



Revised distributional estimates for the recently discovered olinguito (*Bassaricyon neblina*), with comments on natural and taxonomic history

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Understanding a species' distributional limits is a necessary step for developing conservation priorities. The olinguito (Procyonidae: *Bassaricyon neblina*) is a recently described, medium-sized carnivoran found in Northern Andean cloud forests. Here, we provide revised distributional estimates for this species using current ecological niche modeling methods (using Maxent and bioclimatic variables), taking into account sampling bias and using updated locality information including 9 photo-vouchered citizen science records that increased the original data set by 60%. Optimal models were selected via 2 approaches: Akaike's Information Criterion corrected for small sample size (AICc) and performance on withheld data. The AICc-optimal model aligned more closely with current knowledge of the species' elevational limits. This model improves on the previously modeled distribution map for the species, especially in terms of elevational discrimination in the Central Cordillera of Colombia, where high mountain peaks are considered unsuitable. Compared with the original map, the revised map suggests more extensive suitable area in northern Colombia, possibly due to the inclusion of new citizen science records, and highlights 6 priority areas for future sampling that have no olinguito records: the northern portion of the Western Cordillera of Colombia, southern portion of the Western Cordillera of Colombia, western slopes of the Andes in southwestern Colombia, both versants of the middle portion of the Central Cordillera of Colombia, western slopes of the Andes in central and southern Ecuador, and eastern slopes of the Andes in Ecuador. This study improves knowledge of the olinguito's range, increases our understanding of this species' natural and taxonomic history, and provides an example of modeling the distributions of poorly known species with small sample sizes.

Entender los límites de distribución de las especies es un paso necesario para el establecimiento de prioridades de conservación. Recientemente descrito, el olinguito (Procyonidae: *Bassaricyon neblina*) es un carnívoro mediano de los bosques nublados del norte de los Andes. En este trabajo, revisamos la distribución para esta especie usando métodos para Modelamiento de Nicho Ecológico (empleando Maxent y variables bioclimáticas). Para el modelaje, se tuvo en cuenta el sesgo de muestreo y se utilizó información actualizada de localidades de presencia para esta especie incluyendo nueve foto-registros de ciencia ciudadana, aumentando así el set de datos originales en un 60%. Los modelos óptimos fueron escogidos usando dos metodologías: AICc y desempeño con

datos retenidos. El modelo óptimo seleccionado usando el criterio de AICc fue el que mejor se acopló con el conocimiento actual de los límites altitudinales para esta especie. Este modelo mejora la previa estimación de distribución de la especie, especialmente en términos de discriminación altitudinal en la Cordillera Central de Colombia donde los picos de las montañas se consideran como no idóneos. Al comparar con el mapa original, este nuevo mapa sugiere un área idónea más extensa en el norte de Colombia, posiblemente debido a la inclusión de nuevas observaciones de ciencia ciudadana. Este mapa resalta seis áreas prioritarias para futuros muestreos con sin registros de olinguitos: las porciones norte y sur de la Cordillera Occidental de Colombia, la ladera occidental de los Andes en el suroccidente de Colombia, ambas vertientes de la parte central de la Cordillera Central de Colombia, la ladera occidental de los Andes en el centro y sur de Ecuador y la vertiente oriental de los Andes en Ecuador. Este estudio no solo mejora el conocimiento de la distribución del olinguito (como ejemplo al modelar las distribuciones de especies pobremente conocidas, con tamaños de muestra pequeños), sino que también incrementa nuestro entendimiento de su historia natural y taxonómica.

Key words: Andes, citizen science, conservation, distribution, ecological niche modeling, ecotourism, Neotropical, olinguito, Procyonidae

Knowledge of species distributions is a necessary foundation for conservation, especially in the light of global environmental change (Guisan et al. 2013; McKenna et al. 2013). This is particularly important for areas facing strong anthropogenic impacts such as the Northern Andes, a biodiversity hotspot with high endemism. The region's biota is under pressure from various farming practices, illegal logging, and mining, which all result in deforestation (Rodríguez et al. 2012). Despite this, many new species of vertebrates have been discovered in the region in the last 15 years, especially amphibians and birds (Cuervo et al. 2001, 2005; Ocampo-Peñuela and Pimm 2014; Guarnizo et al. 2015; Mendoza et al. 2016), but also some small mammals (Muchhala et al. 2005; Jenkins et al. 2013). The recent discovery of the olinguito (Procyonidae: *Bassaricyon neblina*), a medium-sized mammal, was particularly unexpected, being the first new carnivoran from the Americas described in the last 35 years.

The olinguito is found in the cloud forests of the Colombian and Ecuadorian Andes. This species is thought to be nocturnal, arboreal, and solitary, and has been observed to have a mostly frugivorous diet (Helgen et al. 2013). The olinguito was described in 2013 during a systematic study revising the genus *Bassaricyon*. The analyses involved examination of specimens identified at that time as olingos from various museums. Some were smaller, with longer hair, different pelage color, distinctive craniodental characteristics, and were found at higher elevations than most other olingos. The study determined that this lineage was genetically distinct, having split from other members of the genus ~3.5 million years ago and had been misclassified in museum collections for at least 100 years. The study further noted that some aspects of the olinguito's taxonomic history remained a mystery, related to the possible name "*Bassaricyon osborni*."

With so little known about this new species, assessment of its conservation status has been based primarily on its distribution. Given its restriction to northern Andean cloud forests, which are threatened by high rates of deforestation, loss of habitat is a chief concern (Helgen et al. 2013). Additionally, climate change may pose a significant threat to montane species like the olinguito, as they live within narrow elevational

limits (Ramirez-Villegas et al. 2014). Based on the geographic estimates of a total range of 40,760 km² (Helgen et al. 2013) and projected loss of habitat due to deforestation, this species has recently been given the IUCN status of "Near Threatened" (Helgen et al. 2013, 2016). Modeled distribution maps for the olinguito are also important to guide future field efforts to discover new populations, which are critical for species with so few occurrence records (Pearson et al. 2006). Though geographic estimates for *B. neblina* were generated using ecological niche models (ENMs) in the original description (Helgen et al. 2013), georeferences in some circumstances did not take into account all possible information, the final model did not address sampling bias or model complexity, and it predicted suitability into high-elevation areas above the tree line.

Here, we provide updated distribution maps for the olinguito, with improved ENMs, enhanced georeferencing of historical museum specimens, and the addition of new localities from citizen scientists. We improved upon the original models of Helgen et al. (2013) by reducing the effects of spatial biases in the occurrence data and optimizing model complexity using 2 selection approaches. We obtained more accurate localities for the historical museum records by taking advantage of additional information from collectors' field notes. Finally, we acquired new localities through citizen science, a tool that engages the public to collect scientific data and has seen increasing application over the past 10 years (Dickinson et al. 2010), via photographs that definitively identified olinguitos.

MATERIALS AND METHODS

Occurrence records and georeferencing.—We obtained occurrence records through museum specimens as well as citizen science data. To ensure that georeferences for museum localities used were as accurate as possible, we reexamined field notes (when available) and verbatim locality information from the specimen tags for specimens reported in Helgen et al. (2013; specifically those at the American Museum of Natural History, AMNH; Pontificia Universidad Católica del Ecuador, QCAZ; and the U.S. National Museum of Natural History, NMNH). We then georeferenced the occurrence records by

integrating information from verbatim localities, field notes, museum databases, collection staff (when information about select specimens was not available within museum databases), gazetteers, and topographic maps from time periods close to specimen collection (necessary if place names have changed and to see the placement of older roads).

The publication of the original species description of *B. nebulina* (Helgen et al. 2013) generated a substantial amount of public interest in the olinguito, encouraging naturalists to look for the species themselves. These citizen scientists often contacted 2 of this study's authors (KMH and RK—also authors of Helgen et al. [2013]) to share photographs of suspected olinguitos, allowing us to collate 10 new photo-vouchered records. Many additional submitted photographs represented other species of olingos (*Bassaricyon* spp.) or kinkajous (*Potos* spp.). Olinguitos were distinguished from olingos based primarily on the length and color of their fur, which is a diagnostic trait visible in most photos, as well as the morphology of the tail and the shape of the head in some cases (Helgen et al. 2013).

Environmental data.—The environmental data used for this study were the 19 bioclimatic variables from WorldClim at a resolution of 30 arc-seconds (Hijmans et al. 2005). These variables are derived from monthly temperature and precipitation data, and summarize seasonal and annual aspects of climate. To delineate the area used for model calibration, we defined a species-specific study region in order to avoid including areas with suitable environments that lack records due to dispersal limitations or biotic interactions (Anderson and Raza 2010; Barve et al. 2011). Including such areas can cause ENMs to incorporate a false signal causing the model to indicate these regions as unsuitable (Anderson and Raza 2010). To create the study region, we created circular buffers of 0.7° around each occurrence record (radius chosen to exclude the Eastern Cordillera of Colombia, which is disjunct from the Western and Central Cordilleras), and merged all buffers into a single polygon. We then masked the bioclimatic variables to this study region. This method excluded large biogeographic regions in which the species has not yet been found, such as the Eastern Cordillera in Colombia (likely due to dispersal barriers), while delineating an area large enough to encompass a variety of different environments (Anderson and Raza 2010; Peterson et al. 2011). The resulting polygon was used as the “background” region for ENM construction (see “Model building” below). All geoprocessing analyses were done in R (R Core Team 2015) with the raster package (Hijmans et al. 2016b).

Comparisons of original and newly georeferenced data.—To understand how the climatic signature of the occurrence records changed after thorough georeferencing and the addition of citizen science data, we compared long-term averages of annual precipitation and annual mean temperature across the 2 data sets. We generated a smoothed kernel density plot of the temperature and precipitation values for a slightly more extensive geographic region (minimum convex polygon around occurrence records, buffered by 0.7°) in R (R Core Team 2015) with the MASS package (Venables et al. 2002). We then plotted both

sets of occurrence records (Helgen et al. 2013 and the present study) in this space to compare their occupied environmental space. Similarly, we compared the minimum and maximum temperature and precipitation values for each locality data set.

Spatial thinning.—To reduce artifactual clustering of records due to biased sampling typical of biodiversity data sets, we applied a spatial filter on the full georeferenced data set using the R package spThin (Aiello-Lammens et al. 2015; 1,000 repetitions). Considering the environmental heterogeneity of the area, steep elevational gradients within the Northern Andes, and likely degree of sampling bias in the region, we chose a relatively coarse thinning distance of 10 km. Such filtering should help reduce the effects of sampling bias and, in turn, artifactual spatial autocorrelation, while retaining as many occurrence records as possible (Anderson and Raza 2010; Boria et al. 2014).

Model building.—We modeled the olinguito's potential distribution using Maxent, a machine learning, presence-background ecological niche modeling technique (Phillips et al. 2006), implemented with the R package dismo v. 1.0-15 (Hijmans et al. 2016a). Maxent compares the environmental values at background pixels with those at occurrence records to estimate environmental suitability across geographic space. We randomly sampled 10,000 background localities from the study area. To generate a suite of candidate models with differing levels of complexity, 2 key parameters in Maxent were varied: feature classes and regularization multipliers (Phillips and Dudík 2008; Elith et al. 2010b; Anderson and Gonzalez 2011; Warren and Seifert 2011; Warren et al. 2013; Radosavljevic and Anderson 2014). Feature classes determine the flexibility of the modeled response to the predictor variables, while increasing the regularization multiplier value penalizes model complexity (Phillips and Dudík 2008). We built models of varying complexity that explored different combinations of both parameters with the R package ENMeval (Muscarella et al. 2014). Specifically, we considered linear, quadratic, and hinge feature classes (Elith et al. 2010b), and a range of regularization multipliers from 0.5 to 4.0 in 0.5 increments.

Over the suite of candidate models built, we assessed performance using an $n - 1$ jackknife approach, a special case of k -fold cross validation where n is the number of occurrence records (Pearson et al. 2006). The jackknife method is particularly relevant for species with small sample sizes, as it allows all records to be used during model calibration instead of losing valuable records entirely via data splitting (Shcheglovitova and Anderson 2013). Here, all occurrence records but one are used to train the model in each iteration, and the withheld record is used for testing. As each occurrence record is used once for testing, n models are generated, and evaluation statistics for each iteration are averaged across all n models.

Model selection.—To select the optimal model, we implemented 2 approaches proposed in the literature (Warren and Seifert 2011; Shcheglovitova and Anderson 2013; Radosavljevic and Anderson 2014). For the first, we tested model performance on withheld data through the use of sequential criteria on 2 evaluation statistics. The first statistic

considered was the average omission rate (OR), or the proportion of localities that fall outside the model prediction. As we had confidence that our detailed georeferencing procedures resulted in relatively low spatial uncertainty for the occurrence records, we calculated OR using the minimum training presence (MTP) threshold, or the lowest suitability value for an occurrence record used to calibrate the model. Among the subset of models with the lowest OR, we then further assessed performance using the average value of the test AUC (area under the curve of the receiving operator characteristic plot—Fielding and Bell 1997). The test AUC is a measure of how well the model discriminates testing data from background pixels (i.e., the higher the test AUC value, the greater the chance the testing data have a higher score than a randomly selected background pixel—Fielding and Bell 1997; Warren and Seifert 2011). The model with the highest test AUC, after selecting for lowest OR, was then chosen as optimal (Radosavljevic and Anderson 2014).

The second method of model selection used Akaike's Information Criterion corrected for small sample size (AICc), which has been shown to be useful in selecting optimal settings for Maxent models (Warren and Seifert 2011). This method penalizes overly complex models and helps choose those with an optimal number of parameters. However, it is not strictly appropriate to be used with machine learning techniques, as the number of model parameters may not correctly estimate the degrees of freedom and it does not take parameter weights into account (Warren and Seifert 2011; Warren 2013). Despite this, AICc may still be useful in an ecological niche modeling framework as it can quantify model complexity and goodness of fit without requiring external evaluation data. Low scores indicate models that predict training data well while maintaining a justified number of parameters given the complexity of the data.

We built the final models using the settings chosen as optimal for each selection method and all spatially filtered occurrence records in Maxent. Finally, we projected both final "optimal" models to a larger study region (bounding box around occurrence records buffered by 5°) from southern Ecuador through the Western and Central Cordilleras of northern Colombia. Areas of the continuous predictions produced by Maxent that had values lower than the MTP were removed to generate estimates of the species' distribution. We also clipped the prediction to remove suitable areas beyond large gaps in suitability that arose after applying the MTP threshold. Furthermore, we removed areas separated by additional possible dispersal barriers. Specifically, we retained suitable areas in the Western and Central Cordillera of Colombia and both slopes of the Andes of Ecuador, but removed: 1) suitable areas to the east of the depression separating the Central and Eastern Cordilleras of Colombia, and 2) the southernmost portion of the range in Ecuador between the Río Jubones and Río Yacuambi where suitable areas narrowed substantially. To assess whether environmental extrapolation was required for projection into areas not part of model calibration, we generated Multivariate Environmental Similarity Surface (MESS) maps (R package dismo—

Elith et al. 2010a; for more information on MESS analyses see Supplementary Data SD6).

RESULTS

Georeferencing.—Georeferencing efforts for the original museum specimens and interfacing with citizen scientists allowed us to collect a larger and more accurate set of occurrence records for the olinguito. First, consultation of specimen tags and field notes led to some corrections and, in several instances, more complete verbatim localities than were reported in the taxonomic revision (Supplementary Data SD1 and SD2). Second, georeferencing efforts led to mostly minor changes in coordinates (for approximately 50% of the museum records), although some had substantial changes (one with a difference in elevation of more than 2,000 m; Supplementary Data SD1). For example, tags from a specimen collected at Las Máquinas, Ecuador, the type locality of *B. neblina* (locality 22; Fig. 1) listed this specimen (AMNH 66753) as having been collected at 2,125 m. We used information from the 1923 field

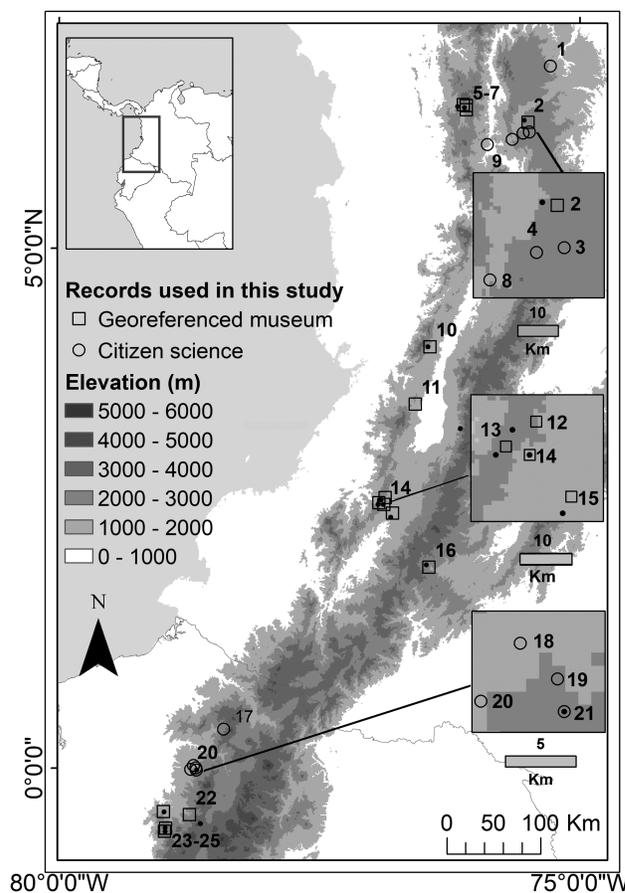


Fig. 1.—Map of occurrence records for the olinguito (*Bassaricyon neblina*), showing all newly georeferenced, unique occurrence records used in this study ($n = 25$; hollow circles and squares) along with those from the taxonomic revision ($n = 16$; black dots). Occurrences are overlaid on a digital elevation map. Data used for this study consist of vouchered museum and citizen science records from both the Colombian and Ecuadorian Andes. Numbers indicate specific localities or clusters mentioned throughout the paper (see Supplementary Data SD1).

notes of collector G. H. H. Tate to relocate the coordinates for this specimen closer to the basecamp (rather than to the east of the Corazón volcano at an elevation of 4,350 m as used in Helgen et al. [2013]). This change in coordinates (and elevation) altered the environmental conditions of the locality considerably (Fig. 2; bottom left).

After georeferencing, we confirmed 15 unique localities that differed in latitude or longitude from the Helgen et al. (2013) museum data set (those authors excluded the locality associated with specimen AMNH 70723; locality 7; Fig. 1). In this study, we secured reliable coordinates for the AMNH 70723 specimen excluded from Helgen et al. (2013), and hence retained it, but excluded a specimen from Los Alpes, Florida, Valle del Cauca, Colombia (Universidad del Valle, UV 12736) due to high georeferencing uncertainty (Supplementary Data SD1). For this specimen, coordinates and elevation (2,250 m) given in Saavedra-Rodríguez et al. (2011) did not match, and we could not find the Los Alpes locality on maps or in gazetteers.

Addition of citizen science records expanded the data set, leading to the inclusion of several areas not represented by museum specimens (9 unique localities plus 1 photo voucher from Helgen et al. [2013] resulted in $n = 10$; Fig. 4; Supplementary Data SD3). Spatial filtering reduced the overall occurrence data set from 25 (Fig. 1) to 16 localities, a majority

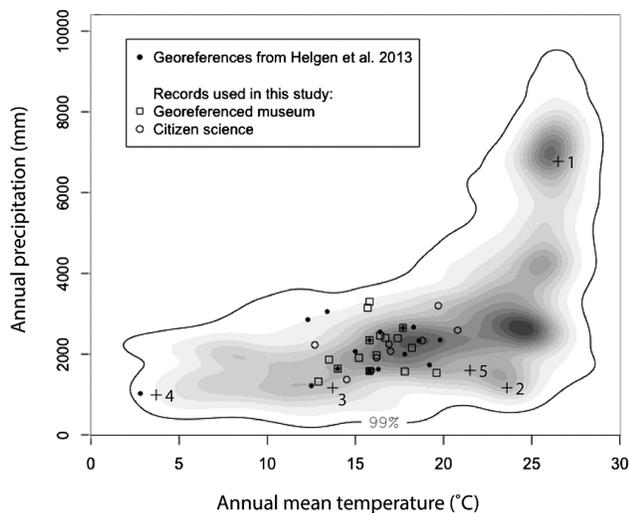


Fig. 2.—Comparison of environmental space for records of the olinguito (*Bassaricyon neblina*). Annual mean temperature and annual precipitation are plotted here for the georeferenced localities reported in the taxonomic revision (Helgen et al. 2013) and the newly georeferenced museum–citizen science localities. Records appear over a kernel density plot of the environments represented in the 100,000 background pixels within a 0.7° buffered minimum convex polygon (MCP) around occurrence records. The darker the gray, the more prevalent the environment within the MCP. All space within the black contour line demarcates the 99% kernel density of environmental conditions within the region. To serve as an altitudinal–environmental reference, well-known cities and locations from the projection region (0.7° bounding box around occurrence records) are indicated with a (+) symbol: 1) Quibdó, Colombia, 50 m; 2) Cali, Colombia, 1,000 m; 3) Quito, Ecuador, 2,700 m; 4) Cotopaxi Volcano, Ecuador, 4,112 m; and 5) Medellín, Colombia, 1,500 m.

of which derived from citizen science records (retained georeferenced museum records: $n = 7$; citizen science records: $n = 9$). Citizen science records came primarily from northern Ecuador and northern Colombia near Medellín. Of note, 1 locality fell about 65 km northeast of Medellín in the Carolina de Príncipe Municipality (locality 1; Fig. 1), extending the known geographic limits of the species approximately 65 km north (for more information on citizen science records see Supplementary Data SD3).

New information on taxonomic and natural history.—By consulting field notes and museum catalogs, we found 2 interesting pieces of information about the taxonomic and natural history of the olinguito not included in the original publication by Helgen et al. (2013).

One aspect concerned the vocalizations of the olinguito. We examined archived field notes from the Field Museum in Chicago for the late Phillip Hershkovitz, a curator there who collected 7 specimens of olinguitos. His field notes mention a *Bassaricyon* that was observed on the night of 23 April 1951 near Río Urrao, Urrao, Colombia (locality 7; Fig. 1). He heard a *Bassaricyon* making a sound that he had never heard an olingo make before. This *Bassaricyon* was whistling, and Hershkovitz noted that it was a “tweet-tweet rather than the tu-weet of *Potos*” and that the timbre of the call was different from that of the kinkajou (*Potos flavus*). Furthermore, he stated that he was able to collect the individual soon after. Indeed, an individual now recognized as an olinguito (FMNH 70722) was entered into Hershkovitz’ catalog on 24 April, the day after he cited hearing this mysterious *Bassaricyon*. As no other *Bassaricyon* was collected by Hershkovitz that day and in that region according to the FMNH Mammal database, we infer that this specimen was the “whistling” *Bassaricyon* obtained the night before, and then processed and labeled by Hershkovitz the subsequent day. Apparently, Hershkovitz was aware that this individual was behaviorally different from olingos he had previously observed, but he did not mention any additional morphological examination of the specimen in the field or museum after it was collected. This adds to information first provided by Poglayen-Neuwall (1976), and later reinterpreted by Helgen et al. (2013), that previously suggested (based on observations of a captive animal) that olinguitos have different characteristic vocalizations than other species of *Bassaricyon*.

We also found additional information about the early 20th century draft name “*Bassaricyon osborni*” (a name that was never formally published), associated with an olinguito specimen that had “Type” written on the skull (AMNH 32609), as discussed by Helgen et al. (2013). Helgen et al. (2013) observed that “this [label] may demonstrate a century-old intention, later discarded (probably by J. A. Allen or H. E. Anthony, see below), to name this taxon after Osborn” (i.e., Henry Fairfield Osborn, a paleontologist and President of the American Museum of Natural History). Upon examining the original specimen catalog from 1911, we now confirm that this had been the intention of J. A. Allen, curator of birds and mammals at the time. In the catalog alongside the specimen listing was written “Type: Allen.” Allen never published regarding this specimen, but

Helgen et al. (2013) later honored this forgotten intention when they named a subspecies of olinguito as *Bassaricyon neblina osborni*, though they ultimately chose a different (and more complete) type specimen for this taxon (FMNH 88476).

We also obtained additional information about the natural history of the olinguito through correspondence with local residents and researchers from Ecuador and Colombia and from other citizen scientists. For example, according to one correspondent, Gary Schiltz, olinguitos are seen eating fruit and are often found frequenting hummingbird feeders (G. Schiltz, in litt.). Schiltz often saw the olinguito in the backyard of his home near the Mindo Cloud Forest Reserve (Figs. 4E and 4F), and also stated that employees of the Bellavista Cloud Forest Reserve (about 10 km northeast) set up banana feeders specifically for the olinguito's use at night (G. Schiltz, in litt.). A researcher within the Caldas Municipality of the Department of Antioquia (Colombia) found the olinguito within a *Cupressus* sp. plantation, a tree species that is not native to Colombia (J. D. Sánchez, in litt.; Fig. 4G). It was previously thought that the olinguito may be a pristine forest specialist, but it seems that they may inhabit other types of habitat as well, although this is a single observation so far. Furthermore, we obtained multiple videos and images of the olinguito on the ground instead of within the canopy or understory, and there have been several confirmed instances of olinguitos being struck by cars (C. Delgado-Vélez, in litt.). Whether they are descending to the ground to forage for food or to move to different patches of suitable forest is unknown, but this indicates vehicular traffic as a source of mortality and another potential threat to the species.

Environmental comparison of original and newly georeferenced data sets.—The newly georeferenced museum and citizen science data show a tighter distribution of localities in environmental space than for the original ones from the taxonomic revision, meaning that the environments at each occurrence record are more similar in this data set (Fig. 2). For locality 22 (Fig. 1), this made a major difference in the associated environmental conditions (Fig. 2, bottom left). Notably, citizen science records also occur in warmer, wetter areas than in the original set of museum records. Similarly, examinations of the minimum and maximum values of each bioclimatic variable for the 2 data sets (Table 1) indicated that several variables, especially those describing temperature, had much lower values in the data set from the taxonomic revision than for the new one. Most of those extreme temperature values were driven downward by the Las Máquinas locality (locality 22; Fig. 1) that was formerly placed incorrectly to the east of the Corazón Volcano, Ecuador, at 4,350 m (Supplementary Data SD1).

Niche models.—Model building in ENMeval resulted in 32 candidate models with different feature class–regularization multiplier combinations. Here, we briefly present and compare the 2 respective models identified as optimal based on AICc scores and the sequential criteria (OR then test AUC)—neither of which corresponded to default settings. We then concentrate further consideration on the model that best matched known elevational associations for the species. Specifically, the sequential criteria resulted in selection of feature class Hinge with a

regularization multiplier of 3 as the optimal settings (hereafter H3; MTP OR: 0.0588; test AUC: 0.7189; Δ AICc: 23.68). Suitable areas extend from the northern extents of the Western and Central Andes of northern Colombia through to the Western and Eastern Andes of southern Ecuador. In addition, this model prediction shows regions of high elevation as suitable for the species (including areas at the peaks of mountains greater than 3,000 m predicted as suitable; Supplementary Data SD5A).

In contrast, the AICc criterion resulted in selection of feature classes linear and quadratic with regularization multiplier 1 (hereafter LQ1; MTP OR: 0.1176; test AUC: 0.7019; Δ AICc: 0). In comparison with the H3 model chosen via sequential criteria, the AICc-selected model predicts areas of higher elevation as less suitable. This prediction excludes most mountain peaks and crests higher than 3,000 m in elevation (Supplementary Data SD5B). Like the H3 model, the LQ1 model also shows low-elevation areas (1,300 m and below) as unsuitable, but has an overall narrower band of suitability due to the absence of suitable high-elevation areas. This model was chosen for all

Table 1.—The range of values of each variable used in ecological niche modeling of the olinguito (*Bassaricyon neblina*) for both the newly georeferenced data set and that from Helgen et al. (2013). Variables with asterisks are those that were incorporated in the final distribution model (nonzero lambda weights in Maxent model). Temperature variables are measured in °C, with the exception of isothermality (a unitless ratio) and temperature seasonality, which is the standard deviation of values in °C multiplied by 100 (Hijmans et al. 2005). Precipitation variables are measured in mm except for precipitation seasonality, the unitless coefficient of variation (Hijmans et al. 2005).

Bioclimatic variables	Georeferenced museum–citizen science records	Records from Helgen et al. (2013)
Annual mean temperature	12.7–20.8	2.8–19.8
Mean diurnal range	8.9–13.2	8.3–13.2
Isothermality	80–92	84–92
Temperature seasonality*	10.7–49.7	13.8–36.3
Max temperature of warmest month	17.6–27.1	7.8–26.8
Min temperature of coldest month*	6.5–15.2	–1.9–13.6
Temperature annual range	9.9–15.5	9.7–15.5
Mean temperature of wettest quarter	12.5–21.1	3.0–19.4
Mean temperature of driest quarter	12.4–20.6	2.2–19.9
Mean temperature of warmest quarter	12.9–21.3	3.0–20.0
Mean temperature of coldest quarter*	12.4–20.2	2.2–19.4
Annual precipitation	1320–3297	1025–3054
Precipitation of wettest month*	196–493	146–464
Precipitation of driest month*	18–121	18–120
Precipitation seasonality	20–64	23–64
Precipitation of wettest quarter	497–1341	374–1237
Precipitation of driest quarter	92–399	90–421
Precipitation of warmest quarter	267–989	244–957
Precipitation of coldest quarter	92–1341	90–1143

further interpretation because it has more reasonable predictions in high-elevation areas. The elevations predicted as suitable in the H3 model were much too high, as the maximum elevation record for the species is 2,890 m (locality 22; Fig. 1; for further explanation of models and parameter weights see Supplementary Data SD4a and SD4b).

After removing various areas in the prediction beyond likely dispersal barriers, the model showed intuitive and reasonable geographic patterns in suitability. The areas of highest suitability include: 1) northern Ecuador, stretching between Imbabura and Cotopaxi provinces; 2) northern Colombia within the Western and Central Andes of the Antioquia Department; and 3) the center of the Western and Central Cordilleras of Colombia within the Cauca Department (Fig. 3A). The model also predicts a long stretch of less suitable area along the eastern slope of the Central Cordillera of Colombia. Most environments within the projection region were also present within the study region used for model calibration, simplifying interpretations (MESS analysis; Supplementary Data SD6). Some lowland areas did show heavy extrapolation into non-analog conditions (i.e., between the Central and Eastern Cordilleras of Colombia, east of the Eastern Cordillera of Colombia, and southwestern Ecuador). However, because these non-analog areas corresponded to environmental conditions far beyond

those considered suitable for the species, the possible issue of extrapolation did not pose a significant complicating factor in the interpretation of the model projection (MESS analysis; Supplementary Data SD6).

DISCUSSION

Understanding the distributions of newly discovered or poorly studied species is essential for short- and long-term conservation planning. Geographic distributions are often the most important sources of information used to determine the IUCN threat category for a species (IUCN 2012). Therefore, making better-informed, accurate geographic estimates for a species is a vital tool for delimiting areas of special conservation concern. Here, we generated a niche model for the olinguito that more accurately depicts potentially suitable areas for the species than previous estimates. However, these estimates are conservative in that they only include suitable and likely accessible areas that are not found beyond large gaps in suitability and likely dispersal barriers, which excludes suitable regions distant from areas without observations of the species (such as southern Ecuador and northern Peru). Furthermore, we highlight regions in need of greater sampling aimed at the discovery of new populations, which is an important use of ENMs in terms of conservation science.

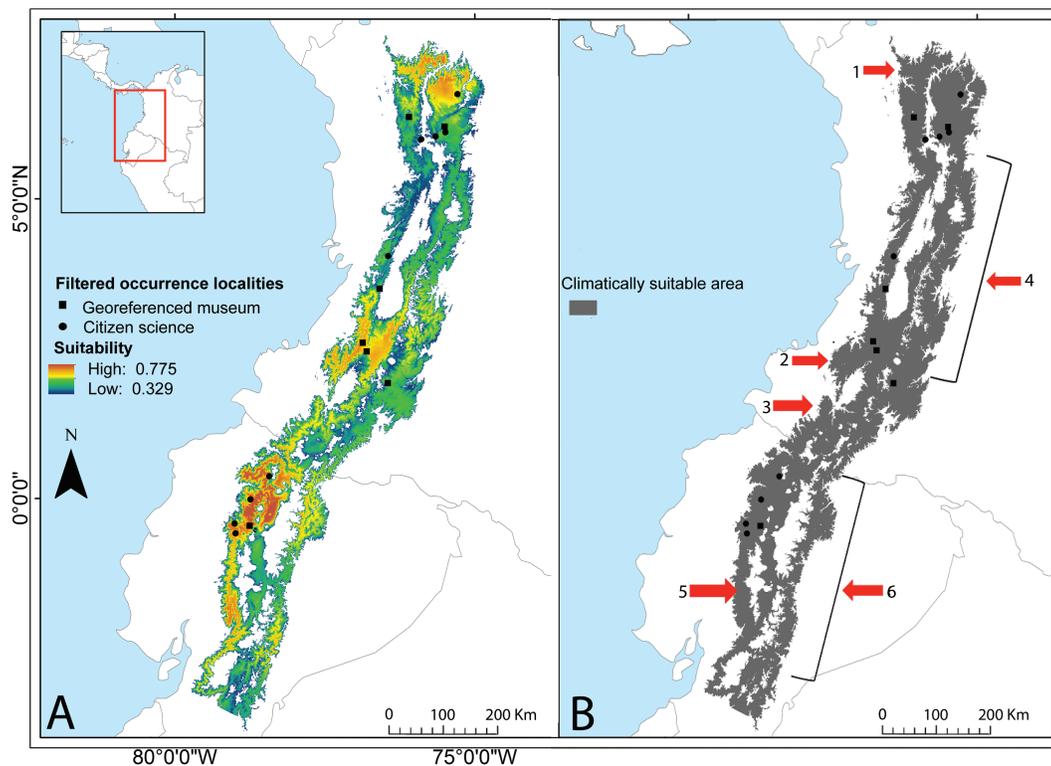


Fig. 3.—A) Final Maxent prediction of climatically suitable areas for the olinguito (*Bassaricyon neblina*). The prediction illustrated here was chosen as optimal via the Akaike's Information Criterion corrected for small sample size (AICc) approach, and then projected to a larger study region from southern Ecuador to the Western and Central Cordilleras of Colombia. Areas below the minimum training presence were clipped from the model (suitability lower than 0.329). B) Final binary model showing climatically suitable areas in need of future sampling (arrows). These areas lack occurrence records, possibly due to sampling bias. These areas include: northern portion of the Western Cordillera of Colombia (1), southern portion of the Western Cordillera of Colombia (2), western slopes of the Andes in southwestern Colombia (3), both versants of the middle portion of the Central Cordillera of Colombia (4), western slopes of the Andes in central and southern Ecuador (5), and eastern slopes of the Andes in Ecuador (6).

Model interpretation.—The final model, made using newly georeferenced museum and citizen science data, shows better elevational discrimination than the model from the taxonomic revision, and also predicts patterns that align more closely with what is expected for a species restricted to the cloud forest in terms of climate and elevation (Foster 2001; Jarvis and Mulligan 2011). The earlier study predicted suitable areas within the Central Cordillera of Colombia substantially above 3,000 m, whereas in the present model those mountain peaks have low suitability. As the highest elevation for an olinguito record is 2,890 m, it is reasonable to discount models that predict suitable areas substantially higher. In addition, researchers such as G. H. H. Tate and P. Hershkovitz made an effort to collect small and mid-sized mammals in high-elevation areas (Anthony 1921, 1923, 1924; also see records of other species in AMNH and FMNH Mammal Databases consulted 2016) at about the same time they collected olinguito specimens, indicating that the lack of high-elevation records is not solely due to collection bias.

The differences between our model and the original from Helgen et al. (2013) are likely due to multiple factors. In addition to modeling protocols, these also include corrected georeferences, addition of citizen science records, and the chosen threshold for the prediction maps. For the corrected georeferences, elevational changes were probably most important, as differences in elevation can mean large discrepancies in environmental conditions (as seen for the Las Máquinas locality, AMNH 66753; Fig. 2: bottom left). Furthermore, new citizen science records associated with warmer areas (Fig. 2) likely played a role in the final model deeming cold, high-elevation areas as unsuitable. Present results also predict more extensive suitable areas in northern Colombia (Fig. 3A), possibly due to the addition of citizen science data (4 new records in this area; Fig. 1). Lastly, the low threshold used to make the binary range maps (mean equal training sensitivity and specificity: 0.160) in the original study (Helgen et al. 2013) may have been too low, leading to overprediction in high-elevation areas.

The differences in suitability for high-elevation areas between the H3 model (chosen here via sequential criteria) and our final model (LQ1 chosen via AICc approach) are potentially a general rule of these 2 approaches to model selection (Galante et al. 2017). The sequential criteria first select the models with the lowest OR. As low omission is prioritized, this can sometimes result in selection of models that overpredict suitable areas. Furthermore, for the LQ1 model, one of the highest contributing variables (as assessed by lambda weights; Supplementary Data SD4a) was temperature of coldest quarter (Bio 11). For this model, the species' response curve for this variable showed an increase in suitability with higher temperature (leading to low modeled suitability at the highest-elevation areas). In contrast, the H3 model shows no temperature-related variable with a similar response (Supplementary Data SD4b). This evidently caused the H3 model to predict high suitability for high-elevation areas. Our final selection of the LQ1 model based upon the lack of biological realism for the H3 model in

geographic space also corresponds to an intuitive pattern in environmental space.

The final model (Fig. 3A) highlights 6 high-suitability areas with no vouchers that should be high priority for sampling: the northern portion of the Western Cordillera of Colombia (1; Fig. 3B), southern portion of the Western Cordillera of Colombia (2; Fig. 3B), western slopes of the Andes in southwestern Colombia (3; Fig. 3B), both versants of the middle portion of the Central Cordillera of Colombia (4; Fig. 3B), western slopes of the Andes in central and southern Ecuador (5; Fig. 3B), and the eastern slopes of the Eastern Andes in Ecuador (6; Fig. 3B). These are areas that the model predicts as climatically suitable, but lack occurrence records. This is possibly due to sampling bias and thus indicates the need for further investigation that may uncover more olinguito populations.

The distributional estimates of the species signal possible important aspects of its ecology. Cloud forests around the world can exhibit a range of conditions (Foster et al. 2001; Jarvis and Mulligan 2011), but the climate is usually humid and moderately cool, with average precipitation of 2,000 mm/year and average temperatures of 17.7°C (Jarvis and Mulligan 2011). Here, the final model (Fig. 3A) indicates areas with high precipitation and temperatures ranging from cool to moderately warm as suitable. Areas with extreme conditions (i.e., very cold, high-elevation areas; very warm, low-elevation areas; and areas with extremely high precipitation such as the Chocó) are deemed unsuitable. Thus, these results make intuitive sense for a tropical cloud forest animal.

Cloud forest species like the olinguito are particularly vulnerable to climate change, largely due to their narrow elevational requirements (Ramirez-Villegas et al. 2014) and geographic restriction by the cloud layer and tree line (Foster 2001; Rehm and Feeley 2015). This information reinforces the concern that climate change likely constitutes a threat to this species as temperatures in these areas increase. Patterns regarding ongoing changes in precipitation also constitute a key factor for this species, but they are less resolved in climate change projections (Kirtman et al. 2013).

Citizen science and flagship species.—Citizen science has the potential to lead to diverse kinds of knowledge, especially for charismatic easy-to-observe species. The description of the olinguito as a new species (Helgen et al. 2013) received extensive global publicity, with photographs featured heavily in news stories. This publicity helped establish the olinguito as an additional flagship species for the Northern Andes, alongside the spectacled bear (*Tremarctos ornatus*), serving as a charismatic representative around which to increase conservation efforts (Ríos-Uzeda et al. 2006). This publicity also served to encourage citizens to look for olinguitos, and to contact KMH and RK with possible records. Such information led to the interesting discovery that olinguitos were sometimes observed to be active during the day. This pattern of some diurnal activity is also seen in the northern olingo (*Bassaricyon gabbi*) in Monteverde, Costa Rica, where the species is often fed by humans near the tourist lodge there (Helgen et al. 2013). It is currently unclear if the olinguito demonstrates this same behavior only due to



Fig. 4.—Photo vouchers for various citizen science localities of olinguitos (*Bassaricyon neblina*) found in Colombia and Ecuador. A) La Herradura, Antioquia Department, Colombia (photo credit: Iván Muñoz); B) Paz de las Aves, a private reserve near Nanegalito, 65 km North of Quito, Ecuador (photo credit: Kristof Zyskowski); C) Siempre Verde cloud forest reserve, adjacent to Cotacachi-Cayapas Ecological Reserve, Ecuador (photo credit: Alex Reynolds); D) Mesenia-Paramillo reserve, Antioquia Department, Colombia (photo credit: Gustavo Suárez); E and F) “Los Loros Locos,” private reserve near Mindo, Ecuador (photo credit: Gary Schiltz); G) *Cupressus* plantation (native understory), Caldas, Antioquia Department (photo credit: Paula Saravia and Juan David Sánchez); H) San Sebastián-La Castellana (local reserve), Envigado, Antioquia Department, Colombia [photo credit: Juan David Sánchez]; I) El Saladito, Envigado, Antioquia Department, Colombia (photo credit: Juan David Sanchez); J) Tandayapa Bird Lodge, Quito, Ecuador (Helgen et al. 2013; photo credit: Mark Gurney).

proximity to feeders or humans, and if this represents a bias by birdwatchers only photographing during the day, highlighting the need for future camera-trapping studies that would not include such a sampling bias.

In total, our correspondence with residents, tourists, and researchers in Colombia and Ecuador led to 9 new unique occurrence records, increasing the available data set by 60% and substantially improving our understanding of this species' distribution. This shows the direct potential for citizen science to contribute to our understanding of flagship species, especially those new to science. These records also offer examples of how the olinguito has already contributed to conservation of the region. One conservation group ([SavingSpecies 2015](#)) has used the olinguito photograph from their region to raise funds to buy critical cloud forest habitat in Antioquia, Colombia near Jardín, which is needed to connect 2 other preserves (www.savingspecies.org). Furthermore, a majority of our citizen science records came from ecotourism lodges such as in the Paz de las Aves Reserve ([Fig. 4B](#)), Bellavista Cloud Forest Reserve, and the Tandayapa Bird Lodge in Ecuador ([Fig. 4J](#)), many of which use olinguito photographs in advertisements. This highlights the potential for olinguitos to attract more visitors to the region. As such, ecotourism has potential to create a self-sustaining conservation program for the species ([Brightsmith et al. 2008](#)), protecting land not only for olinguitos, but also for other species inhabiting Andean cloud forests, both known and unknown to science.

Future directions.—ENMs built on climate data are important tools for understanding species distributions both in the present and the future, and can make useful predictions about the potential effects of climate change, which have strong implications for species conservation. Building upon the updated occurrence records and niche models provided here, future research should consider deforestation and anthropogenic climate change in updating the formal IUCN conservation assessment for the species under criteria related to the extent of occurrence ([IUCN 2012](#)). Because the distribution of the olinguito is likely to be continually constricted by both climate change and deforestation, further analysis of their current and future distributions is necessary, along with the inclusion of more citizen science localities. A promising avenue for obtaining new citizen science records for the olinguito is through an established iNaturalist project ([Kays 2014](#)) where locals and researchers can upload their own sightings and corresponding localities for the species. Including new records obtained through both iNaturalist and public outreach in these future analyses may lead to a different IUCN prognosis.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Information used to georeference museum occurrence records.

Supplementary Data SD2.—Data sources for georeferencing of all museum records mentioned in the taxonomic revision ([Helgen et al. 2013](#)).

Supplementary Data SD3.—All citizen science localities are included here, along with their associated sighting dates, sources, and coordinates.

Supplementary Data SD4a.—Coefficients of environmental variables for both *Bassaricyon neblina* Maxent models ordered by weight.

Supplementary Data SD4b.—Response curves for the 3 highest contributing environmental variables for each of the 2 selected *Bassaricyon neblina* Maxent models.

Supplementary Data SD5.—Maps showing high-elevation areas predicted as climatically suitable by both model selection approaches (AICc and performance on withheld data).

Supplementary Data SD6.—Multivariate Environmental Suitability Surface (MESS) analysis.

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