar to those reported for other *Oreotrochilus* species (Dorst 1962, Langer 1973, Carpenter 1976, Areta *et al.* 2006), including a previous description of a *O. cyanolaemus* nest

(Molina *et al.* 2021). Like the nests we found, *Oreotrochilus* species nest in sites protected from harsh environmental conditions prevalent in the high Andes, such as caves and rock wall cracks (Dorst 1962, Carpenter 1976, Bodrati *et al.* 2003, Areta *et al.* 2006). Some *Oreotrochilus* use human infrastructure as nesting sites, including buildings and bridges (Carpenter 1976, Solano-Ugalde 2008), increasing the availability of nesting sites in human-altered areas; we unsuccessfully searched for nests in such places, indicating that *O. cyanolaemus* may only use natural support. Overall, it remains to be determined which factors are involved in breeding success of *O. cyanolaemus*, how females select nesting sites, and if there is a strong competition for such sites. Lastly, all active nests were found during the rainy season (January–March), corresponding with previous observations on the species (Molina *et al.* 2021), and similar to other bird species in the paramos of southern Ecuador (Ortiz-Crespo 2000, Carrasco-Ugalde *et al.* 2022).

Our estimated geographical range of *O. cyanolaemus* is smaller than previously thought (Sornoza-Molina *et al.* 2018), suggesting that finer resolution data and more locality records provide more accurate distribution estimations. The small distributional range of *O. cyanolaemus*, one of the smallest ranges in the Trochilidae occurring in mainland South America, is likely the result of a complex geological history that includes the uplift of Andean mountain ranges and the emergence of low valleys where drier climates prevail (Sornoza-Molina *et al.* 2018). Our modelling provides evidence that environmental conditions are not even across the Chilla-Tioloma-Fierro Urco mountain range, and that the species is more likely found in the central and western portions of this range. The Chilla-Tioloma-Fierro Urco range might act as a barrier for humidity moving eastwards from the Pacific Ocean, resulting in rain-shadowed valleys to the east of this range (Oñate-Valdivieso *et al.* 2018). Consequently, its easternmost portion is influenced by the drier climate of the inter-Andean valley (Oñate-Valdivieso *et al.* 2018), which precludes the occurrence of optimal habitat for *O. cyanolaemus*. However, we want to highlight that our distribution range comes from a modelling procedure that has strengths and weaknesses (see Phillips and Dudik 2008, Syfert *et al.* 2013), and future studies, with refined modelling techniques (e.g. presence/absence models), should validate our findings. We also expect that data on new occurrence localities for the species, during months not covered by this study, will improve our knowledge of the distribution range and ecology of *O. cyanolaemus*.

Conservation

O. cyanolaemus is considered a “Critically Endangered” species at the national (Freile *et al.* 2019) and international levels (BirdLife International 2022), the latter assessment based on an estimate of 80–110 mature individuals, living in one subpopulation, i.e. criterion C2a(ii). Although our field methods do not allow for calculations of absolute population size, we generally agree with that estimation. Given the extensive survey effort we performed across the entire known distributional range of the species, and the amount of remaining shrubby habitat in the paramo of the region, we do not expect that large new populations of *O. cyanolaemus* will be found. Moreover, our encounter rates and habitat suitability model indicate that the western and central portions of its distribution (Chilla and Cerro de Arcos areas) are likely the most important for the species, and conservation efforts should focus on those areas.

The species’ population is considered to be declining because of habitat loss. Long-term monitoring is desirable to understand the

extent of this purported decline, and the effects that habitat loss and degradation have on the species survival. Likewise, immediate conservation actions are critical beyond land purchase and protection, as small preserves will not safeguard the entire range of the species, which is pivotal to prevent further population declines. Large-scale conservation planning involving local communities and promoting local pride for the species, i.e. using *O. cyanolaemus* as a conservation emblem for the region, as has already been done by local initiatives, is recommended, along with further studies of its ecology and its responses to habitat and climatic changes. Our observations on the habitat used by males and females, along with nesting microhabitat, will aid ongoing and future efforts to seclude shrubby habitat patches, and to control camping activities and fires in potential and known nesting sites. Further, our information on the main feeding plants can be crucial for habitat restoration efforts, both assisted restoration and natural regeneration, with the caveat that we still lack phenological information about plants and the temporal variations in visits by *O. cyanolaemus*. We suggest further ecological studies about this “Critically Endangered” species aiming to understand key questions like breeding success, population demography and trends, seasonal differences in habitat use, and its specific responses to habitat change.

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References

- Abrahamczyk, S., Poretschkin, C. and Renner, S. S. (2017) Evolutionary flexibility in five hummingbird/plant mutualistic systems: testing temporal and geographic matching. *J. Biogeogr.* **44**: 1847–1855.
- Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B. and Anderson, R. P. (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* **38**: 541–545.
- Altshuler, D. L. and Dudley, R. (2003) Kinematics of hovering hummingbird flight along simulated and natural elevational gradients. *J. Exp. Biol.* **206**: 3139–3147.
- Anderson, R. P. and Raza, A. (2010) The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. *J. Biogeogr.* **37**: 1378–1393.
- Areta, J. I., Vila Moret, S., Mazar Barnett, J. and Casañas, H. (2006) Primer registro de nidificación del Picaflor Andino Castaño (*Oreotrochilus adela*) en la Argentina. *Nuestras Aves* **51**: 21–23.
- Astudillo, P. X., Tinoco, B. A. and Siddons, D. (2015) The avifauna of Cajas National Park and Mazán Reserve, southern Ecuador, with notes on new records. *Cotinga* **37**: 1–11.
- Bennett, J. R., Maloney, R. and Possingham, H. P. (2015) Biodiversity gains from efficient use of private sponsorship for flagship species conservation. *Proc. R. Soc. Lond. B Biol. Sci.* **282**: 20142693.
- BirdLife International (2022) Species Factsheet: *Oreotrochilus cyanolaemus*. Accessed online 10 January 2022 from www.birdlife.org.
- Bodrati, A., Mérida, E. and Montenegro, L. (2003) Nidificación del picaflor andino común (*Oreotrochilus leucopleurus*) en el parque nacional El Leoncito, provincia de San Juan, Argentina. *Nuestras Aves* **45**: 26–28.
- Carpenter, F. L. (1976) Ecology and evolution of an Andean hummingbird (*Oreotrochilus estella*). Berkeley, CA, USA: University of California Press.

- Carrasco-Ugalde, A., Molina, P., Pacheco, D. and Tinoco, B. (2022) Nesting biology of an Ecuadorian endemic hummingbird, the endangered Violet-throated Metal-tail *Metallura baroni*. *Rev. Ecuatoriana Ornitol.* **8**: 31–40.
- Corley-Smith, G. T. (1969) A high altitude hummingbird on the volcano Cotopaxi. *Ibis* **111**: 17–22.
- Didan, K. (2015) MYD13Q1 MODIS/Terra Vegetation Indices 16-Day L3 Global 250m. Sioux Falls, SD, USA: NASA EOSDIS Land Processes DAAC.
- Dorst, J. (1962) Nouvelles recherches biologiques sur les Trochilidés des hautes Andes péruviennes (*Oreotrochilus estella*). *Oiseau* **32**: 95–126.
- Feinsinger, P. and Colwell, R. K. (1978) Community organization among Neotropical nectar-feeding birds. *Am. Zool.* **18**: 779–795.
- Fick, S. E. and Hijmans, R. J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**: 4302–4315.
- Fjeldså, J. and Krabbe, N. (1990) *Birds of the high Andes*. Copenhagen, Denmark: Zoological Museum, University of Copenhagen; Svenborg, Denmark: Apollo Books.
- Freile, J. F., Santander, T., Carrasco, L., Cisneros-Heredia, D. F., Guevara, E. A., Sánchez-Nivicela, M. and Tinoco, B. A. (2019) *Lista roja de las aves del Ecuador continental*. Quito, Ecuador: Ministerio del Ambiente, Aves y Conservación, Comité Ecuatoriano de Registros Ornitológicos, Universidad del Azuay, Red Aves Ecuador and Universidad San Francisco de Quito.
- Galante, P. J., Alade, B., Muscarella, R., Jansa, S. A., Goodman, S. M. and Anderson, R. P. (2018) The challenge of modeling niches and distributions for data-poor species: a comprehensive approach to model complexity. *Ecography* **41**: 726–736.
- García-Meneses, P. M. and Ramsay, P. M. (2014) *Puya hamata* demography as an indicator of recent fire history in the páramo de El Ángel and Volcán Chiles, Ecuador-Colombia. *Caldasia* **36**: 53–69.
- Guevara, L., Gerstner, B. E., Kass, J. M. and Anderson, R. P. (2018) Toward ecologically realistic predictions of species distributions: a cross-time example from tropical montane cloud forests. *Glob. Chang. Biol.* **24**: 1511–1522.
- Hejl, S. J., Verner, J. and Bell, G. W. (1990) Sequential versus initial observations in studies of avian foraging. *Stud. Avian Biol.* **13**: 166–173.
- Hijmans, R. J. and van Etten, J. (2012) raster: Geographic Analysis and Modeling with Raster Data. R package version 2.0-12.
- Hornung-Leoni, C. T., González-Gómez, P. L. and Troncoso, A. J. (2013) Morphology, nectar characteristics and avian pollinators in five Andean *Puya* species (Bromeliaceae). *Acta Oecol.* **51**: 54–61.
- Jabaily, R. S. and Sytsma, K. J. (2013) Historical biogeography and life-history evolution of Andean *Puya* (Bromeliaceae). *Bot. J. Linn. Soc.* **171**: 201–224.
- James, F. C. and Shugart Jr, H. H. (1970) A quantitative method of habitat description. *Audubon Field Notes* **24**: 727–736.
- Langer S. (1973) Zur Biologie des Hochlandkolibrius *Oreotrochilus estella* in den Anden Boliveins. *Bonn. Zool. Beitr.* **24**: 24–47.
- Menezes, J. C. T. and Marini, M. Á. (2017) Predators of bird nests in the Neotropics: a review. *J. Field Ornithol.* **88**: 99–114.
- Miller, G. A. and Silander, J. A. (1991) Control of the distribution of giant rosette species of *Puya* (Bromeliaceae) in the Ecuadorian paramos. *Biotropica* **23**: 124–133.
- Molina, P. A., Pacheco, D. O., Carrasco, A. and Tinoco, B. A. (2021) On the breeding biology of the Blue-throated Hillstar (*Oreotrochilus cyanolaemus*), a recently discovered species from southern Ecuador. *Wilson J. Ornithol.* **132**: 1007–1014.
- Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M. and Anderson, R. P. (2014) ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods Ecol. Evol.* **5**: 1198–1205.
- Oñate-Valdivieso, F., Fries, A., Mendoza, K., González-Jaramillo, V., Pucha-Cofrep, F., Rollenbeck, R. and Bendix, J. (2018) Temporal and spatial analysis of precipitation patterns in an Andean region of southern Ecuador using LAWR weather radar. *Meteorol. Atmos. Phys.* **130**: 473–484.
- Ordóñez-Delgado, L., Ramón-Vivanco, C. and Ortiz-Chalán, V. (2019) Systematic review of the state about the knowledge of the vertebrates of the Podocarpus National Park. *La Granja* **30**: 7–18.
- Ortiz-Crespo, F. (2000) The nest of the Rainbow Star-frontlet, *Coeligena iris*. *Bull. Br. Ornithol. Club* **120**: 205–208.
- Ortiz-Crespo F. and Bleiweiss R. (1982) The northern limit of the hummingbird genus *Oreotrochilus* in South America. *Auk* **99**: 376–378.
- Phillips, S. J. and Dudík, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**: 161–175.
- R Core Team (2021) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.
- Restrepo-Chica, M. and Bonilla-Gómez, M. A. (2017) Dinámica de la fenología y visitantes florales de dos bromelias terrestres de un páramo de Colombia. *Rev. Mex. Biodivers.* **88**: 636–645.
- Rivadeneira, G., Ramsay, P. M. and Montúfar, R. (2020) Fire regimes and pollinator behaviour explain the genetic structure of *Puya hamata* (Bromeliaceae) rosette plants. *Alp. Bot.* **130**: 13–23.
- Roberge, J. M. and Angelstam, P. (2004) Usefulness of the umbrella species concept as a conservation tool. *Conserv. Biol.* **18**: 76–85.
- Solano-Ugalde, A. (2008) High in the Andes: colonial nesting of Ecuadorian Hillstar (*Oreotrochilus chimborazo*: Trochilidae) under a bridge. *Ornitol. Colomb.* **6**: 86–88.
- Sornoza-Molina, F., Freile, J. F., Nilsson, J., Krabbe, N. and Bonaccorso, E. (2018) A striking, critically endangered, new species of hillstar (Trochilidae: *Oreotrochilus*) from the southwestern Andes of Ecuador. *Auk* **135**: 1146–1171.
- Syfert, M. M., Smith, M. J. and Coomes, D. A. (2013) The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS One* **8**: e55158.
- Tinoco, B. A., Astudillo, P. X., Latta, S. C. and Graham, C. H. (2009) Distribution, ecology and conservation of an endangered Andean hummingbird: the Violet-Throated Metal-tail (*Metallura baroni*). *Bird Conserv. Internatn.* **19**: 63–76.
- Varadarajan, G. S. (1990) Patterns of geographic distribution and their implications on the phylogeny of *Puya* (Bromeliaceae). *J. Arnold Arbor.* **71**: 527–552.
- Welton, L. J., Siler, C. D., Bennett, D., Diesmos, A., Duya, M. R., Dugay, R., Rico, E. B. R., et al. (2010) A spectacular new Philippine monitor lizard reveals hidden biogeographic boundary and a novel flagship species for conservation. *Biol. Lett.* **6**: 654–658.
- Woods, S. and Ramsay, P. M. (2001) Variability in nectar supply: implications for high-altitude hummingbirds. Pp. 209–217 in P. M. Ramsey ed. *The ecology of Volcán Chiles: high-altitude ecosystems on the Ecuador-Colombia border*. Plymouth, UK: Pebble and Shell.
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. and Smith, G. M. (2009) *Mixed effects models and extensions in ecology with R*. New York, USA: Springer.