PONTIFICIA UNIVERSIDAD CATÓLICA DEL ECUADOR

FACULTAD DE CIENCIAS EXACTAS Y NATURALES

ESCUELA DE CIENCIAS BIOLÓGICAS

Description and Conservation status of a new subspecies of *Xenodacnis parina* (Aves: Thraupidae) from the Ecuadorian Andes.

Tesis previa a la obtención del título de

Magíster en Biología de la Conservación

JUAN MANUEL AGUILAR ULLAURI

Quito, 2016

Certifico que la tesis de Maestría en Biología de la Conservación del candidato Juan Manuel Aguilar Ullauri ha sido concluida de conformidad con las normas establecidas; por lo tanto, puede ser presentada para la calificación correspondiente.

Tjitte de Vries

Director de Tesis

Quito, 31 de Marzo 2016

ACKNOWLEDGEMENTS

This study was made with financial aid from EcoCiencia, EcoFondo and PBIC-CTA. I thank Andrea Nieto for field assistance, Daniel Rivas for bioacoustics instructions, John V. Moore and Niels Krabbe for song information; and also Francisca Hervas, Luna Figuero, Dolly Muñoz, Diego Pacheco, Juan F. Freile, Francisco Sanchez and Boris A. Tinoco for support and contributions to this manuscript; also thanks to Diego García Olaechea from the CORBIDI museum staff at Lima Peru. This investigation benefited from the direction of Tjitte de Vries, and the reviews from Santiago Burneo and Alejandra Camacho, all generously contributed with this manuscript.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

1. ABSTRACT

Xenodacnis is a Thraupid genus distributed in tropical high Andes. Its single member, *X. parina*, occurs in disjunct Andean ranges along paramo in southern Ecuador to puna from southern Peru. The population in Ecuador is separated by ca. 450 km from the nearest populations in Peru and its taxonomic affinities have not been evaluated since its discovery in 1980s at Cajas National Park. There are no major morphometric and plumage coloration differences reported in the genus *Xenodacnis*, I use criteria from integrative taxonomy to show that the isolated population from Ecuador withholds environmental and male song differences, compared to Peruvian subspecies, suggesting a different taxonomic treat, that was confirmed with morphometric differences, reporting bigger sizes; all these criterion place *Xenodacnis parina* from Ecuador as the most distinct member of the species. I propose this new subspecies of *Xenodacnis parina* and use new information to evaluate its conservation status according to the IUCN Red List criteria.

Key words: Andes, new subspecies, paramo, puna, taxonomy, *Xenodacnis*.

2. RESUMEN

Xenodacnis es un género de Tráupido distribuido en los altos Andes tropicales. Su único miembro, *X. parina*, ocurre en rangos discontinuos a lo largo de los Andes en los páramos del suroeste del Ecuador y la puna del Perú. La población en Ecuador está separada por aproximadamente 450 km de la población más cercana en el Perú, y sus afinidades taxonómicas aún no han sido evaluadas desde su descubrimiento en los años 1980s en el Parque Nacional Cajas. Sin mayores diferencias en medidas morfométricas y de color del plumaje reportadas en el género Xenodacnis, se recurrió a criterios de la taxonomía integrativa para demostrar que la población aislada de Ecuador muestra diferencias ambientales y en los cantos de los machos, comparada con las subespecies del Perú; sugiriendo un trato taxonómico diferente, lo que se confirmó con diferencias morfométricas, reportando tamaños más grandes; todos estos criterios dejan a la población de *Xenodacnis parina* de Ecuador como el miembro con más diferencias dentro de la especie. Propongo una nueva subespecie de *Xenodacnis parina* y uso la nueva información generada para evaluar su estado de conservación de acuerdo a los criterios de la lista roja de la IUCN.

Palabras clave: Andes, nueva subespecie, páramo, puna, taxonomía, *Xenodacnis*.

3. INTRODUCTION

In avian taxonomy, comparative morphology has been the most valid criteria to define species limits under the biological species concept (Sangster 2014, Padial et al. 2010). In mountain ranges such as the Andes, bird speciation is mostly allopatric (Fjeldså et al. 2012) and morphological differences are not always evident (Winger and Bates 2015, Gutiérrez-Pinto et al. 2012). This has lead to an underestimation of species diversity, and morphologically cryptic species are often incorrectly lumped under a single species with presumptive widespread distribution (e.g. Avendaño et al. 2015, Lara et al. 2012).

The integrative taxonomy employs independent criteria, such as environmental, bioacoustics or morphological characters to define species limits (Gill 2014, Sangster 2014, Dayrat 2005). When analyzed, these criterions can also explain the origin, evolutionary trajectory and distribution of populations (Gill 2014). Integrative taxonomy allows the application of explicit protocols to discriminate between candidate species and deep intraspecific lineages (Padial et al. 2010, Vieites et al. 2009).

Some bird species populations, in separate mountains along high Andes have been traditionally regarded as single polytypic species (Fjeldså et al. 2012, Sedano and Burns 2010, Helbig et al. 2002, Weigend 2002). They are often isolated and adapted to local conditions and resources with the consequent niche differentiation among mountains (Fjeldså et al. 2012, Vuilleumier 1969). These differentiated “populations” are in fact diagnosable, as independent evolutionary lineages that could be granted species status (Andersen et al. 2014). These differences in bird species composition have already been described between the Andes from northern Peru and Southern Ecuador (Cabot and de Vries 2009).

Xenodacnis parina (Cabanis 1873, Passeriformes, Thraupidae) is an Andean species inhabiting isolated mountain ranges that could represent a complex of two or more species. It is distributed discontinuously in Ecuador and Peru between 3000 and 4400 m (Hilty 2011). Its diet is specialized and consists on small insects and extra floral nectar found beneath the leaves of *Gynoxys* shrubs (Compositae) (Aguilar and Iñiguez 2015, Ridgely and Greenfield 2001). It was described by Cabanis in 1873 with the type locality "Maraynioc", Junín department, in central Peru (Ortiz 2002, Bond and Meyer de Schauensee 1939). Later, Bond and Meyer de Schauensee (1939) described a different species from the northern Andes of Peru: *Xenodacnis petersi*, with two subspecies, *X. petersi petersi* (type locality Yánac, Ancash department, west central Peru) and *X. petersi bella* (type locality Atuén, Amazonas department, northern Andes Peru). Zimmer (1942) and Zimmer and Mayr (1943) established size and color as diagnosable differences, with greater sizes in *X. petersi*. With no further revisions on the genus, *X. petersi* has remained as a junior synonym of *X. parina* (Zimmer and Mayr 1943); currently considered a single species with three subspecies (*X. parina bella*, *X. parina parina* and *X. parina petersi*), reported in Amazonas, Ancash, Apurimac, Arequipa, Ayacucho, Cajamarca, Cuzco, Junín and Lima departments in Peru (Gill and Donsker 2014, Remsen et al. 2013, Hilty 2011, Schulenberg et al. 2007).

Ridgely (1980) reported *X. parina* from southern Ecuador in Azuay province at Cajas National Park (Figure 1), a 2130 km^2 isolated mountain massif of paramo with numerous valleys and lakes (Beltrán et al. 2009). He did not assign the population as a subspecies but Hilty (2011) mentioned that it may be referable to *X. parina bella*. Due to the lack of information on the Ecuador population, its taxonomic status is uncertain (Ridgely and Greenfield 2001), and considered endangered in the country (Ortiz 2002), although locally abundant, the species is consider globally under least concern conservation status (BirdLife International 2015.

Across the Andes, the distribution of *Xenodacnis* is interrupted by a low and dry region, known as the North Peru Low, between 3° S and 8° S (Figure 1). It starts with the depression of the Jubones River valley and ends at the Huancabamba River valley with the elevation of northern high Andes of Peru (Weigend 2004, Weigend 2002); The North Peru Low has been proposed as an important barrier for the dispersion of birds along the Andes (Winger and Bates 2015, Gutiérrez-Pinto et al. 2012, Parker et al. 1985, Vuilleumier 1969).

In allopatry, bird morphologic differences have been linked with ecological differences like resource acquisition (Tobias et al. 2014); in species with specialized diets, conserved morphologic traits may reflect ecological adaptation (Winger and Bates 2015), making difficult to establish morphologic variation across North Peru Low (Gutiérrez-Pinto et al. 2012, Parker et al. 1985). To give *Xenodacnis parina* from Ecuador a proper taxonomic identity, distribution, environmental niche, bioacoustics and morphologic criterion suggested by Gill (2014) need to be addressed. Environmental niche models have been useful to analyze distribution differences and predict potential occurrences of Andean bird species (Jiguet et al. 2010), which contributes to establish distribution range and to help evaluate conservation status using IUCN Red List Criteria (IUCN 2012). Furthermore, song analysis is also useful to asses taxonomic status in birds (Gill 2014, Sangster 2014), since there is evidence that most genetically distant species present more divergent songs (Sosa-López et al. 2015).

To assign a taxonomic identity and conservation status to *Xenodacnis* population from El Cajas, Ecuador, distribution, environmental and song analysis needs to be accompanied by morphology and plumage coloration differences, which are defining current intra specific limits in *Xenodacnis* subspecies from Peru (Zimmer and Mayr 1943, Zimmer 1942, Bond and Meyer de Schauensee 1939).

4. MATERIALS AND METHODS

4.1 POPULATION SAMPLING

Data from *Xenodacnis* in Ecuador was generated in five daily visits to Cajas National Park, in 2014 (Permiso de investigación: 001-20l4-SGA-PNC-BD-FA-Aguilar), and one previous survey from 2010. Song recordings, and occurrence coordinates, were gathered during fieldwork; morphometric data came from 30 hours of mist netting, capturing and measuring individuals in one day survey; also two individuals were collected; tissue samples and skins were placed at the Museum of Zoology, Pontificia Universidad Católica del Ecuador (QCAZ); some individuals were found dead on the road, if possible, I took measures and prepared the skins in the Museo de Zoología de la Universidad del Azuay, but these individuals were not considered for analysis; Additional data on Ecuador population came from previous studies on this population (Aguilar and Iñiguez 2015) and occurrence localities of *Xenodacnis* from Peru and Ecuador were obtained from online resources (eBird 2012). *X. parina* adult male recordings were downloaded from Xeno-canto Foundation (http://www.xeno-canto.org/) and from Macaulay Library from Cornell Lab Ornithology (http://macaulaylibrary.org/). Morphometric data from *X. parina* subspecies from Peru came from CORBIDI museum specimens at Lima Peru.

4.2 ENVIRONMENTAL NICHE MODELING

Environmental niche models were used to define geographic distribution of suitable environmental conditions among different *Xenodacnis* subspecies from Peru and El Cajas population from Ecuador. Environmental niche models were based on 19 bioclimatic variables, obtained from WorldClim (www.worldclim.org), which included seasonality, averages and extremes in temperature and precipitation across Central and South America (Hijmans et al. 2005) at a resolution of 30 seconds. To avoid spatial autocorrelation, I excluded occurrences within the same locality, separated by distances less than 5 km. Niche models were obtained with a maximum entropy algorithm as implemented in MAXENT v.3.3.3k (Phillips et al. 2006). For all models we used default parameter settings; to test model performance we evaluate if 30% of randomly selected points are predicted by a model performed with remaining fraction of data, with a 10 replicate bootstrap; obtaining a maximum possible test value of the area under the ROC curve (Test AUC). Binary maps of presence and absence of suitable habitat conditions were based on the equal training sensitivity and specificity threshold (Phillips et al. 2006). I obtained one environmental niche model for the species; one for each subspecies from Peru and one for the populations in El Cajas, Ecuador; we also obtained one model with all *Xenodacnis parina* subspecies data from Peru. I created maps showing the distribution of suitable environmental conditions under Equal training sensitivity and specificity threshold from models.

To analyze differences in environmental conditions between Ecuador and the other populations of *X. parina*, I characterized the climate envelope of each group by extracting the bioclimatic values at each occurrence locality. Values from 19 variables were synthesized with a principal components analysis (PCA).

4.3 BIOACOUSTICS ANALYSIS

Song quantitative variables were measured from spectrograms (DFT size = 512 samples) using software Raven v.1.4 (Cornell Lab of Ornithology, Ithaca, New York, USA, 2011). Analysis was performed considering previous work from Bolus (2014) and Lara et al. (2012). We quantified independent sounds in spectrograms as elements within notes, arranged in different phrases and calculated: (1) number of elements (E), (2) mean number of elements per note (E/N), (3) notes per phrase (N/P), (4) element rate (E/T), (5) song duration (T) and (6) the presence of a “rasp” element at the beginning or end of a song (R), in most cases this rasp element was lost spectrogram analysis, but its presence or absence was considered an informative character.

To compare variable response of taxonomic groups, we carried out a PCA with all six variables; first two components were plotted within minimum convex polygons for each population data group; we also tested variables for statistical differences.

4.4 MORPHOLOGICAL VARIATION

Measurements considered are unflattened wing chord, tail from the insertion of the central rectrices to their tips, tarsus, exposed culmen from feather edge to bill tip, bill width and bill depth at nares, measured with a digital Caliper (range: 0-150 mm, accuracy: ± 0.02 mm) following Baldwin et al. (1931) proceedings and suggestions from Winker (1998); weight was also considered. Sex was determined by plumage color dimorphism, and morphological differences between sexes were also analyzed to establish sexual dimorphism characteristics.

Measurements of the *X. parina* population from Ecuador were compared with measurements from six museum specimens of *X. parina* subspecies from Peru and four individuals from Ecuador, all with all with data on six variables included in a PCA and the first two components from analysis were plotted with minimum convex polygons for each sex from each subspecies to illustrate differences between individuals and subspecies; I also tested measurements for statistical differences; and discus this data with morphological measurements given in Bond and Meyer de Schauensee (1939). Color was compared using digital photographs made in the field and museum collections.

4.5 CONSERVATION STATUS

The Red List category of *Xenodacnis* from Ecuador was assessed under the UICN criteria version 3.1 (IUCN 2012): population size reduction (UICN criteria "A"), geographic range (UICN criteria "B") and small population size (UICN criteria "C"). For the assessment we considered confirmed locations, and estimated the extent of occurrence (EEO) and area of occupancy (AOO; IUCN 2012) by measuring the area of a minimum convex polygon generated from all 35 reported localities gathered initially, and the area within extent of occurrence corresponding to Paramo Evergreen Shrub and Grasslands, which includes *Gynoxys* species, and occupies 2054 km^2, mostly in the Andes southwestern Ecuador, according to Ministerio de Ambiente (2013) classification system; I also calculated the area of Paramo Evergreen Shrub and Grasslands overlapping environmental niche model.

To infer population size, I used abundance data from Tinoco et al. (2013), that established a mean of 0.541 individual in 0.2 ha point counts (s.d. ± 1.59), along 20 localities with Paramo Evergreen Shrub and Grasslands at Cajas National Park. Finally, I replicated a 30 hour/net survey from 2010 (Aguilar and Iñiguez 2015) at Ilincocha, Cajas National Park (2°46,8'S; 79°13,86'W), which along with individuals found dead on the road dividing Cajas National Park, allowed to infer changes in population size. All the information generated helped to identify principal treats for the species.

5. RESULTS

5.1 POPULATION SAMPLING

A total of 60 presence localities of *Xenodacnis* were established (Appendix 1): 22 records of *X. parina parina*, 27 of *X. parina petersi*, only three of *X. parina bella* and eight for El Cajas population in Ecuador; one not yet confirmed record from Morona-Santiago Province at Valle de Collanes was also gathered and will not be considered until further confirmation. I obtained 18 individual male recordings shown in Appendix 2; new recordings made during field work were uploaded to Xeno-cato foundation; and gathered measurements of 62 individuals of *Xenodacnis* (Appendix 3) including some additional individuals found dead on Cajas National Park, all measures were not available for some individuals, due to feather molting or because bird were stressed when captured.

5.2 ENVIRONMENTAL NICHE MODELING

Environmental niche model for *X. parina* show the predicted distribution range for the species (Figure 2(A); n = 60, ETSS = 0.296, Test AUC = 0.984), models show the geographic isolation between populations with the distribution of suitable conditions for the Ecuadorian population isolated in Ecuador (Figure 2(B); n = 8, ETSS = 0.477, Test AUC = 0.999) and like ways the model considering all *X. parina* subspecies from Peru with suitable environmental conditions restricted to Peru (Figure 2(B); n = 52, ETSS = 0.251, Test AUC = 0.972), the distance between suitable habitats in El Cajas, Ecuador and Peru from these last two models is 300 km. Environmental niche models from subspecies in Peru show absence of suitable conditions in Ecuador for *X. parina parina* from southern Peru (Figure 2(C and D); n= 22, ETSS = 0.318, Test AUC = 0.975), but show that *X. parina petersi* (Figure 2(C and D); n = 27, ETSS = 0.083, Test AUC = 0.995), presents suitable environmental conditions in Ecuador but these areas hardly overlap *Xenodacnis* from Ecuador niche model. Moreover, *X. parina bella* model could not be tested since this subspecies has only three occurrence localities (Figure 2(C and D); n = 3, ETSS = 0.618) and therefore the model is inaccurate.

The first two components of PCA of bioclimatic variables (Figure 3, Table 1) explain 75% of variance; first component explains 38.8% and has high loadings on precipitation seasonality, daily temperature range and temperature annual range. The second component explains 36.7% of the variation and has the highest loadings in mean temperature of coldest quarter, minimum temperature of the coldest month, and mean temperature of driest quarter. Overall, populations from El Cajas occupy an environmental envelope characterized by higher minimum annual and seasonal temperatures, and higher precipitation, different to environmental conditions from occurrences of subspecies in Peru.

5.3 BIOACOUSTICS ANALYSIS

Measurements of individual male song recordings (Table 2) show that the population from Ecuador has less complex songs with 10 to 12 elements and no more than five notes. Southern songs are more elaborated; *Xenodacnis parina bella* and *X. parina petersi* have similar songs (16 to 29 elements), meanwhile *X. parina parina* has more than 30 elements. These elements also differ between subspecies, rasp element starting songs was audible but did not persisted in all spectrograms (Figure 4: A, B and E), however it was included in song length, as it appeared only on one *X. parina parina* song and all *X. parina* from El Cajas.

The PCA for six acoustic variables is shown in Figure 5, explained 71% of the variation (PC 1 = 47.8%, PC 2 = 23.27%). The PCA shows a separation in acoustic space (Figure 5, Table 3) between Ecuador and other subspecies. First component is mainly represented by the number of elements, followed by presence of rasp element; second component is constructed by song density variables: mean number of elements per note (E/N) and mean number of notes per phrase (N/P). *X. parina petersi* songs are more similar to songs from Ecuador, but maintain statistical differences in number of elements ($t = 3.733$, $p = 0.013$, $n = 6$) and mean number of notes per phrase ($t = 3.199$, $p = 0.02$, $n = 6$), but not in song duration ($t = 2.085$, $p = 0.091$, $n = 6$), explaining more notes per song in similar times.

5.4 MORPHOLOGICAL VARIATION

Ecuador population sexual morphologic dimorphism is shown in Table 4; measurements show that Males are heavier than females ($t = -5.96$, $p = 0.001$, $n = 14$); also, have larger wing chord ($t = -7.54$, $p = 0.0009$, $n = 15$), tail ($t = -6.445$, $p = 0.0001$, $n = 15$) and tarsus ($t = -4.513$, $p = 0.0004$, $n = 15$). Moreover, bill measurement, exposed culmen ($t = -0.2218$, $p = 0.8387$, $n = 4$), bill width ($t = 0$, $p = 1$, $n = 4$), and depth ($t = -1.26$, $p = 0.296$, $n = 4$), do not show differences between sexes. Color sexual dimorphism consists in lustrous prussian blue males with bluish grey under tail coverts. Females are less colorful with prussian blue restricted to the face (chin, lares, orbital feathers and forecrown), bluish grey dorsum, orange throat and breast turning pale brown towards the vent and under the tail covers (Figures 6 and 7); and both sexes have black bill, eye, and legs.

Wing chord is the only information complete for all individuals; statistical differences were analyzed only between six individuals of the *petersi* group and six *Xenodacnis* from El Cajas (three males and three females); bill sizes showed that exposed culmen does not vary (male: $t = 3.027$, $p = 0.099$, $n = 3$; Female: $t = 3.547$, $p = 0.711$, $n = 3$), bill depth varies only in females (male: $t = 3.471$, $p = 0.073$, $n = 3$; Female: $t = 4.697$, $p = 0.042$, $n = 3$), and bill width is different in both sexes (male: $t = 13.17$, $p = 0.005$, $n = 3$; Female: $t = 5.763$, $p = 0.02$, $n = 3$). Also *Xenodacnis* from Ecuador has a bigger wing chord (male: $t = 6.135$, $p = 0.025$, $n = 3$; Female: $t = 6.74$, $p = 0.021$, $n = 3$) and tarsus (male: $t = 7.143$, $p = 0.019$, $n = 3$; Female: $t = 5.52$, $p = 0.03$, $n = 3$); tail was only compared for females and did not prove differences ($t = 3.78$, $p = 0.063$, $n = 3$). Moreover, weight was only analyzed for males, and present the most notorious difference ($t = 10.22$, $p = 0.009$, $n = 3$) between the *petersi* group and *Xenodacnis* from El Cajas, Ecuador.

Since weigth First component of PCA explain 81% variation, and second component 12% considering all six variables from 14 individuals (Table 5), three body size measurements shows that *Xenodacnis* from Ecuador is bigger and the most different form of *Xenodacnis*; second component of PCA is mainly influenced by bill measurements especially by exposed culmen (Figure 8).

5.5 CONSERVATION STATUS

The main threat is the widespread destruction of montane shrubs, fragmentation of *Polylepis* woodlands, afforestation with exotic tree species; and the presence of roads.

X. parina in Ecuador is restricted to 8 locations of Paramo Evergreen Shrub and Grassland, most within Cajas National Park (Fig. 9; 285.4km²), placing it as an important area for its conservation. Area of occupancy is 8.9 km^2, within 285 km^2 of estimated extent of occurrence. Area of Paramo Evergreen Shrub and Grassland overlapping environmental niche model give a population size of 15 959 individuals; however, 2 407 individuals were calculated within area of occupancy; and 77 092 individuals within the estimated extent of occurrence.

Moreover, with a main road across Cajas National Park since 2012, traffic has increased, and we found eight road kills, mainly adult individuals (four adult males, three adult females, and one juvenile), this leads to assume that the number of mature individuals is in constant decline. Replicated mist netting survey in Cajas National Park after a five year period, showed population reduction, with 15 individuals (6 males, 7 females and 2 juveniles) captured in 2010 compared to eight individuals (3 males, 3 females and 2 juveniles) captured in 2014, just 53% of individuals after 4 years, recapturing one banded male that persisted in territory.

Criteria analyzed place *Xenodacnis parina* population from El Cajas, Ecuador, threatened as critically endangered: B2 (a)(b)(v) + c(iv); mainly because it occupies an area (< 10 km²) severely fragmented by roads with an observed decline number of mature individuals.

5.6 TAXONOMIC REVIEW

Morphologic, plumage coloration, bioacoustics and environmental differences, all suggest that the Ecuadorian populations of *Xenodacnis* represent a separate lineage from

Xenodacnis parina described subspecies; more resembled to *petersi* group: *X. parina petersi* and *X. parina bella* (Hilty 2011, Zimmer and Mayr 1943, Zimmer 1942, Bond and Meyer de Schauensee 1939). Niche models also reveal geographic and environmental isolation between Ecuador and the Peruvian populations. The large geographic distance between suitable habitats in both ranges (~300 km) could explain the larger divergence within the genus. Niche models predict overlapping areas between subspecies in Peru (Figure 2) with their environmental and acoustic multivariate space overlapping or adjacent (Figures 3 and 5); therefore, results confirm subspecies status, correctly lumped under a single species.

Songs differ between described subspecies and the population from Ecuador; songs from *X. parina petersi* and *X. parina bella* confirmed their close taxonomic relation. Songs from southern subspecies, *X. parina parina*, confirm its taxonomic distinctiveness and PCA proves that the population of Ecuador is more related to the *petersi* group (Bond and Meyer de Schauensee 1939).

In concordance to bioacoustics and environmental differences; morphological analysis present heavier and larger sizes in *Xenodacnis parina* from Ecuador, also more resembled to the *petersi* group (Bond and Meyer de Schauensee 1939), than to *X. parina parina*. Plumage coloration in males is very similar within the species, mostly lustrous prussian blue, with grayish on vent and anal region (Figures 6 and 7). Female color presents differences, *X. parina parina* females have a full blue cape, different from the crown color pattern from Ecuador and the *petersi* group from northern Peru (for color references see: Schulenberg et al. 2007). However, female color in *X. parina petersi* and *X. parina bella* has more violet blue on chin, also throat and chest are dull ferruginous and abdomen under tail covers are buffy yellow (Bond and Meyer de

Schauensee 1939), different from orange throat and pale brown abdomen and under tail covers of *X. parina* from Ecuador (Figures 6 and 7).

Since Ridgely (1980) reported *X. parina* in southern Ecuador, the taxonomic identity of this population has remained uncertain. Results show geographical consistency in morphology, plumage coloration, environmental niche modeling and bioacoustics analysis, suggesting that the population from Ecuador is the most distant within the genus and does not belong to *X. parina bella*, as stated by Hilty (2011); however, is closest related to the *petersi* group. All information gathered suggests that *Xenodacnis parina* from el Cajas, Ecuador could be defined as different from all described members of the species, and that a taxonomic identity should be granted.

6. DISCUSSION

In allopatry, bird phenotype is not always coherent with species limits (Gutiérrez-Pinto et al. 2012, McKitrick and Zink 1988, Parker et al. 1985), as in the genus *Xenodacnis*. We analyze alternative taxonomic criteria and prove that *X parina* from El Cajas Ecuador and *X. parina* subspecies from Peru, exhibit essential reproductive isolation and would not interbreed if they occur in sympatry (Gill 2014). The criteria used, successfully define subspecies limits for *X. parina* in Ecuador, showing unusual characteristics within the genus, compared to related *Xenodacnis* that coexist in the Andes of Peru. Minor phenotype differences could be explained by a recent colonization, shared foraging ecology and similar ecosystems (Winger and Bates 2015, Tobias et al. 2014).

Information gathered suggests that ancient *Xenodacnis* expanded north, accumulating few phenotype differences due to events of vicariance and co-occurrence during orogeny along new high Andean ecosystems (Winger and Bates 2015, Tobias et al. 2014, Weir 2009). The *petersi* group most likely colonized El Cajas mountain massif heading north through western Andes, in a vicariant event of dispersion followed by isolation, during late Miocene (Weir 2009); and allopatry between *X. parina* from Peru and *X. parina* from Ecuador started 2.7 Ma when northern Andes had already reached modern elevations (Gregory-Wodzicki 2000), and an active Andean drainage systems had already shaped the North Peru Low (Garzione et al. 2008); consequently alike other Andean taxa, speciation occurred during Pleistocene climatic oscillations (Chaves et al. 2013, Lutz et al. 2013, Campagna et al. 2011, Jiguet et al. 2010, Bonaccorso 2009). The areas where high Andean bird species remained isolated during Pleistocene climatic events, had ideal conditions for long-term survival, and birds specialized, to become abundant and a vital element of local fauna (Fjeldså et al. 2012).

Environmental distribution models for *X. parina bella* and *X. parina petersi*, have suitable environmental conditions to occur in Ecuador, leading to assume that before the North Peru Low split current high Andean ecosystems distribution, a population of an ancient *Xenodacnis* of the *petersi* group spread north along favorable environmental conditions, reaching Northern Andes. However, maximum entropy models, all supported current isolation by distance (Wright 1943) with the North Peru Low as a >300 km gap in distribution of *Xenodacnis*; in concordance with other examples of Andean bird allopatric speciation which confirm the North Peru Low as an ecological barrier for Andean birds (Jiguet et al. 2010, Bonaccorso 2009).

Separate niche models for each *X. parina* subspecies from Peru show continuous sympatric areas between them along the Andes (Figure 2), suggesting these populations may have sympatric areas of occurrence. Moreover, due to restricted distributions, and insufficient information on some populations, perhaps in the future, with more localities reported, we could generate a better prediction of *X. parina bella* distribution range. In Ecuador *Xenodacnis* is found at altitudes between 3300 m and 4100 m; very restricted compared to *Xenodacnis* in Peru, ranging from 2000 m to 4800 m. The continuous sympatric areas predicted for subspecies along the Andes of Peru and the wide altitudinal range (Figure 2), suggests these population may have interbred recently, and should be left as subspecies until molecular data is analyzed.

Environmental differences show clear separation between puna in Central Andes from Peru and paramo from Cajas mountain massif at Northern Andes; the variables that best explained *Xenodacnis* suitable habitat were seasonal precipitation and temperature values; this is congruent to differences between humid paramo and puna, which is more seasonal and xeric (Tovar et al. 2013, Luteyn 1999), proving isolation by environment (Wang and Bradburd 2014). Moreover, the models showed that *X. parina* from Ecuador could also occupy suitable environmental conditions outside current range in Ecuador, and suggest the need for further explorations to confirm northern occurrence of the species. Finally, more than 200 occurrence records were gathered for *X. parina* from El Cajas Ecuador, and an estimated the extend of occurrence based on IUCN (2012) from all these records; furthermore, all occurrences fall within only eight named localities established in Cajas mountain massif (Figure 9). The northern and not yet confirmed record in Morona-Santiago Province at Valle de Collanes (Apendix 1); does not overlap any model for habitat suitability or ecosystems from this analysis.

Song analysis helped to establish an initial rasp note as the most notable and diagnosable difference in *X. parina* acoustic repertory. Song elaborateness, demonstrate geographic concordance, finding more elaborated songs in *X. parina parina*, and the simplest songs in *X. parina* from El Cajas Ecuador; one basic song element for identification from El Cajas is the presence of rasp note to start songs, while in Peruvian populations is uncommon and usually precedes more elaborated central notes of the song. We did not evaluate element types, but each population presented unique elements, more similar among songs from Peru (Figures 4 and 5).

Xenodacnis parina allopatric subspecies prove that in environments with similar selection pressures, bird species do not accelerate phenotypic divergence by divergent selection (Winger and Bates 2015). Morphologically, data from Bond and Meyer de Schauensee (1939) also place the Ecuadorian population as heavier and with larger wing chord and tarsus (only the tale is larger in X. *parina petersi*; according to: Bond and

Meyer de Schauensee 1939). The southernmost and smallest form is *X. parina parina* (Zimmer 1942, Bond and Meyer de Schauensee 1939). Measurements support environmental and song analysis, showing that the Ecuadorian population is the most distinct form of *Xenodacnis parina* (Fig. 8); *X. parina* males from El Cajas Ecuador, have developed greater sizes, weighing almost twice compared with males from other subspecies (Appendix 3), and lighter fledgling individual found at Cajasis is heavier than all adult *X. parina* individual from Peru.

Molecular information on *X. parina* from El Cajas Ecuador is available from Burns (1997) LSUMZ B7760; and phylogeny presented by Burns et al. (2014) and Barker et al. (2012), place it with *Phrygilus*, *Idiopsar*, *Diuca*, *Haplospiza*, and *Acanthidops* (Passeriformes: Thraupidae); in a clade of Andean specialist (Campagna et al. 2011). Due to the presence of sympatric areas for subspecies in Peru, higher genetic distances across North Peru Low should be expected (Gutiérrez-Pinto et al. 2012).

The taxonomic analysis presented, proposes *X. parina* from El Cajas Ecuador as a new subspecies, endemic to El Cajas mountain massif in Ecuador, specialized in feeding by gleaning on foliage of *Gynoxys cuicochensis* (Aguilar and Iñiguez 2015), a endemic plant from Ecuador (Montúfar and Pitman 2003), suggesting that *Xenodacnis parina* in Peru interacts with different resources; these specialized interactions suggest a reduction in the ability of the species to move through the landscape and support isolation by environment, two drivers of speciation in tropical Andes (Winger and Bates 2015, Smith et al. 2014, Wang and Bradburd 2014).

Being a mono-specific genus, *Xenodacnis* taxonomic limits still need to be addressed; we suggest *X. parina* from El Cajas Ecuador should be granted subspecies status, since there is evidence of speciation, placing *X. parina* population from El Cajas, Ecuador, as the most distinct within this genus. Splitting *Xenodacnis* will also contribute to paramo and puna conservation; this new subspecies along with Violet throated metaltail (*Metallura baroni*), also a Cajas massif endemic (Tinoco et al. 2009), place Cajas plateau as an endemic bird area EBA, with two endemic bird lineages with limited distribution within it (Herzog et al. 2012); the area has previously been identified as a key area for conserving the avifauna of *Polylepis* forests, where extra conservation efforts are needed (Fjeldså 2002). *Xenodacnis* from El Cajas has been considered endangered in Ecuador (Ortiz 2002), however, with more information, our evaluation suggests critically endangered category (B2 (a)(b)(v) + c(iv)); criterion mainly involved an area of occupancy (Figure 9: < 10 km^2) severe fragmented by roads (IUCN 2012; criteria B). Furthermore, observed population size reduction (IUCN 2012; criteria A) and small population size criteria (IUCN 2012; criteria C), place the species as endangered. Road kills found in Cuenca-Guayaquil highway, situate the roads shown in figure 9, as a major threat for this subspecies.

Ornithology has provided arguments from ecological and physiological effects of current climate change on wildlife (Crick 2004), some mountain species environmental tolerance thresholds have modified their distribution and this could lead to local extinctions (Wilson et al. 2005, Crick 2004); being a top Andean specialist, the case of *X. parina* from El Cajas Ecuador could be of peculiar interest to study and monitor climate change and habitat transformation effects on Andean birds.

7. CONCLUSION

X. parina population from El Cajas Ecuador is the more distinct form, within the *Xenodacnis* genus; which main area of conservation is Cajas National Park (Ortiz 2002); threats are widespread destruction of paramo and montane shrubs and fragmentation of *Polylepis* woodlands; moreover, the road Cuenca-Guayaquil dividing Cajas National Park is considered a major threat for the species. Currently under least concern conservation criteria (BirdLife International 2015), granting *Xenodacnis* population from El Cajas a taxonomic identity involves assists the conservation criterion, reinforces the endemic bird pattern for Cajas mountain massif, and provides a contribution to understand high Andean bird speciation patterns and the mechanisms that lead the avian diversity of the region. Type localities for described *Xenodacnis parina* subspecies fall within the Peruvian distributions ranges. Therefore, we conclude that *Xenodacnis* from el Cajas Ecuador represents a subspecies not yet described; for which I give a proper description in the following section.

8. SUBSPECIES DESCRIPTION

Xenodacnis parina cajaensis subsp. nov.
Azulito del Cajas (Spanish name)
Cajas Dacnis (English name)

Holotype. Adult male: QCAZ 4624 (dry skin and tissue), collected at Toreadora, El Cajas National Park, Azuay, Ecuador (2.7833 S; 79.2166 W, elevation ~4000 m). Collected and prepared by Juan M. Aguilar on June 12, 2014. Tissue samples are available as QCAZ 4624, and type locality male song as XC203152.

Diagnosis. The subspecies shows geographic isolation, is restricted to shrubby vegetations with *Gynoxis cuicochensis* in Ecuadorian southwestern paramo, *Xenodacnis parina cajaensis* subsp. nov. is more similar to the *petersi* group (*X. parina bella*, and *X. parina petersi*). Differences in color are appreciable on female, with Orange throat and pale brown vent in *Xenodacnis parina cajaensis* subsp. nov., different from ferruginous vent in all *X. parina* subspecies from Peru. Adult male song is a short series of liquid whistles (five to nine notes in two phrases), usually preceded by a hissing rasp element, absent in different and more elaborated songs of other *X. parina* subspecies,. *Xenodacnis parina cajaensis* subsp. nov. inhabits paramo ecosystem with different environmental conditions than others *X. parina* subspecies that inhabit puna ecosystem. *Xenodacnis parina cajaensis* subsp. nov. is more similar to closer geographic relatives; however, the *petersi* group (*X. parina bella*, and *X. parina petersi*) is more related to *X. parina parina*; pointing *Xenodacnis parina cajaensis* subsp. nov. as the biggest subspecies weighting as much as twice compared to Peruvian relatives; and besides geographic distribution, size as the most diagnosable intra-specific characteristic.

Etymology. *Xenodacnis* comes from Greek, *xeno* meaning something strange, different or foreign; and Dacnis as a different genus in Thraupidae, composed mainly by bluish species. Parina is the specific name; and the intra specific epithet cajaensis refers to the location where *Xenodacnis* is found in Ecuador.

Holotype Description. Male; color above is lustrous prussian blue with some black on few wing covers and edges of all primary and secondary edges and tail feathers; ventral region is grayish with deep violet-blue in vent feathers edges, turning darker bellow rump and under tail coverts, has grey anal region; also has black bill, eye, and legs. Mass, 23.1 g; unflattened wing chord, 81.5 mm; tail, from the insertion of the central rectrices to their tips, 65 mm; tarsus, 28.9 mm; exposed culmen, 8.2 mm; bill width, 5 mm; bill depth at the base 4,3 mm.

Designation and description of paratypes. Adult female: QCAZ 4625 (skin and tissue), collected at Toreadora, El Cajas National Park, Azuay, Ecuador (2.7833 S; 79.2166 W, elevation ~4000 m) and prepared by Juan M. Aguilar on June 12, 2014; mass, 18 g; wing (chord), 75 mm; tail, from the insertion of the central rectrices to their tips, 60 mm; tarsus, 26.7 mm; exposed culmen,7.9 mm; bill with, 4.6 mm; bill depth at the base, 4.4 mm. the specimen shows prussian blue chin, lares, orbital feathers and fore crown, with few blue feathers extending irregularly through crown, nape and coverts, on a bluish grey back, color on throat and breast is orange with whitish vent and under tail covers; both sexes have black bill, eye and legs. Additional paratypes are: adult male: MZUA.AV.000013 (dry skin) and Adult female: MZUA.AV.000037 (dry skin) from El Cajas National Park, Azuay, Ecuador (2.7767 S; 79.2595 W, ~4000 m). Collected and prepared by JMA on June 12, 2014.

Distribution and Ecology. Endemic from Ecuador inhabits Paramo Evergreen Shrub and Grasslands at Cajas mountain massif plateau from 3300 to 4100 m. at the south western edge of the northern Andes, between the Cañar River to the north, Jubones River in the south, Giron-Paute inter Andean valley in the east, and western Andean slope. *Xenodacnis parina cajaensis* subsp. n. feeds on mites and extra floral nectar secretions under neath the leaves of *Gynoxys cuicochensis* shrubs, always in small territorial groups; presents sexual color dimorphism with bigger males, more conspicuous and vocal than females. Juveniles resemble females but with irregular molt patterns.with males. Presence of brood patches indicate reproductive seasons in September and June, with chicks found in September.

9. LITERATURE CITED

Andersen, M.J., Nyári, Á.S., Mason, I., Joseph, L., Dumbacher, J.P., Filardi, C.E. and Moyle, R.G. 2014. Molecular systematics of the world's most polytypic bird: the *Pachycephala pectoralis*/*melanura* (Aves: Pachycephalidae) species complex. Zoological Journal of the Linnean Society 170 (3): 566-588.

Aguilar, J.M. and Iñiguez, X. 2015. *Xenodacnis* (*Xenodacnis parina*) un ave especialista en los páramos del sur oeste del Ecuador. Ornitología Neotropical 26:1-70.

Avendaño, J.E., Cuervo, A.M., López-O J.P., Gutiérrez-Pinto, N., Cortés-Diago, A., Cadena, C.D. 2015. A new species of tapaculo (Rhinocryptidae: Scytalopus) from the Serranía de Perijá of Colombia and Venezuela. The Auk 132 (2): 450-466.

Baldwin, S.P., Oberholser, H.C. and Worley, L.G. 1931. Measurements of birds. Scientific Publication Cleveland Museum of Natural History II. Oxford, Mississippi, USA.

Barker, F.K., Burns, K.J., Klicka, J., Lanyon, S.M. and Lovette, I.J. 2012. Going to extremes: contrasting rates of diversification in a recent radiation of new world passerine birds. Systematic biology 62 (2): 298-320.

Beltrán, K., Salgado, S., Cuesta, F., León-Yánez, S., Romoleroux, K., Ortiz, E., Cárdenas, A. and Velástegui, A. 2009. Distribución Espacial, Sistemas Ecológicos y Caracterización Florística de los Páramos en el Ecuador. EcoCiencia, Proyecto Páramo Andino y Herbario QCA. Quito, Ecuador.

Birdlife International. 2015. Species factsheet: *Xenodacnis parina*. http://www.birdlife.org

Bolus, R.T. 2014. Geographic variation in songs of the Common Yellowthroat. The Auk 131: 175-185.

Bonaccorso, E. 2009. Historical Biogeography and Speciation in the Neotropical Highlands: Molecular Phylogenetics of the Jay Genus *Cyanolyca*. Molecular Phylogenetics and Evolution 50: 618-632.

Bond, J. and Meyer de Schauensee, R. 1939. Description of New Species and Subspecies of *Xenodacnis*. Notulae naturae of the Academy of Natural Sciences of Philadelphia 40: 1-2.

Burns, K.J., Shultz, A.J., Title, P.O., Mason, N.A., Barker, F.K., Klicka, J., Lanyon, S.M. and Lovette, I.J. 2014. Phylogenetics and diversification of tanagers (Passeriformes: Thraupidae), the largest radiation of Neotropical songbirds. Molecular Phylogenetics and Evolution 75: 41-77.

Burns, K.J. 1997. Molecular systematics of tanagers (Thraupinae): evolution and biogeography of a diverse radiation of neotropical birds. Molecular Phylogenetics and Evolution 8 (3): 334-348.

Cabot, J. and de Vries, T. 2009. A new subspecies of Gurney's Hawk *Buteo poecilochrous*. Bulletin of the British Ornithologists' Club 129 (3): 149-164.

Campagna, L., Geale, K., Handford, P., Lijtmaer, D.A., Tubaro, P.L. and Lougheed, S.C. 2011. A molecular phylogeny of the Sierra-Finches (*Phrygilus*, Passeriformes): extreme polyphyly in a group of Andean specialists. Molecular Phylogenetics and Evolution 61: 521-533.

Chaves, J.A., Hidalgo, J.R. and Klicka, J. 2013. Biogeography and evolutionary history of the Neotropical genus *Saltator* (Aves: Thraupini). Journal of Biogeography 40: 2180-2190.

Crick, H.Q.P. 2004. The impact of climate change on birds. Ibis 146: 48-56.

Dayrat, B. 2005. Towards integrative taxonomy. Biological Journal of the Linnean Society 85: 407-415. DOI: 10.1111/j.1095-8312.2005.00503.x

eBird. 2012. eBird: An online database of bird distribution and abundance [on-line application]. eBird, Ithaca, New York. Available at http: // www.ebird.org [Assessed 10 July 2015]

Fjeldså, J., Bowie, R.C.K. and Rahbek, C. 2012. The role of mountain ranges in the diversification of birds. Annual Review of Evolution, Ecology and Systematics 43: 249-265.

Fjeldså, J. 2002. Key areas for conserving the avifauna of *Polylepis* forests. Ecotropica 8 (2): 125-131.

Garzione, C.N., Hoke, G.D., Libarkin, J.C., Withers, S., MacFadden, B., Eiler, J., Ghosh, P. and Mulch, A. 2008. Rise of the Andes. Science 320: 1304-1307.

Gill, F. and Donsker, D. (Eds). 2014. IOC World Bird List (v 4.1). IOC World Bird List. Available at http://www.worldbirdnames.org/ [Assessed 11 May 2015]

Gill, F. 2014. Species taxonomy of birds: Which null hypothesis? The Auk 131: 150-161.

Gutiérrez-Pinto, N., Cuervo, A.M., Miranda, J., Perez-Eman, J.L., Brumfield, R.T. and Cadena, C.D. 2012. Non-monophyly and deep genetic differentiation across low-elevation barriers in a Neotropical montane bird (*Basileuterus tristriatus*; Aves: Parulidae). Molecular Phylogenetics and Evolution 64 (1): 156-165.

Gregory-Wodzicki, K.M. 2000. Uplift history of the Central and Northern Andes: a review. Geological Society of America Bulletin 112 (7): 1091-1105.

Helbig, A.J., Knox, A.G., Parkin, D.T., Sangster, G. and Collinson, M. 2002. Guidelines for assigning species rank. Ibis 144: 518-525.

Herzog, S.K., Martinez, R., Jørgensen, P.M. and Tiessen, H. 2012. Cambio climático y biodiversidad en los Andes tropicales. IAI and SCOPE, Paris.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. and Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965-1978. DOI: 10.1002/joc.1276

Hilty, S. 2011. Tit-like Dacnis (*Xenodacnis parina*). In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E (eds.). 2014. Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona. Available at http://www.hbw.com/species/tit-dacnis-xenodacnis-parina [Assessed 10 July 2015]

IUCN. 2012. IUCN Red List Categories and Criteria: Version 3.1.Second edition. Gland, Switzerland and Cambridge, UK: IUCN. iv + 32pp.

Jiguet, F., Barbet-Massin, M. and Henry, P-Y. 2010. Predicting potential distributions of two rare allopatric sister species, the globally threatened *Doliornis* cotingas in the Andes. Journal of Field Ornithology 81 (4): 325-339.

Lara, C.E., Cuervo, A.M., Valderrama, S.V., Calderón, F.D. and Cadena, C.D. 2012. A new species of wren (Troglodytidae: *Thryophilus*) from the dry Cauca River Canyon, northwestern Colombia. The Auk 129: 537-550.

Luteyn, J.L. 1999. Páramos: a checklist of plant diversity, geographical distribution and botanical literature. Memoirs of The New York Botanical Garden, Volume 84.

Lutz, H.L., Weckstein, J.D., Patané, J.S., Bates, J.M. and Aleixo, A. 2013. Biogeography and spatio-temporal diversification of *Selenidera* and *Andigena* toucans (Aves: Ramphastidae). Molecular Phylogenetics and Evolution 69: 873-883.

McKitrick, M.C. and Zink, R.M. 1988. Species concepts in ornithology. Condor 90: 1-14.

Ministerio del Ambiente. 2013. Sistema de Clasificación de los Ecosistemas del Ecuador Continental. Ministerio del Ambiente del Ecuador, Subsecretaría de Patrimonio Natural. Quito, Ecuador.

Montúfar, R. and Pitman, N. 2003. *Gynoxys cuicochensis*. The IUCN Red List of Threatened Species. 2003: e.T38077A10091560. Available at http://www.iucnredlist.org/details/38077/0 [Assessed 11 March 2016]

Ortiz, F. 2002. Tit-like Dacnis (*Xenodacnis parina*). Pp. 182 in: Granizo, T. (Ed.). Libro Rojo de las Aves del Ecuador. SIMBIOE, Conservación, Internacional, EcoCiencia, Ministerio del Ambiente, UICN. Serie de Libros Rojos del Ecuador, tomo 2. Quito, Ecuador.

Padial, J.M., Millares, A., De la Riva, I. and Vences, M. 2010. The integrative future of taxonomy. Frontiers in Zoology 7:1-16.

Parker III, T.A., Schulenberg, T.S., Graves, G.R. and Braun, M.J. 1985. The avifauna of the Huancabamba region, northern Peru. Pp. 169-197 in Buckley, P.A., Foster, M.S., Morton, E.S., Ridgely, R.S., and Buckley F.G. (Eds.). Neotropical

Ornithology. Ornithological Monographs number 36. American Ornithologists' Union, Washington D.C, USA.

Peterson, A.T. 2006. Taxonomy is important in conservation: A preliminary reassessment of Philippine species-level bird taxonomy. Bird Conservation International 16: 155-173.

Phillips, S.J., Anderson, R.P. and Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modeling 190: 231-259.

Remsen, J.V.Jr., Cadena, C.D., Jaramillo, A., Nores, M., Pacheco, J.F., Pérez-Emán, J., Robbins, M.B., Stiles, F.G., Stotz, D.F. and Zimmer, K.J. 2013. Classification of the bird species of South America. American Ornithologists Union. Available at http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm [Assessed 11 March 2016]

Ridgely, R.S. and Greenfield, P.J. 2001. The birds of Ecuador: status, distribution and taxonomy. Cornell Univ. Press, Ithaca, New York, USA.

Ridgely, R.S. 1980. Notes on some rare or previously unrecorded birds in Ecuador. American Birds 34: 242-48.

Sangster, G. 2014. The application of species criteria in avian taxonomy and its implications for the debate over species concepts. Biological Reviews 89: 199-214.

Schulenberg, T.S., Stotz, D.F., Lane, D.F., O'Neill, J.P. and Parker III, T.A. 2007. Birds of Peru. Princeton University Press, Princeton, New Jersey, USA.

Sedano, R.E. and Burns, K.J. 2010. Are the Northern Andes a species pump for Neotropical birds? Phylogenetics and biogeography of a clade of Neotropical tanagers (Aves: Thraupini). Journal of Biogeography 37 (2): 325-343.

Smith, B.T., McCormack, J.E., Cuervo, A.M., Hickerson, M.J., Aleixo, A., Cadena, C.D., Pérez-Emán, J., Curtis, W., Burney, C.W., Xie, X., Harvey, M.G., Faircloth, B.C., Glenn, T.C., Derryberry, E.P., Prejean, J., Fields, S. and Brumfield, R.T. 2014. The drivers of tropical speciation. Nature 515 (7527): 406-409.

Sosa-López, J.R., Martínez Gómez, J.E. and Mennill, D.J. 2015. Divergence in mating signals correlates with genetic distance and behavioural responses to playback. Journal of evolutionary biology 29 (2): 306–318.

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 Metaltail (*Metallura baroni*). Bird Conservation International 19 (01): 63-76.

Tobias, J.A., Cornwallis, C.K., Derryberry, E.P., Claramunt, S., Brumfield, R.T. and Seddon, N. 2014. Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. Nature 506 (7488): 359-363.

Tovar, C., Arnillas, C.A., Cuesta, F. and Buytaert, W. 2013. Diverging Responses of Tropical Andean Biomes under Future Climate Conditions. PLoS ONE 8 (5): e63634.

Vieites, D.R., Wollenberg, K.C., Andreone, F., Kohler, J., Glaw, F. and Vences, M. 2009. Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. Proceedings of the National Academy of Sciences of the United States of America 106: 8267-8272.

Vuilleumier, F. 1969. Pleistocene speciation in birds living in the high Andes. Nature 223: 1179-1180.

Wang, I.J. and Bradburd, G.S. 2014. Isolation by environment. Molecular ecology, 23 (23): 5649-5662.

Weigend, M. 2002. Observations on the biogeography of the Amotape-Huancabamba Zone in northern Peru. The Botanical Review 68 (1): 38-54.

Weigend, M. 2004. Additional observations on the biogeography of the Amotape–Huancabamba Zone in northern Peru, Defining the south-eastern limits. Revista Peruana de Biología 11 (2): 127-134.

Weir, J.T. 2009. Implications of genetic differentiation in Neotropical montane forest birds. Annals of the Missouri Botanical Garden 96 (3): 410-433.

Wilson, R.J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R. and Monserrat, V.J. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. Ecology Letters 8: 1138-1146.

Winger, B.M., Bates J M (2015) The tempo of trait divergence in geographic isolation: avian speciation across the Marañon Valley of Peru. Evolution 69:772-782.

Winker, K. 1998. Suggestions for measuring external characters of birds. Ornitologia Neotropical 9: 23-30.

Wright, S. 1943. Isolation by distance. Genetics 28(2): 114.

Zimmer, J.T. and Mayr, E. 1943. New species of birds described from 1938 to 1941. The Auk 60 (2): 249-262.

Zimmer, J.T. 1942. Studies of Peruvian birds, No. 43. Notes on the genera *Dacnis, Xenodacnis, Coereba*, *Conirostrum*, and *Oreomanes*. American Museum Novitates 1193 (43): 1-16.

10. FIGURES

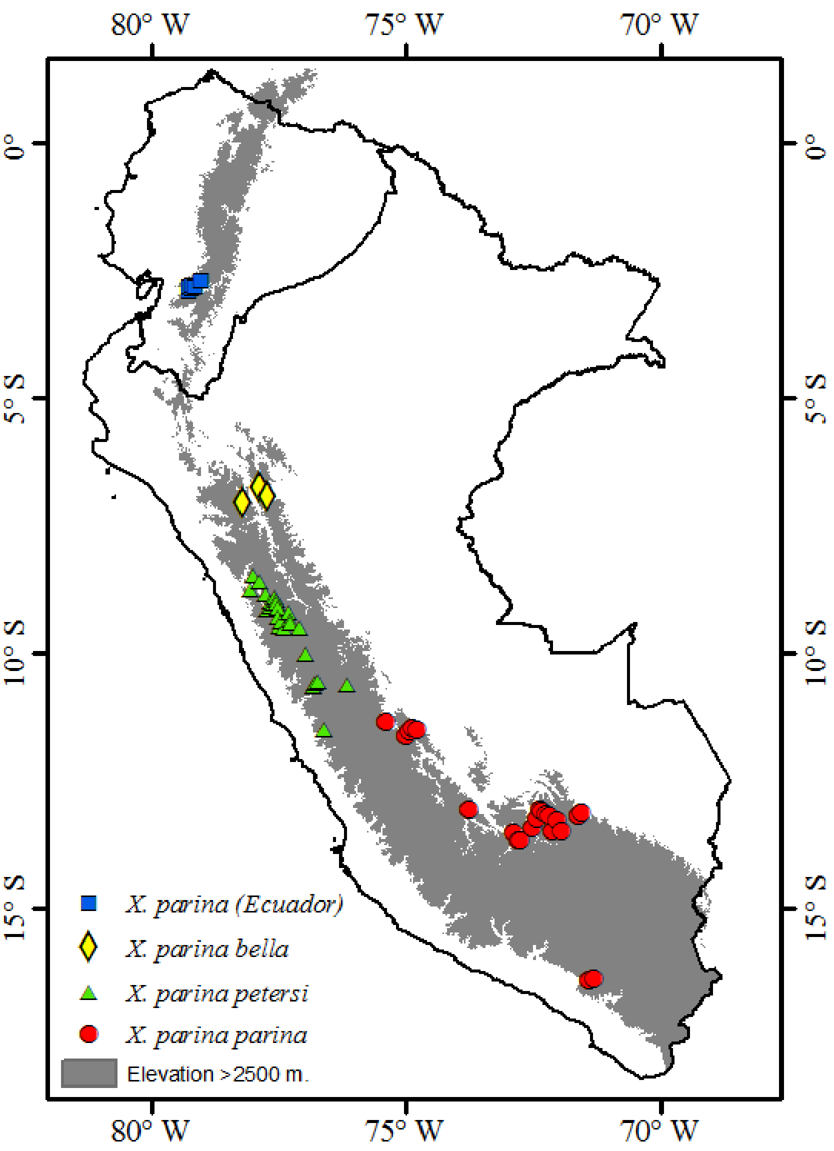

Figure 1. *Xenodacnis parina* distribution. Symbols are localities obtained from Global Biodiversity Information Facility (GBIF) and records from this study.

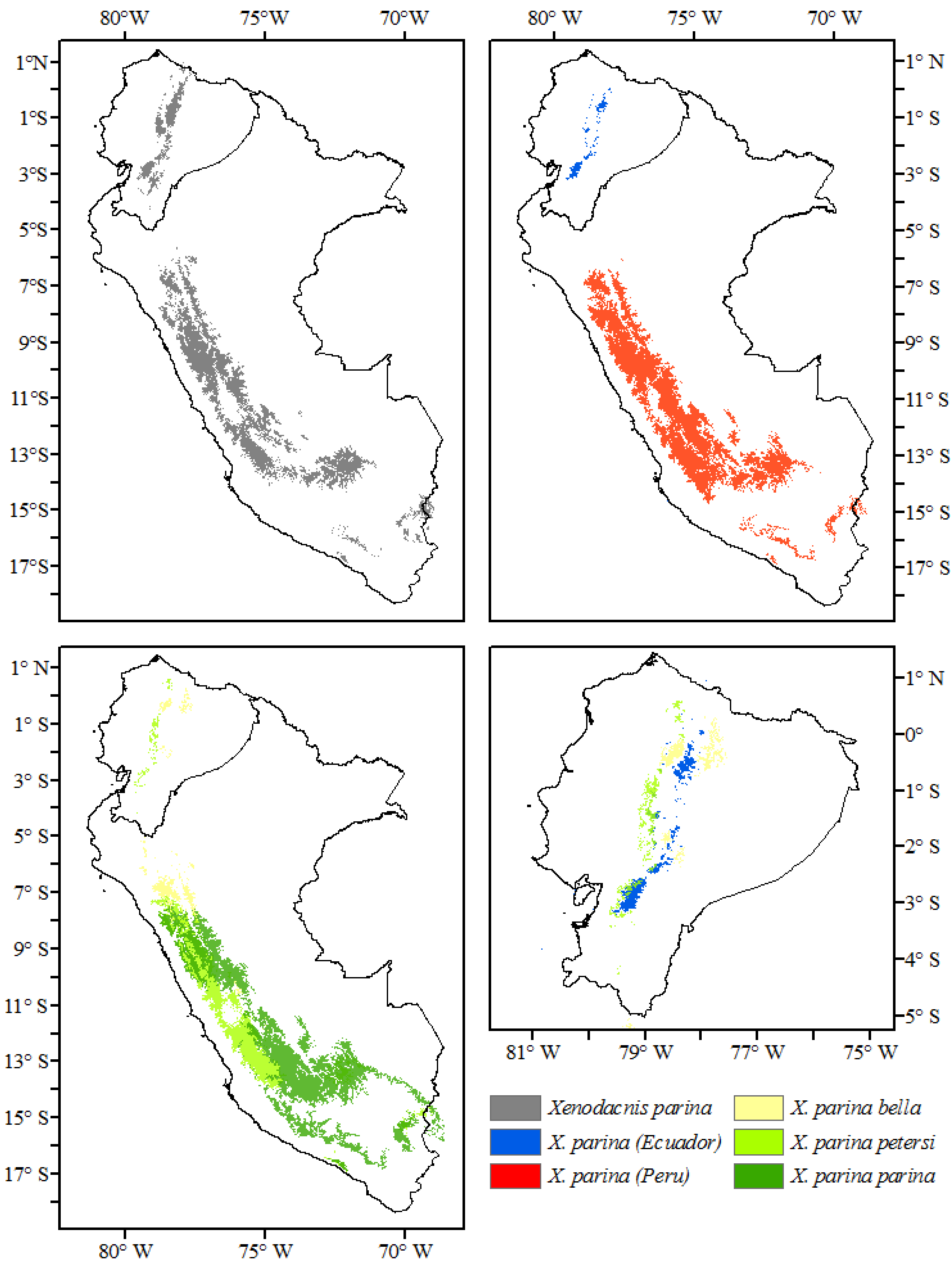

Figure 2. Habitat suitability for *Xenodacnis parina* based on environmental niche models**.** A: habitat suitability for *X. parina*; B: habitat suitability for *X. parina* from Ecuador and for all *X. parina* from Peru; C: habitat suitability for Peruvian subspecies; and D: distribution of suitable environmental conditions for the population from Ecuador and the Peruvian subspecies in Ecuador.

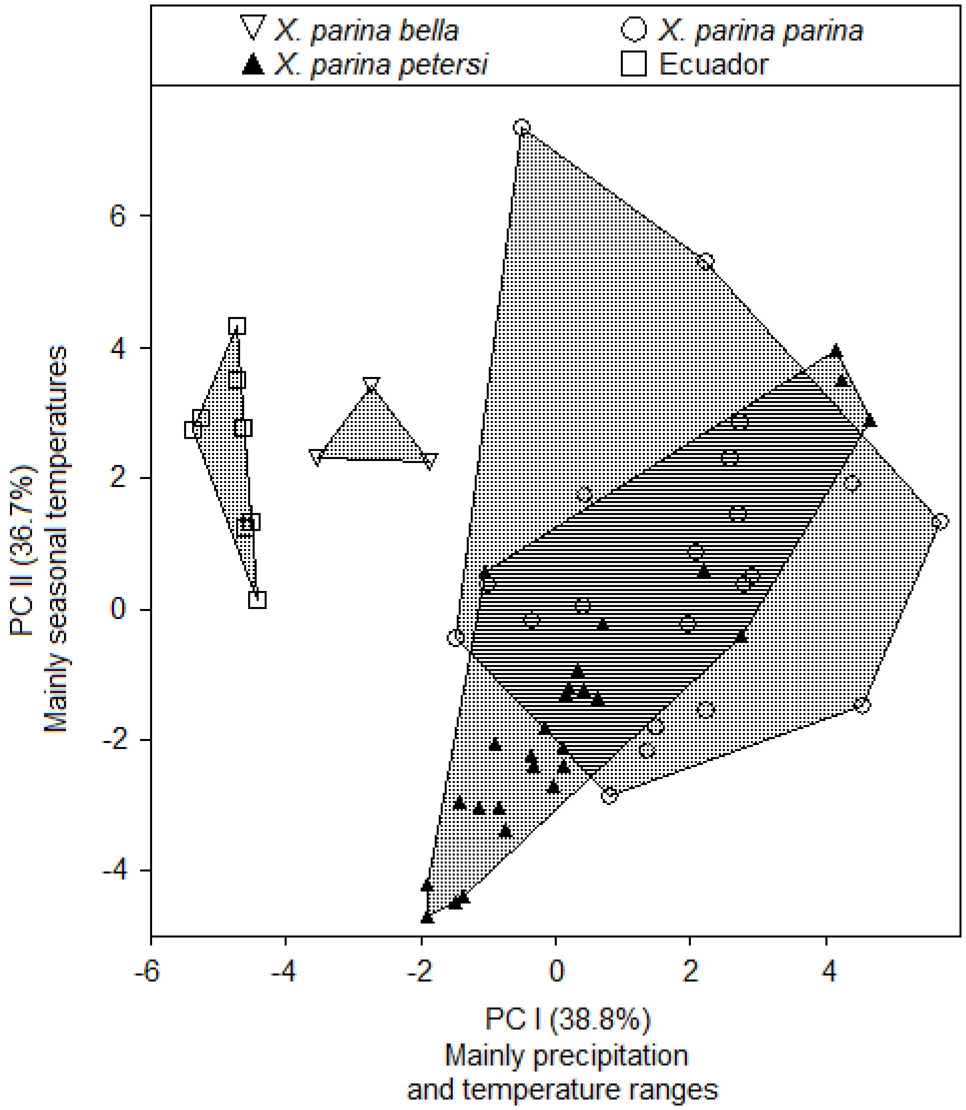

Figure 3. Graphic output of first two components from PCA. Multivariate space based on 19 environmental variables for the 59 locations where *Xenodacnis parina* have been recorded. Shaded areas are convex polygons for each subspecies.

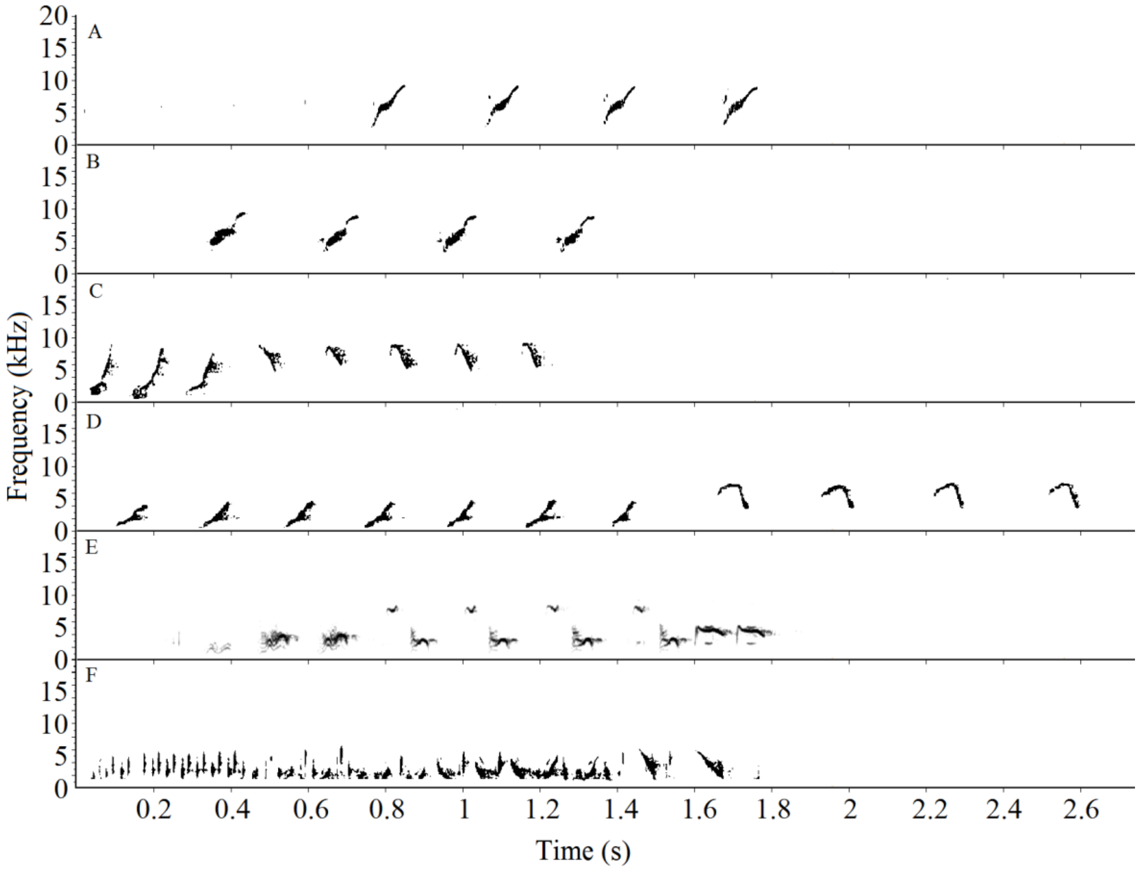

Figure 4. *Xenodacnis parina* male spectrograms. A and B: *X. parina* population from El Cajas, Ecuador; C: *X. parina bella*, from Amazonas, Peru; D: *X. parina petersi*, from Ancash, Peru; E and F: *X. parina parina*, from Cuzco and Arequipa, Peru.

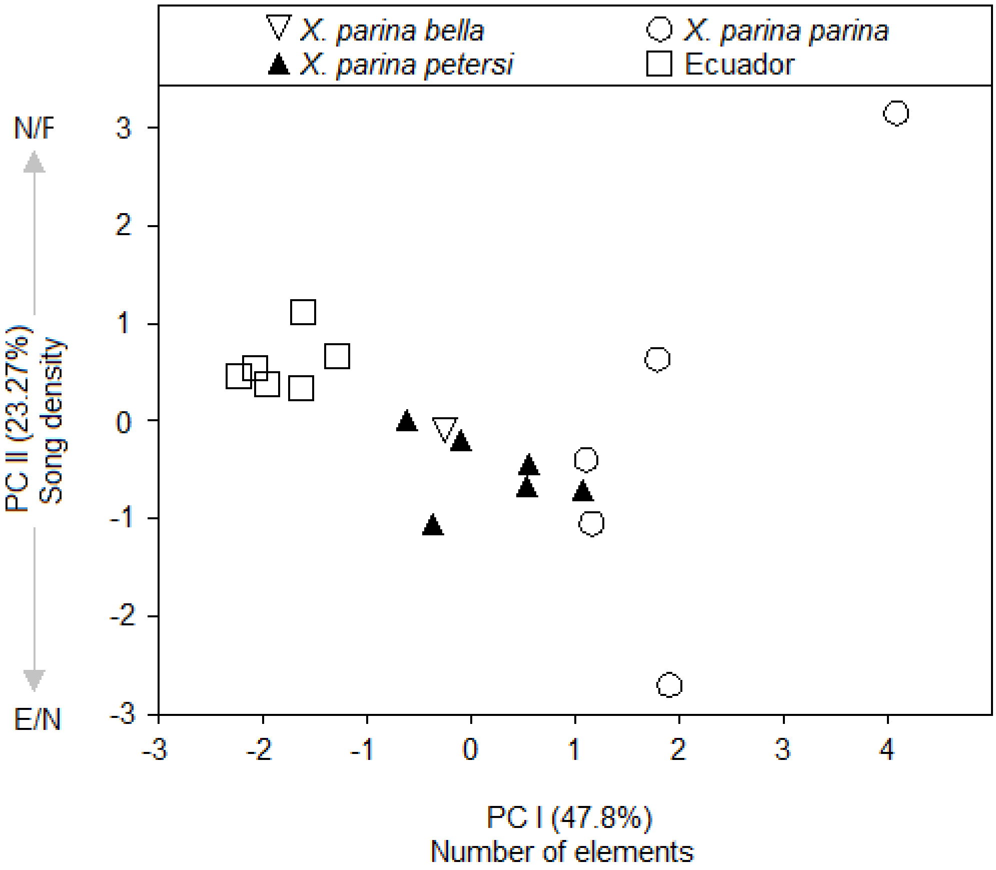

Figure 5. Graphic output of first two principal components from PCA of six acoustic variables from songs of *Xenodacnis*.

Figure 6. Photography of *Xenodacnis parina* from Cajas National Park, Ecuador. Female (left) and male (right) photographed during field work.

Figure 7. *Xenodacnis parina* specimens. Male (above) and female (below) from Cajas National Park.

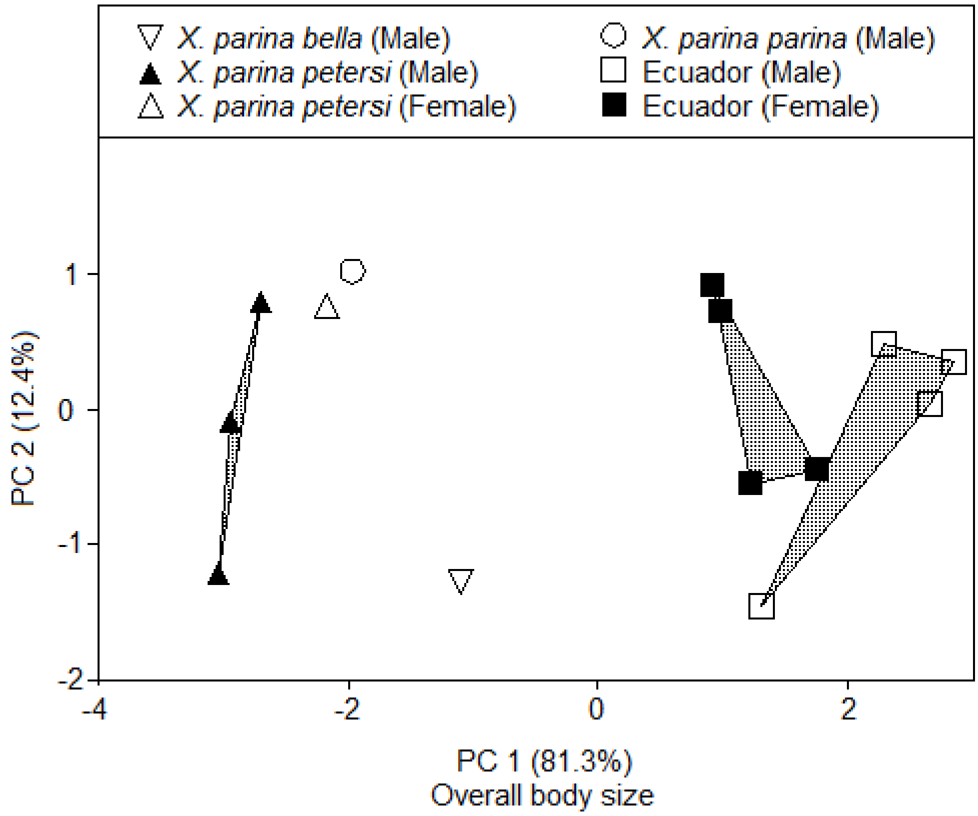

Figure 8. Graphic output of first two principal components from PCA of six morphological variables of *Xenodacnis parina*.

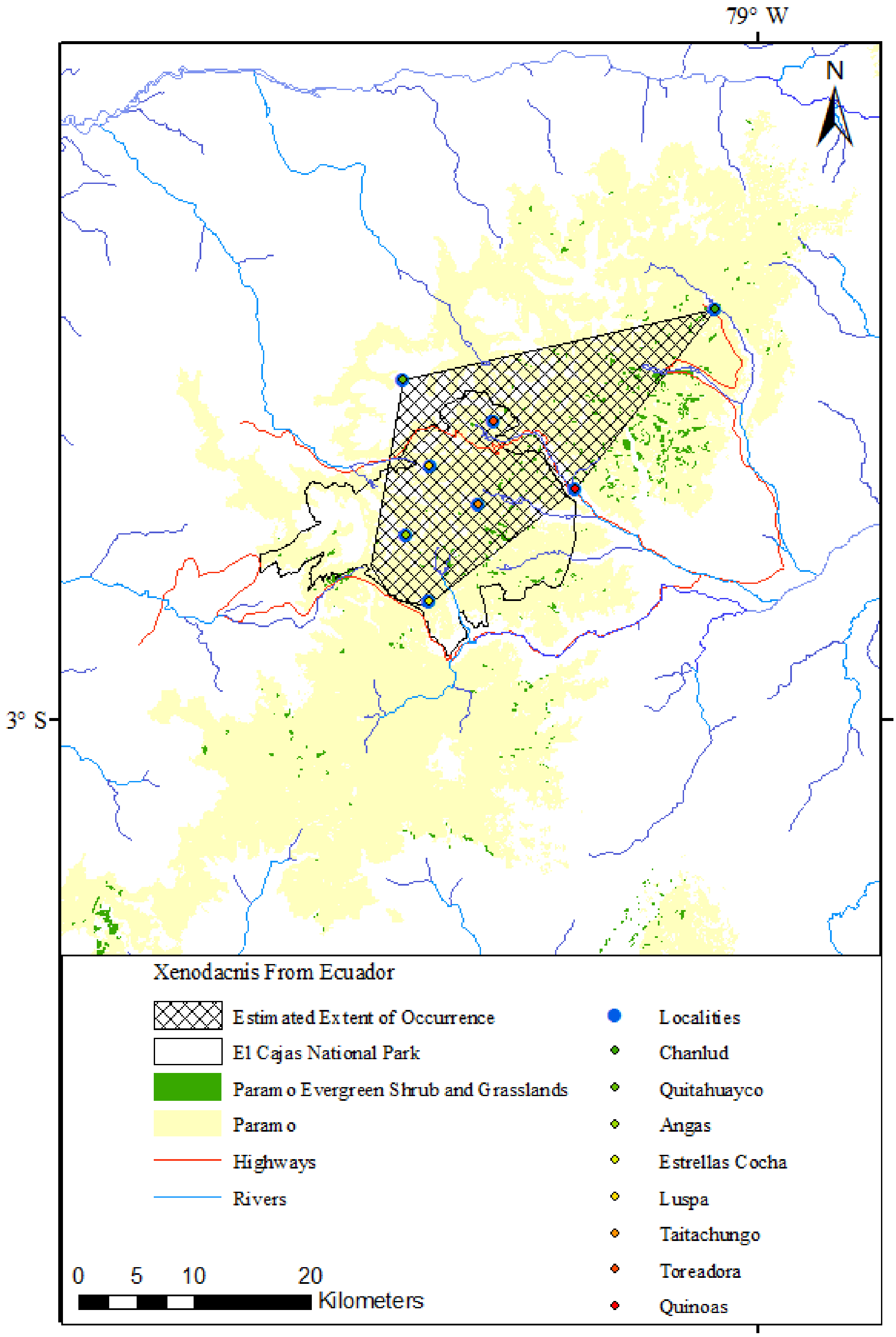

Figure 9. Current distribution of *Xenodacnis* in paramo ecosystem at El Cajas mountain massif, Ecuador. Map presents eight occurrence localities, UICN (2013) estimated extent of occurrence from all occurrence records and Ecosystems from Ministerio de Ambiente (2013).

11. TABLES

Table 1. Variables and PCA loadings from environmental multivariable analysis. Variables contribution to PCA first two components.

Variables	PC I	PC II
BIO1 = Annual Mean Temperature	0.2044	0.3098
BIO2 = Mean Diurnal Range	0.3023	-0.1146
BIO3 = Isothermality	-0.1885	0.2177
BIO4 = Temperature Seasonality	0.2293	-0.1981
BIO5 = Max Temperature of Warmest Month	0.2693	0.2369
BIO6 = Min Temperature of Coldest Month	0.03852	0.3724
BIO7 = Temperature Annual Range	0.2915	-0.1444
BIO8 = Mean Temperature of Wettest Quarter	0.227	0.2921
BIO9 = Mean Temperature of Driest Quarter	0.1821	0.3254
BIO10 = Mean Temperature of Warmest Quarter	0.2233	0.2938
BIO11 = Mean Temperature of Coldest Quarter	0.1799	0.3258
BIO12 = Annual Precipitation	-0.2643	0.1041
BIO13 = Precipitation of Wettest Month	-0.1322	-0.02566
BIO14 = Precipitation of Driest Month	-0.2636	0.2361
BIO15 = Precipitation Seasonality	0.3105	-0.1264
BIO16 = Precipitation of Wettest Quarter	-0.1479	-0.002215
BIO17 = Precipitation of Driest Quarter	-0.2781	0.2268
BIO18 = Precipitation of Warmest Quarter	-0.1627	-0.1362
BIO19 = Precipitation of Coldest Quarter	-0.2717	0.2276

Table 2. Song measurements of *Xenodacnis Parina*. Six bioacoustics variables obtained of 18 male song recordings from different populations. Code ML for songs obtained at Maculay Library and XC at Xeno-cato foundation.

Catalog	Subspecies	E	E/N	N/P	E/T	T	R
XC36777	*X. parina parina*	67	1.29	17.33	0.02	1.56	0
XC69730	*X. parina parina*	41	1.37	7.5	0.06	2.29	0
ML33844	*X. parina parina*	44	3.14	4.67	0.03	1.53	1
ML33842	*X. parina parina*	30	3.33	4.5	0.04	1.19	0
ML33851	*X. parina parina*	40	4.44	3	0.05	2.06	0
XC14800	*X. parina bella*	16	2.00	4	0.07	1.18	0
ML10472	*X. parina petersi*	18	2.00	4.5	0.09	1.56	0
ML33956	*X. parina petersi*	29	2.64	5.5	0.07	1.96	0
ML33954	*X. parina petersi*	24	2.18	5.5	0.10	2.49	0
ML82176	*X. parina petersi*	24	2.18	5.5	0.09	2.10	0
ML33958	*X. parina petersi*	15	1.67	4.5	0.11	1.70	0
ML33957	*X. parina petersi*	16	2.67	3	0.10	1.58	0
XC243293	*X. parina* Ecuador	12	1.50	4	0.14	1.74	1
XC206262	*X. parina* Ecuador	15	1.67	4.5	0.09	1.42	1
XC203152	*X. parina* Ecuador	10	1.67	3	0.13	1.29	1
XC206263	*X. parina* Ecuador	12	1.71	3.5	0.13	1.56	1
XC206264	*X. parina* Ecuador	14	1.75	4	0.12	1.75	1
XC5525	*X. parina* Ecuador	12	1.33	4.5	0.09	1.11	1

Table 3. *Xenodacnis parina* male song multivariate PCA. Variance and variable contribution to the first two components of the analysis.

PC	Eigenvalue	% variance	Variables	Component 1	Component 2
1	2.86777	47.796	E	0.5552	0.1514
2	1.39609	23.268	E/N	0.2119	-0.7158
3	1.07185	17.864	N/P	0.414	0.5813
4	0.541607	9.0268	E/T	-0.524	0.03673
5	0.10655	1.7758	T	0.2057	-0.2354
6	0.016134	0.2689	R	-0.3983	0.2645

Table 4. Morphological variation in adult *Xenodacnis parina* from Ecuador. Number of individuals measured (n), mean values and standard deviation (SD).

	Male			**Female**		
	n	Mean	SD	n	Mean	SD
Weight (g)	17	20.259	±1.209	16	17.463	±1.541
Wing Chord (mm)	18	79.194	±2.504	17	74.147	±2.178
Tail (mm)	18	61.222	±2.798	17	56.529	±3.165
Tarsus (mm)	18	28.178	±0.886	17	26.700	±1.086
Bill height (mm)	8	4.221	±0.090	5	4.140	±0.241
Bill width (mm)	8	4.929	±0.409	5	4.860	±0.329
Exposed culmen (mm)	8	8.084	±0.266	5	8.020	±0.164

Table 5. *Xenodacnis parina* morphological multivariate PCA. Variance and variable contribution to the first two components of the analysis.

PC	Eigenvalue	% variance	Variables	PC I	PC II
1	4.87917	81.32	Wing Chord (mm)	0.436	-0.0376
2	0.745053	12.418	Tail (mm)	0.4295	-0.1996
3	0.140798	2.3466	Tarsus (mm)	0.4326	-0.1128
4	0.125745	2.0957	Exposed culmen	0.2888	0.8832
5	0.0559923	0.9332	Bill height (mm)	0.4066	-0.3882
6	0.0532381	0.8873	Bill width	0.4354	0.1234

APPENDIX

Appendix 1. *Xenodacnis parina* occurrence localities. Occurrence coordinates in decimal degrees, from online resources (eBird 2012) and personal observations. Data is separated at least 5 km, avoiding spatial autocorrelation for environmental analysis.

Population	Country	State/Province	Locality	Longitude	Latitude
X. p. parina	Perú	Arequipa	Chiquata	-71.4200	-16.4200
X. p. parina	Perú	Arequipa		-71.3275	-16.4181
X. p. parina	Perú	Apurímac		-72.7950	-13.6776
X. p. parina	Perú	Apurímac		-72.7861	-13.6759
X. p. parina	Perú	Apurímac		-72.8868	-13.5180
X. p. parina	Perú	Cuzco	Anta	-72.1500	-13.4833
X. p. parina	Perú	Cuzco		-71.9635	-13.4815
X. p. parina	Perú	Cuzco		-72.5498	-13.4473
X. p. parina	Perú	Cuzco		-72.0509	-13.2931
X. p. parina	Perú	Cuzco		-72.4623	-13.2584
X. p. parina	Perú	Cuzco	Quenuamont	-72.2167	-13.1975
X. p. parina	Perú	Cuzco		-71.6429	-13.1848
X. p. parina	Perú	Cuzco		-72.2784	-13.1637
X. p. parina	Perú	Cuzco		-71.5746	-13.1316
X. p. parina	Perú	Cuzco		-72.3491	-13.1151
X. p. parina	Perú	Cuzco		-72.3857	-13.0782
X. p. parina	Perú	Ayacucho		-73.7765	-13.0737
X. p. parina	Perú	Junín		-75.0177	-11.6237
X. p. parina	Perú	Junín	Toldopampa	-74.9430	-11.5310
X. p. petersi	Perú	Lima		-76.6108	-11.4945
X. p. parina	Perú	Junín		-74.7977	-11.4908
X. p. parina	Perú	Junín	Toldopampa	-74.8980	-11.4650
X. p. parina	Perú	Junín	Maraynioc	-75.4000	-11.3667
X. p. petersi	Perú	Lima	Maticuna	-76.8333	-10.6500
X. p. petersi	Perú	Pasco		-76.1726	-10.6183
X. p. petersi	Perú	Lima	Yaui	-76.8000	-10.5833
X. p. petersi	Perú	Lima		-76.7469	-10.5622
X. p. petersi	Perú	Huánuco		-76.9717	-10.0319
X. p. petersi	Perú	Ancash		-77.0958	-9.5128
X. p. petersi	Perú	Ancash		-77.3896	-9.5076
X. p. petersi	Perú	Ancash		-77.4793	-9.4968

X. p. petersi	Perú	Ancash		-77.2672	-9.4239
X. p. petersi	Perú	Ancash		-77.4606	-9.3794
X. p. petersi	Perú	Ancash		-77.2728	-9.3639
X. p. petersi	Perú	Ancash		-77.5034	-9.2866
X. p. petersi	Perú	Ancash		-77.3015	-9.2187
X. p. petersi	Perú	Ancash		-77.5544	-9.1567
X. p. petersi	Perú	Ancash	Huascaran National Park	-77.7300	-9.1500
X. p. petersi	Perú	Ancash		-77.5297	-9.1110
X. p. petersi	Perú	Ancash		-77.6530	-9.0801
X. p. petersi	Perú	Ancash		-77.6081	-9.0375
X. p. petersi	Perú	Ancash	Morococha	-77.5456	-9.0278
X. p. petersi	Perú	Ancash		-77.6682	-8.9876
X. p. petersi	Perú	Ancash		-77.5556	-8.9719
X. p. petersi	Perú	Ancash		-77.5664	-8.9192
X. p. petersi	Perú	Ancash		-77.7592	-8.8342
X. p. petersi	Perú	Ancash		-78.0485	-8.7548
X. p. petersi	Perú	Ancash	Yanac; Quebrada Tutapac	-77.8700	-8.6200
X. p. petersi	Perú	Ancash	Yanac	-78.0000	-8.5000
X. p. bella	Perú	Cajamarca		-78.2129	-7.0256
X. p. bella	Perú	Amazonas	Atuen	-77.7306	-6.9167
X. p. bella	Perú	Amazonas	Atuen	-77.8667	-6.7500
X. parina	Ecuador	Azuay	El Cajas National Park	-79.2553	-2.9091
X. parina	Ecuador	Azuay	El Cajas National Park	-79.2727	-2.8576
X. parina	Ecuador	Azuay	El Cajas National Park	-79.2167	-2.8333
X. parina	Ecuador	Azuay	Quinoas	-79.1414	-2.8218
X. parina	Ecuador	Azuay	El Cajas National Park	-79.2544	-2.8036
X. parina	Ecuador	Azuay	El Cajas National Park	-79.2054	-2.7698
X. parina	Ecuador	Azuay	Machangara; Chanlud	-79.0334	-2.6819
X. parina	Ecuador	Azuay	Northwest from Cajas National Park	-79.2751	-2.7377
X. parina	Ecuador	Morona-Santiago	Valle de Collanes	-78.4328	-1.6721

Appendix 2. Male song recordings used for bioacoustics analysis. Code ML for Maculay Library and XC for Xeno-cato foundation, the song for *X. parina bella* is the only available.

Code	Recordist	State/Prov.	Population	Sex	Catalog #
1	Huw Lloyd	Cuzco	*parina*	Male	XC36777
2	Frank R. Lambert	Cuzco	*parina*	Male	XC69730
3	Theodore A. Parker, III	Arequipa	*parina*	Male	ML33844
4	Theodore A. Parker, III	Arequipa	*parina*	Male	ML33842
5	Theodore A. Parker, III	Arequipa	*parina*	Male	ML33851
6	Todd Mark	Amazonas	*bella*	unknow	XC14800
7	Theodore A. Parker, III	Ancash	*petersi*	Male	ML10472
8	Theodore A. Parker, III	Ancash	*petersi*	Male	ML33956
9	Theodore A. Parker, III	Ancash	*petersi*	Male	ML33954
10	Paul K. Donahue	Ancash	*petersi*	Male	ML82176
11	Theodore A. Parker, III	Ancash	*petersi*	Male	ML33958
12	Theodore A. Parker, III	Ancash	*petersi*	Male	ML33957
13	John V. Moore	Azuay	Ecuador	Male	XC243293
14	Juan M. Aguilar	Azuay	Ecuador	Male	XC206262
15	Juan M. Aguilar	Azuay	Ecuador	Male	XC203152
16	Juan M. Aguilar	Azuay	Ecuador	Male	XC206263
17	Juan M. Aguilar	Azuay	Ecuador	Male	XC206264
18	Nick Athanas	Azuay	Ecuador	Male	XC5525

Appendix 3. Morphological measurements of *Xenodacnis parina*. Details of individuals measured of subspecies from Peru and from Ecuador population, including age (A, adult; Y, juveniles; U, unknown) and sex (M, males; F, females; U, unknown). Museum abbreviations: CORBIDI, Deposito de material biológico del Perú; MZUA, Museo de Zoología de la Universidad del Azuay; QCAZ, Museo de Zoología de la Pontifica Universidad Católica del Ecuador. Data from literatura came from *a*) Aguilar and Iñiguez (2015) and *b*) Bond and Meyer de Schauensee (1939).

Population	Source	Prov/State	Age	Sex	Exposed culmen	Bill depth	Bill width	Wing Chord	Tail	Tarsus	Weight
Ecuador	a	Azuay	A	F				73	53	27.6	16
Ecuador	a	Azuay	A	F				73	54	27.7	17
Ecuador	a	Azuay	A	F				77	58	27.38	18
Ecuador	a	Azuay	A	F				70	56	25.84	16
Ecuador	a	Azuay	A	F				74	55	27.9	16
Ecuador	a	Azuay	A	F				76	53	27.7	17
Ecuador	a	Azuay	A	F				73	54	26.14	20
Ecuador	a	Azuay	A	F				70	53	26.83	16
Ecuador	a	Azuay	A	F				78	58	27.15	
Ecuador	a	Azuay	A	F				73	54	26.83	17
Ecuador	a	Azuay	A	F				74	56	27.53	17
Ecuador	a	Azuay	A	M				82	60	28.2	19
Ecuador	a	Azuay	A	M				80	56	27.9	20
Ecuador	a	Azuay	A	M				80	58	29.6	19.5
Ecuador	a	Azuay	A	M				74	58	30.2	18
Ecuador	a	Azuay	A	M				80	60	27.9	21
Ecuador	a	Azuay	A	M				82	59	27.49	20
Ecuador	a	Azuay	A	M				82	62	27.9	19
Ecuador	a	Azuay	A	M				79	58	27.64	20
Ecuador	a	Azuay	A	M				81	61	28.07	20
Ecuador	a	Azuay	A	M				80	63	27.71	21
Ecuador	a	Azuay	U	F				75	54	25.4	16
Ecuador	a	Azuay	Y	U				75	54	25.63	15
Ecuador	a	Azuay	Y	U				75	56	27.43	19
Ecuador	a	Azuay	Y	U				76	58	26.45	
X. parina bella	b	Amazonas	A	F				68.5			
X. parina bella	b	Amazonas	A	F				74			
X. parina bella	b	Amazonas	A	M	8			75.5	60	23.5	

X. parina bella	b	Amazonas	A	M				76.5			
X. parina parina	b		A	F				58			
X. parina parina	b		A	F				58			
X. parina parina	b		A	M				61.5			
X. parina parina	b		A	M				66.5			
X. parina petersi	b	Ancash	A	F				71			
X. parina petersi	b	Ancash	A	F				71			
X. parina petersi	b	Ancash	A	F				75			
X. parina petersi	b	Ancash	A	M	9			82.5	66	27	
X. parina petersi	b	Ancash	A	M				78			
X. parina petersi	b	Ancash	A	M				79			
X. parina petersi	b	Ancash	Y	M				74.5			
X. parina petersi	b	Ancash	Y	M				77.5			
X. parina petersi	CORBIDI AB-001422	Junin	A	F	7.57	3.56	3.19	58	56	20	10.2
X. parina bella	CORBIDI AB-001665	Ancash	A	M	7.4	3.99	3.43	69	58	24	11.2
X. parina petersi	CORBIDI AB-001686	Lima	A	F	7.85	3.42	3.01	66	54	20	
X. parina petersi	CORBIDI AB-011862	Junin	A	F	7.16	3.62	2.86	62	53	22.6	9.2
X. parina parina	CORBIDI AB-011863	Cusco	A	M	8.05	3.65	3.34	63	53	22.84	11.1
X. parina petersi	CORBIDI AB-011864	Junin	A	M	7.98	3.73	3.24	60	53	22.64	12.3
X. parina petersi	CORBIDI AB-011865	Junin	A	M	7.46	3.7	3.11	62		23.65	13.3
Ecuador	Field Data 2014	Azuay	A	F	8.2	3.8	4.8	76	60	26.9	19.1
Ecuador	Field Data 2014	Azuay	A	F	7.9	4.3	5.4	76	63	26.3	21.2
Ecuador	Field Data 2014	Azuay	A	F	8.2	4	4.9	73	60	26.5	18
Ecuador	Field Data 2014	Azuay	A	M	8.3	4.2	4.9	79	63	29.1	21
Ecuador	Field Data 2014	Azuay	A	M	8.3	4.3	5.5	79	66	28.3	21.4
Ecuador	Field Data 2014	Azuay	A	M	7.6	4.3	4.3	75	64	28.3	21.2
Ecuador	Field Data 2014	Azuay	Y	F	7.9	4.2	4.6	74.5	60	23.5	17.1
Ecuador	Field Data 2014	Azuay	Y	M	7.8	4.3	4.7	78	61	27	21.2
Ecuador	Field Data 2014	Azuay	Y	M	8.3	4.1	4.7	75	61	26.5	19.9
Ecuador	Field Data 2014	Azuay	Y	M	8.2	4.1	5.5	77	62	28.7	19.1
Ecuador	MZUA.AV.000013	Azuay	A	M	7.97	4.17	4.83	81	65	27.8	
Ecuador	MZUA.AV.000037	Azuay	A	F	8	4.2	4.6	74	55	25.6	
Ecuador	QCAZ 4624	Azuay	A	M	8.2	4.3	5	81.5	65	28.9	23.1
Ecuador	QCAZ 4625	Azuay	A	F	7.9	4.4	4.6	75	60	26.7	18