Expanded Distribution and Predicted Suitable Habitat for the Critically Endangered Yellow-tailed Woolly Monkey (*Lagothrix flavicauda*) in Peru

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Submission date: 5/19/22

ABSTRACT

The Tropical Andes Biodiversity Hotspot holds a remarkable number of species at risk of extinction due to anthropogenic habitat loss, hunting and climate change. One of these species, the Critically Endangered yellow-tailed woolly monkey (*Lagothrix flavicauda*), was recently sighted in Junín region, 206 kilometres south of its previously known distribution. The range extension, combined with continued habitat loss, calls for a re-evaluation of the species' distribution and available suitable habitat. Here, we present novel data from surveys at 53 sites in the regions of Junín, Cerro de Pasco, Ayacucho and Cusco. We encountered *L. flavicauda* at 9 sites, all in Junín, and the congeneric *L. l. tschudii* at 20 sites, but never in sympatry. Using these new localities along with all previous geographic localities for the species, we made predictive Species Distribution Models based on Ecological Niche Modelling using a generalized linear model and maximum entropy. Each model incorporated bioclimatic variables, forest cover, vegetation measurements, and elevation as predictor variables. Model evaluation showed >80% accuracy for all measures. Precipitation was the strongest predictor of species presence. Habitat suitability maps illustrate potential corridors for gene flow between the southern and northern populations, although much of this area is inhabited by *L. l. tschudii*. An analysis of the current protected area (PA) network showed ~47% of remaining suitable habitat is unprotected. With this, we suggest priority areas for new protected areas or expansions to existing reserves that would conserve potential corridors between *L. flavicauda* populations. Further surveys and characterization of the distribution in intermediate areas, combined with studies on genetic flow, are still needed to protect this species.

Key Words (7/8 used): *Oreonax*, Maxent, Generalized Linear Modelling, Conservation, Species Distribution Modelling (SDM), Range Expansion

Introduction

Changes in species' distributions are of major concern for conservationists due to the continual expansion of human populations and land use (Hansen *et al.* 2001; Newbold *et al.* 2014; Dai *et al.* 2021) that shift, contract, or fragment a species' geographic range. Such altered ranges may isolate populations, enhancing the likelihood of inbreeding depression or local extinction (Ewers and Didham 2005; Calkins *et al.* 2021; Solórzano-Garcia *et al.* 2021). Information on the relative distributions of different populations of a species can reveal what types of landscapes or species community composition—in the case of competitive exclusion—act as geographic or ecological barriers to gene flow (Case and Taper 2000; Blair and Melnick 2012; Sales *et al.* 2019; Pázstor *et al.* 2020). To conserve natural biodiversity in the face of expanding land use by humans, conservation management must operate on a landscape scale, understanding species-ecosystem relationships and species' responses to habitat change (Bellamy *et al*. 2013; Robillard *et al.* 2015; Xioa *et al.* 2019). Informed management planning involves understanding the true current distribution of a species and the necessary habitat components to predict how distribution changes will occur in the future, and the best possible options for area protection.

The yellow-tailed woolly monkey (*Lagothrix flavicauda*) is considered Critically Endangered and amongst the most threatened primate species in the world (Mittermeier *et al.* 2012; Shanee *et al.* 2021), making it a key focus of conservation initiatives in northern Peru (Shanee *et al.* 2018). The Tropical Andes Biodiversity Hotspot (TABH), to which the species is endemic, is among the top five hotspots predicted to lose the most biological diversity due to continued anthropogenic activities (Brooks *et al.* 2002). In northern Peru, the greatest threat to species and habitats in the TABH is habitat destruction for cattle ranching, logging, and other, mainly small

70 scale, economic activities, fuelled by a growing human population and aided by the construction
71 of highways and incentivized access to lands (Oliveira *et al.* 2007; Shanee 2011; Shanee 2012;
72 Programa Bosques 2015; GIZ 2016; Laurance 2018; Shanee and Shanee 2016). With this migrant
73 economic development, roads are continuously built to access new areas, creating a cycle of
74 increasing deforestation for the extraction of resources and settlement (Gallice, Larrea-Gallegos
75 and Vázquez-Rowe 2019). Hunting of primates for bushmeat and the pet trade is also putting *L.*
76 *flavicauda* and other species at further risk (Shanee 2011; Shanee 2012; Shanee *et al.* 2017).

77 The geographic range of *L. flavicauda* – long thought to be restricted to the northern regions
78 of Amazonas and San Martín and neighbouring areas of Huánuco, La Libertad, and Loreto – has
79 been continuously re-evaluated through survey efforts (Mittermeier, de Macedo-Ruiz, Luscombe
80 1975; Graves *et al.* 1980; Leo Luna 1980; Parker and Barkley 1981; Butchart *et al.* 1995; Shanee
81 *et al.* 2007; Shanee 2016; Shanee 2011). Recent observations in the region of Huánuco have found
82 *L. flavicauda* populations as far as the south eastern border with the region of Pasco (Aquino *et al.*
83 2015; Aquino, Garcia and Charpentier 2016). Camera trap observations led to the discovery of a
84 new population of *L. flavicauda* in 2018 (McHugh *et al*. 2020). This new population, in the
85 Inchatoshi Kametsha Conservation Concession, Junín, is about 206 km south of the previously
86 known southern range limit for the species (McHugh *et al.* 2020), with no sightings in intermediate
87 areas.

88 *Lagothrix flavicauda* is generally restricted to montane forests between 1,400 to 2,800 m
89 above sea level (m.a.s.l.) along the eastern slopes of the Andes (Aquino *et al*. 2017, Shanee 2011),
90 with occasional occurrences below this elevation (Allgas *et al.* 2014; Paterson and Lopez Wong
91 2014). Their preferred habitat depends on local climate and forest composition (Shanee 2016;
92 Almeyda-Zambrano *et al.* 2019), and they are able to survive at least for a time in moderately

93 disturbed habitats when hunting pressure is low (Aquino *et al*. 2015; Shanee and Shanee 2015).
94 This may be, in part, due to a flexible diet consisting of flowers, leaf petioles, epiphytic roots,
95 vertebrates, and soil, although they are predominantly frugivorous. Fruits make up almost half of
96 their dietary intake, which is dominated by a handful of species and genera with large fleshy fruits
97 (Shanee and Shanee 2011, Shanee 2014; Fack *et al.* 2018), making food tree density and phenology
98 important factors for sustaining viable populations. Previous studies suggest that the protected area
99 (PA) network in northern Peru is insufficient to protect *L. flavicauda* from the consequences of
100 human population growth, habitat degradation, and climate change (Buckingham and Shanee
101 2009; Shanee 2016). As the number of PAs in Peru change, along with our knowledge of primate
102 species distributions, it is critical to re-assess their coverage with current data.

103 Many conservation and research initiatives use *L. flavicauda* as a flagship species in Peru
104 (Shanee *et al*. 2018). Although these have led to an increasing number of private, communal, and
105 state PAs within the species distribution (Shanee *et al.* 2017; Shanee *et al.* 2020), they have
106 predominantly focused on populations in Amazonas and San Martín (Shanee and Shanee 2015).
107 Field surveys are vital to determining the species' distribution and habitat preferences outside these
108 well-studied regions; however, they are often expensive, time consuming, and can be unfeasible
109 depending on the terrain, access, and public order limitations (Young 1996; Shanee and Shanee
110 2016). Predictive species distribution modelling (SDM) can highlight optimal areas for field
111 surveys through comparison of the ecological conditions found within a given species' known
112 range, with those across a wider area, showing where conditions are most favourable for the
113 species presence (Phillips, Anderson and Schapire 2006; Ramirez-Villegas *et al.* 2014; Guisan,
114 Thuiller and Zimmerman, 2017).

Species' distributions are predicated on three main conditions: the species must have the means to disperse into and out of a habitat, the habitat must have the correct combination of environmental variables to make it suitable, and the abiotic conditions must be able to maintain necessary species interactions (Guisan *et al.* 2017). SDM considers the second condition by using known habitat parameters to determine which are most important to the distribution of the focal species, and uses them to locate potentially suitable habitat (Dong *et al*. 2019; Cianfranni *et al.* 2010; Liu *et al.* 2019). Such modeling may be used to prioritize search efforts when financial or human resources are not available for surveying a region of interest in person. For endangered species, analyzing correlations between these variables and known species occurrences can highlight conditions which the species requires for its long-term survival in the region of interest, and can be used to develop more effective conservation strategies. With this, conservationists can determine why a species may not be present in a particular area (Liu *et al.* 2019) or increase research and conservation effort in areas that appear to be suitable (LaRue and Nielsen 2008).

Here we compare the results of two SDM approaches—Generalized Linear Modelling (GLM) and Maximum Entropy (MaxEnt)—using the results of our recent field surveys in central and southern Peru. We created SDMs combining these novel localities with all previous records to create the most complete SDM for the species to date. We use the results of these approaches to highlight remaining suitable *L. flavicauda* habitat, particularly in its less-studied southern range. Finally, we evaluate the current Peruvian PA network's coverage of suitable habitat within the species' distribution, noting priority areas for new PAs, conservation corridors, and future surveys between the northern and recently-discovered Junín populations.

Methods

Population Surveys

We conducted five surveys between May 2019 and May 2021. Due to Covid-19 related travel restriction, no surveys were conducted between May and December 2020, with the May 2020 survey being cut short due to implementation of national quarantine measures. Surveys were carried out in the regions of Ayacucho, Cerro de Pasco, Cusco, and Junín. Survey sites were selected based on preliminary MaxEnt models which used previously published localities, and updated with new sightings as the study progressed, with sites selected considering access routes, land ownership and researcher safety.

Survey efforts followed methods of previous surveys for the species (Shanee 2011). We gathered locality data along existing trail systems with local residents as field guides. Occasionally new trails were opened to enter new areas; however, this was typically avoided to minimize habitat disturbance. We visited sites for 2-9 days, with effort determined by available habitat size, and the possibility of *L. flavicauda* being found or confirmation of its presence. We recorded localities and points of visual or audio detection of all primates with a handheld GPS. We also gathered secondary evidence from local informants in and around the areas visited. Using images and verbal descriptions of *Lagothrix* spp. we cross-referenced information from multiple informants at each site.

Species Distribution Modelling

We selected two standard SDM methods— GLM and MaxEnt. To avoid overestimation of suitable habitat, we limited prediction outputs to between -80° W and -65° W, and -5° S and -15° S. We filtered this to only include areas between 1,000 and 3,500 m.a.s.l., i.e., within the species'

161 altitudinal range, which includes the entirety of the eastern slopes of the Peruvian Andes. Models
162 used presence points from our own surveys combined with localities from recent published studies,
163 i.e., ≤10 years (Shanee 2011; Allgas *et al*. 2015; Aquino *et al*. 2016; Aquino *et al.* 2017; McHugh
164 *et al.* 2020), and an additional six localities from the Global Biodiversity Information Facility
165 (GBIF Secretariat 2021) (Fig. 1; Table S1).

166 Environmental data were all from publicly available sources (Table S2). We used the 19
167 bioclimatic variables from *WorldClim2*, available in the R package raster v. 3.1-5 (Hijmans *et al.*
168 2020) and elevation data from the NASA Shuttle Radar Topography Mission (SRTM; v. 4) at 30-
169 meter resolution. We used forest cover data from the Global Forest Change (v. 1.7) dataset of
170 percent tree cover from the year 2000, in which tree cover is given as a gradient of percentage
171 canopy connectivity per 30 m pixel for vegetation taller than 5 m. Forest loss and gain between
172 the years 2000 and 2018 were also analyzed, but were excluded from the model due to an
173 insufficient number of areas experiencing any recorded loss or gain (fewer than 10 pixels within
174 the study region, which did not coincide with the location of any presence points). We also used
175 the Vegetation Health Product (VHP) dataset, at 1 km resolution, from the NOAA Centre for
176 Satellite Applications and Research, which has been created from an algorithm providing estimates
177 of moisture, thermal, and wind conditions in combination with infrared imaging to achieve an
178 estimate of vegetation conditions in response to weather impacts. All data layers were re-sampled
179 to 30 m resolution.

180

181 *Generalized Linear Model*

182 All GLMs were evaluated in R (v. 3.5.2; R Core Team 2018). We modelled the ecological
183 niche of *L. flavicauda* as a binomial response variable of presence/pseudoabsence using a binomial

184 variance and logistic link function. We randomly selected pseudoabsence points to counter
185 sampling bias from the lack of absence data existing for the species using the *randomPoints*
186 function in the *dismo* package v.1.1-4 (Hijmans *et al.* 2017), generating 355 in the study area
187 within an elevation mask including only areas within the altitudinal range. All presence points
188 were excluded from the background point extraction process. We then extracted and standardized
189 values from all environmental layers at each pseudoabsence and presence point to be used in the
190 models. Models were built excluding correlated predictor variables based on Pearson's *r* value (±
191 0.75). Our final model was selected using the corrected Akaike Information Criterion (AICc)
192 procedure (Akaike 1973; Hurvich and Tsai 1993).

193 We evaluated the predictive ability of our model using the area under the ROC curve
194 (AUC), which summarizes model accuracy by giving the probability that the model ranks random
195 presence sites over pseudoabsence sites. We calculated the AUC by building the models from a
196 training set, and then applying it to the remainder of the data as a test set to evaluate predictive
197 performance (Fielding and Bell 1997; Hirzel *et al.* 2006). Due to the relatively small number of
198 presence points, we bootstrapped this process 1000 times using multiple distributions of presence
199 data in the training and testing sets (Hein *et al.* 2007; Guisan *et al.* 2017). We also tested model
200 accuracy using Cohen's kappa statistic and percent accuracy from a confusion matrix as a
201 threshold-dependent method of evaluation (Guisan *et al.* 2017). Using training and test data, we
202 set a probability threshold so that any point with a presence probability of 0.4 or higher was marked
203 as a presence when establishing a confusion matrix of model predictions. The kappa statistic value
204 ranges from -1 (complete disagreement between predicted and actual values) to 0 (predictions
205 equated to random chance), to +1 (complete agreement with actual values).
206

207 *Maximum Entropy Model*

208 The MaxEnt model was created and evaluated in MaxEnt Programming Software (v. 3.4.4;
209 Phillips 2006) and re-evaluated in R. We applied default settings to our MaxEnt run, with the
210 following exceptions: background predictions were written for evaluation and mapping purposes
211 and we selected a random test percentage of 25% of our presence points. We used the same non-
212 correlated variables as in the GLM. MaxEnt measures variable contribution by permutation
213 importance determined by randomly permuting the values of each variable among the training
214 points, measuring the resulting decrease in training AUC, and normalizing these values to give a
215 percentage (Phillips *et al.* 2006). MaxEnt evaluates the model using a ROC curve and calculating
216 the model AUC. We corroborated the given value by bootstrapping the AUC calculation 1000
217 times in R using the background prediction values.

218

219 *Suitable Habitat Classification and Protected Area Assessment*

220 To assess habitat suitability, we assigned habitat based on the predicted probability of
221 species presence to categories of "Good" (P(robability of species presence) between 0.25 and
222 0.75), "Very Good" (P>0.75), and "Low" (P<0.25), with "Good" and "Very Good" being
223 considered suitable habitat. To incorporate the probable impact of hunting into our results, we
224 considered habitat within 1 km of human settlement to have high hunting pressure for *L. flavicauda*
225 (Shanee 2016). We used data from Humanitarian OpenStreetMap Team (2020) to distinguish
226 human settlements, and deemed any suitable habitat within a 1 km buffer of settlement as low
227 suitability. We overlaid the suitable habitat predicted by both models to find where the predictions
228 intersected. Finally, we conducted an analysis of the PA coverage of suitable *L. flavicauda* habitat
229 by overlaying the Peruvian PA network from the World Database of Protected Areas (WDPA;

230 UNEP-WCMC 2020) with the habitat predictions and calculated the percent of habitat that was
231 considered Good or Very Good within the network. This was repeated with the network of non-
232 governmental conservation concessions in Peru, downloaded from the National Forestry Service
233 (SERFOR), as these concessions are not included in the WDPA files.
234
235 *Data Accessibility*
236 All open-source data used for modelling are openly accessible via the links provided in
237 the references. Presence data, prediction results, and all code can be found at
238 https://doi.org/10.5061/dryad.dz08kps0g.
239

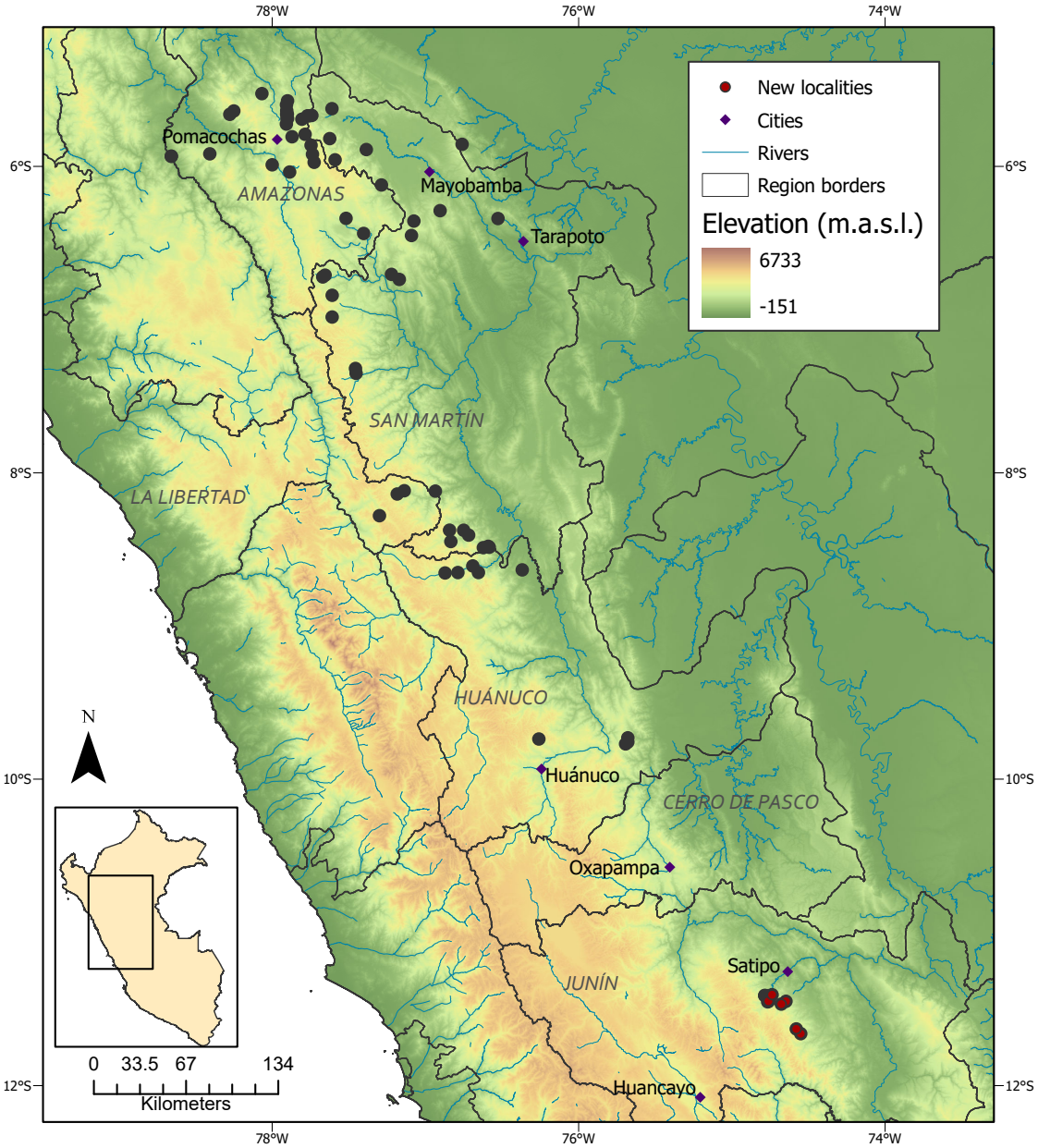

Fig. 1 *Lagothrix flavicauda* occurrences used as presence points in habitat suitability modelling (HSM) in this study.

Results

Population Surveys

In total we surveyed 53 new sites in central and southern Peru. We encountered *L. flavicauda* at 9 of these sites, all to the north of the Mantaro river in Junín (Fig. 2). In surveys south of this point we did not find any evidence of the species, from our own surveys or from local

informants, suggesting a possible southern limit for the species between ~11.6 and ~12° south (Table 1). We recorded the congeneric Peruvian woolly monkey (*L. lagotricha tschudii*) at 20 sites, both north and south of the southern *L. flavicauda* population. At no sites were the species sympatric.

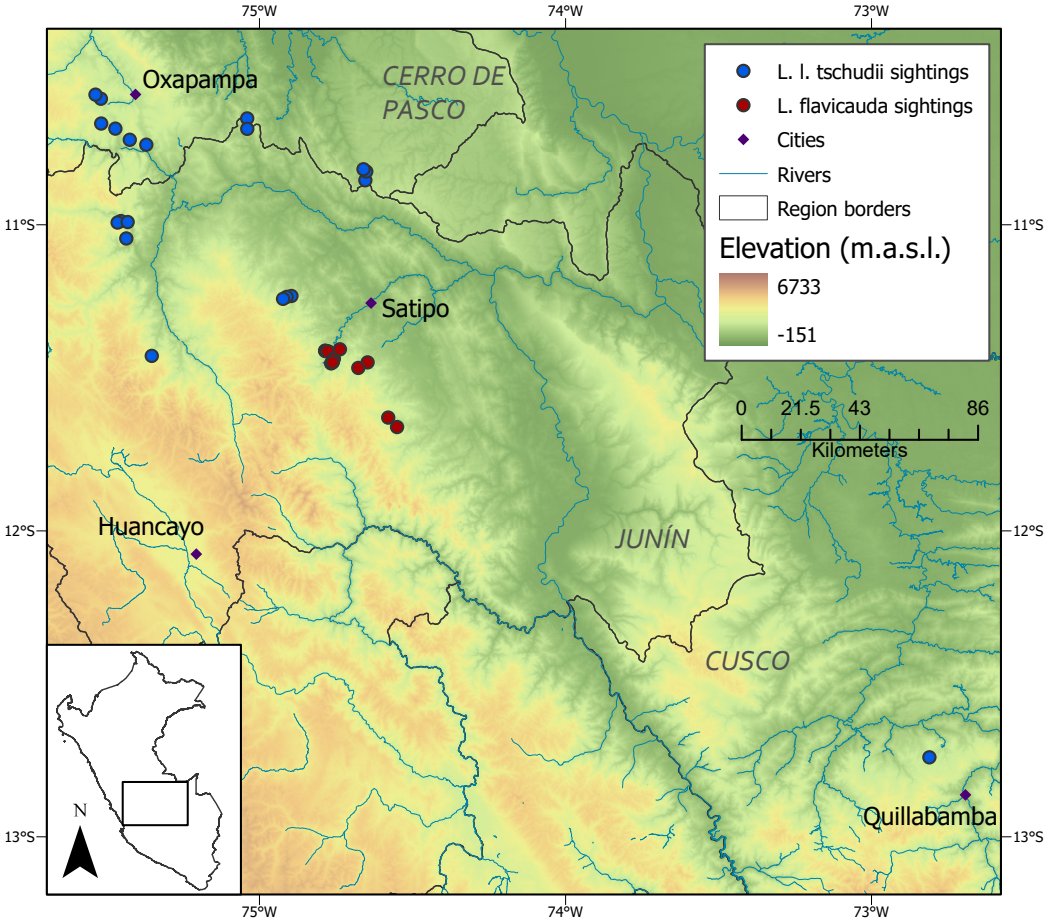

Fig. 2 Survey results for *L. flavicauda* and *L. lagotricha tschudii*.

Table 1. Coordinates where *L. flavicauda* and *L. l. tschudii* were found in our surveys.

Region	Species	Longitude	Latitude	m.a.s.l.
Junín	*L. flavicauda*	-74.7659	-11.4530	2179
Junín	*L. flavicauda*	-74.7568	-11.4378	1869
Junín	*L. flavicauda*	-74.7609	-11.4490	1866
Junín	*L. flavicauda*	-74.6467	-11.4496	1609
Junín	*L. flavicauda*	-74.6770	-11.4678	1825
Junín	*L. flavicauda*	-74.7609	-11.4490	1866
Junín	*L. flavicauda*	-74.5504	-11.6610	2012

Junín	*L. flavicauda*	-74.5793	-11.6301	2067
Junín	*L. flavicauda*	-74.7372	-11.4069	1422
Pasco	*L. l. tschudii*	-75.4709	-10.6859	1410
Pasco	*L. l. tschudii*	-75.3698	-10.7384	1257
Pasco	*L. l. tschudii*	-75.4238	-10.7223	1323
Pasco	*L. l. tschudii*	-75.5182	-10.5882	1612
Pasco	*L. l. tschudii*	-75.5358	-10.5748	2088
Pasco	*L. l. tschudii*	-75.5171	-10.6693	2349
Junín	*L. l. tschudii*	-75.4529	-10.9879	1771
Junín	*L. l. tschudii*	-75.4635	-10.9928	2490
Junín	*L. l. tschudii*	-75.4307	-10.9911	1622
Junín	*L. l. tschudii*	-75.4352	-11.0447	1672
Junín	*L. l. tschudii*	-75.3518	-11.4285	2365
Junín	*L. l. tschudii*	-74.8955	-11.2327	1609
Junín	*L. l. tschudii*	-74.9112	-11.2358	1795
Junín	*L. l. tschudii*	-74.9229	-11.2421	1080
Pasco	*L. l. tschudii*	-74.6540	-10.8546	1465
Pasco	*L. l. tschudii*	-74.6510	-10.8259	1410
Pasco	*L. l. tschudii*	-74.6600	-10.8186	1257
Pasco	*L. l. tschudii*	-75.0401	-10.6526	1323
Pasco	*L. l. tschudii*	-75.0399	-10.6866	1612
Cusco	*L. l. tschudii*	-72.8110	-12.7401	1948

Species Distribution Modelling

After the multicollinearity reduction, the GLM with the lowest AICc (242) contained elevation, mean diurnal temperature range, isothermality, precipitation of wettest month, precipitation seasonality, precipitation of coldest quarter, percent forest cover and VHP as predictor variables. These were the variables used in both model types. The suitable habitat predicted by the two models overlapped by 47.5%, with the GLM being more conservative in the southern regions (Fig. 3).

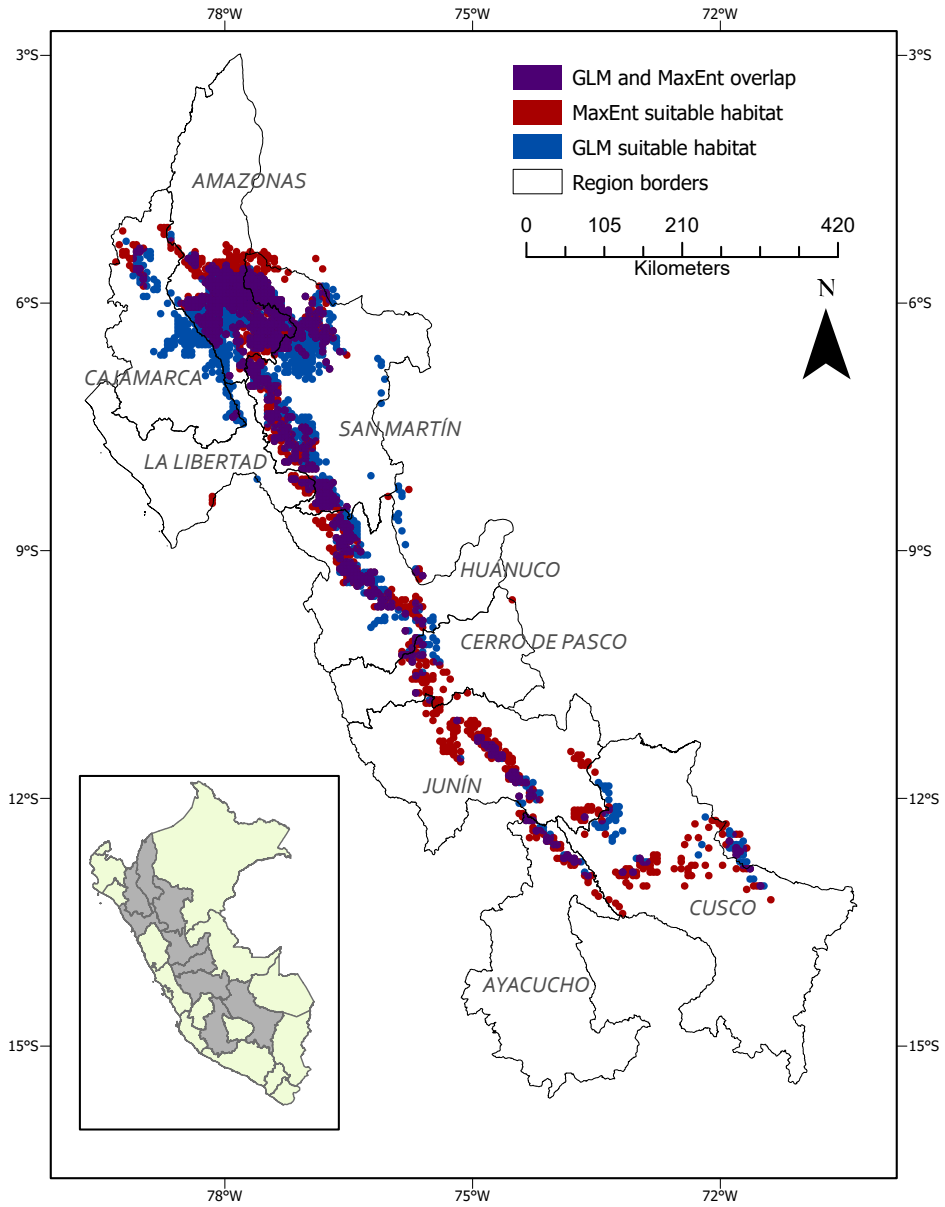

Fig 3. Suitable habitat (Good and Very Good) as indicated by the GLM, MaxEnt model, and their overlap.

Generalized Linear Modelling

The GLM found all predictor variables to be significantly associated with the likelihood of *L. flavicauda* presence with the exceptions of isothermality and forest cover. The variable most

highly associated with *L. flavicauda* habitat was precipitation seasonality, which had a negative relationship. Precipitation of the wettest month had the strongest positive correlation (Table 2).

Table 2. Correlation coefficients and standard error of residual deviances for each standardized predictor variable in the GLM. Estimates indicate the average change in the response variable associate with a one unit increase in the (standardized) predictor variable. Shading indicates significant association.

Predictor	Estimate	Standard Error	P value
Intercept	-6.228	1.008	<0.0005
Elevation	-0.768	0.249	0.00201
Bio2	0.983	0.466	0.0349
Bio3	0.616	0.327	0.0600
bio13	1.653	0.738	0.0251
bio15	-11.019	2.309	<0. 0005
bio19	-4.831	1.107	<0. 0005
Forest Cover	0.441	0.306	0.149
VHP	- 1.256	0.247	<0.0005

Based on the GLM, 1.4% of the study area was found to be Very Good habitat, and 11.4 % was considered Good (Table 3). Only a very small proportion of remaining habitat was within the 1 km human settlement buffer (Table 3). Suitable habitats in the southern regions of the *L. flavicauda* range run north-south through central Huánuco and Pasco, but coincide with areas where the species has been found to be absent, or where *L. l. tschudii* was found instead (this study; Aquino *et al.* 2017, 2019). In Junín, additional areas of Good habitat are present around and immediately south of the newly discovered populations. Of all Very Good and Good habitat, 17.72% and 25.95%, respectively, were found to be within Peru's current PA network (Table 3),

289 most of which are in PAs in the northern regions of the study area, while much of the area between
290 the northern and Junín populations remains unprotected.

291 A single iteration of the threshold-independent AUC calculation gave an AUC of 0.93 (Fig.
292 S1). The bootstrapped evaluation gave a slightly lower mean AUC of 0.89 (95% CI 0.86-0.95).
293 Applying the GLM to the training dataset with a 0.4 threshold produced predictions with 81.76%
294 accuracy. The model was better able to correctly predict the pseudoabsences (86.36%) than
295 presences (59.26%), likely due to the larger amount of pseudoabsence points in the test dataset
296 (Table S3). The kappa statistic (0.47) indicated that the model produced predictions in good
297 agreement with the test data, though this was not significant (p=0.70).

298 **Table 3.** Percentages of the study area that the GLM and MaxEnt model considered to be Very
299 Good, Good and unsuitable and the amount of each habitat type within the protected area (PA)
300 network in Peru.
301

Modeling Approach	Habitat Suitability	Within Study Region (% of region- before human settlement)	Within Study Region (% of region- after human settlement)	Within PAs (% of habitat)
GLM	Unsuitable	87.10	87.33	14.32
	Good	11.47	11.28	25.95
	Very Good	1.43	1.39	17.72
MaxEnt	Unsuitable	86.01	86.2	13.79
	Good	11.66	11.49	21.5
	Very Good	2.33	2.31	38.1

302

303 *MaxEnt Model*

304 The MaxEnt model corroborated that precipitation seasonality had a strong negative
305 correlation with species presence (Table 4). There were some differences in variable importance
306 in comparison to the GLM results, including relatively low importance of Precipitation of Coldest

Quarter (Table 2). The AUC for the MaxEnt model was 0.95 (Fig. S2) and corroborated by the mean AUC from bootstrap (0.95; 95% CI 0.93-0.97), indicating greater accuracy than the GLM.

The MaxEnt model suggested a higher percentage of Good and Very Good habitats compared to the GLM (Table 3; Fig. 4a), with percentages minimally effected after removing areas within the human settlement buffer. Suitable habitat in the southern regions of the study area included more Good habitat running north to south in Junín (Fig. 4b). Overlaying the PA network also showed more suitable habitat overall within the network compared to the GLM, with 21.5% and 38.1% of Good and Very Good being within PAs, respectively (Table 3; Fig. 5a), though much of the suitable habitat in the southern portion of the species' range remains unprotected (Fig. 5b).

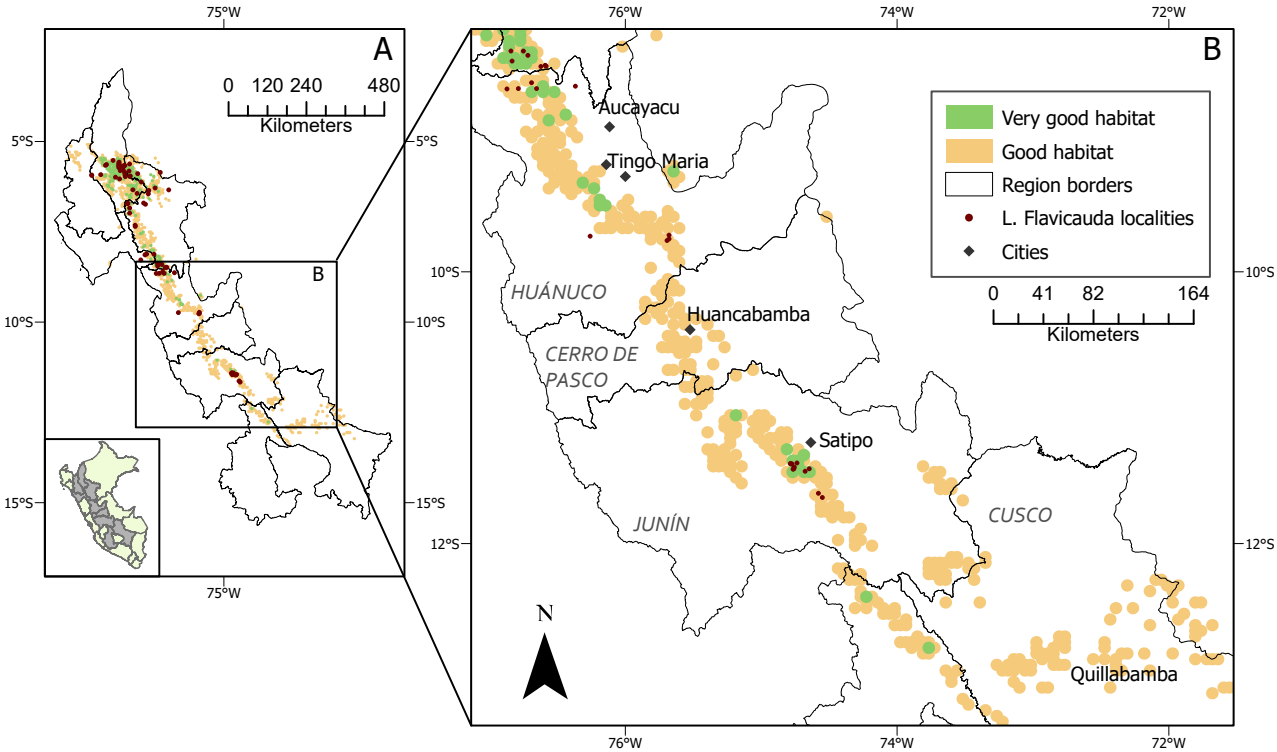

Fig. 4 Habitat suitability maps for *L. flavicauda* as predicted by the MaxEnt model a.) throughout the described study area and b.) within the regions surrounding the southernmost *L. flavicauda* occurrences.

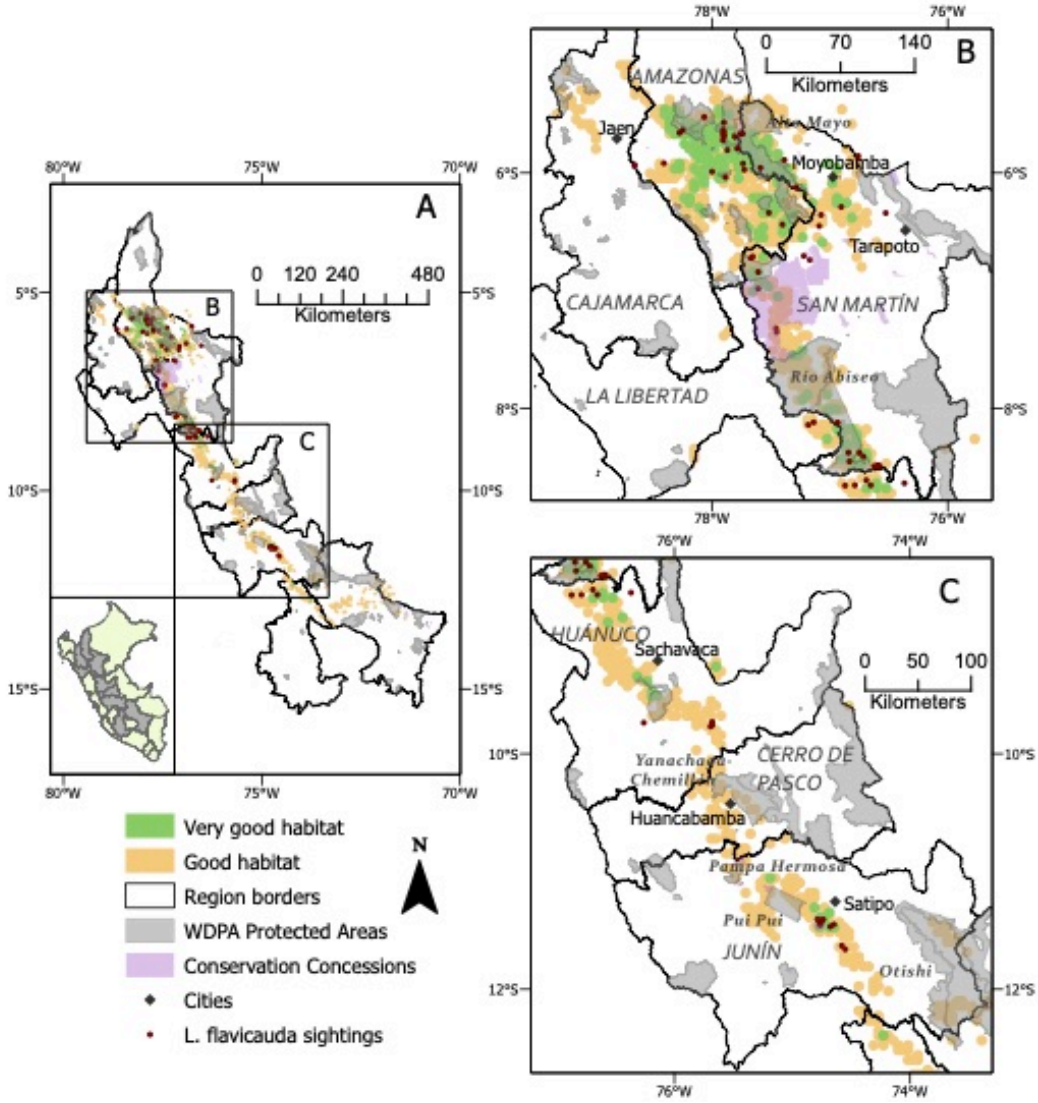

Fig. 5 PA network coverage over habitat suitability as predicted by the Maxent model a.) over the entire study area and b.) within the regions surrounding the southernmost *L. flavicauda* occurrences

Discussion

We carried out the first survey of *L. flavicauda* in the recently discovered southern expansion of its known range (McHugh *et al.* 2020), and our results suggest that this is a very localized population isolate of the species. Models of suitable habitat including the regions south

of Huánuco and our new occurrence records provide important information on the habitat availability for the species, thereby providing insight into priority areas for focused conservation efforts and placement of conservation corridors and new protected areas. Our use of free, open-source modelling platforms will make updating and refining this analysis relatively simple with the addition of novel presence data. Our updated suitable habitats will hopefully lead to the discovery of more *L. flavicauda* populations, possibly connecting the northern and southern distributions.

Our surveys discovered multiple new sightings of *L. flavicauda* in central Junín, but only of *L. l. tschudii* in Cerro de Pasco, northern Junín and northern Cusco, and neither *Lagothrix* taxa in Ayacucho. The lack of encounters or secondary evidence of *L. flavicauda* in areas with evidence of *L. l. tschudii* may be due, in large part, to competitive exclusion. *L. l. tschudii* has been found to be one of the most abundant high-altitude species in previous surveys in Cerro de Pasco and Huánuco (Aquino *et al.* 2019), and inhabits forests with niche conditions and at elevations suitable for *L. flavicauda* (Aquino *et al.* 2016; Serrano-Villavicencio *et al.* 2021). When comparing the suitable habitat in our models with our observations of *L. l. tschudii*, we found that most are in areas well-suited to the species (Fig. 6), paralleling the work of Aquino *et al.* (2016) which indicated that *L. flavicauda* occupied similar but separate, higher-altitude habitats than *L. l. tschudii*. While competitive exclusion may explain the replacement of either *Lagothrix* taxa with its congener, further surveys are needed to rule out possible sympatry in other areas, and to confirm the absence of both taxa in Ayacucho, with future models incorporating both species.

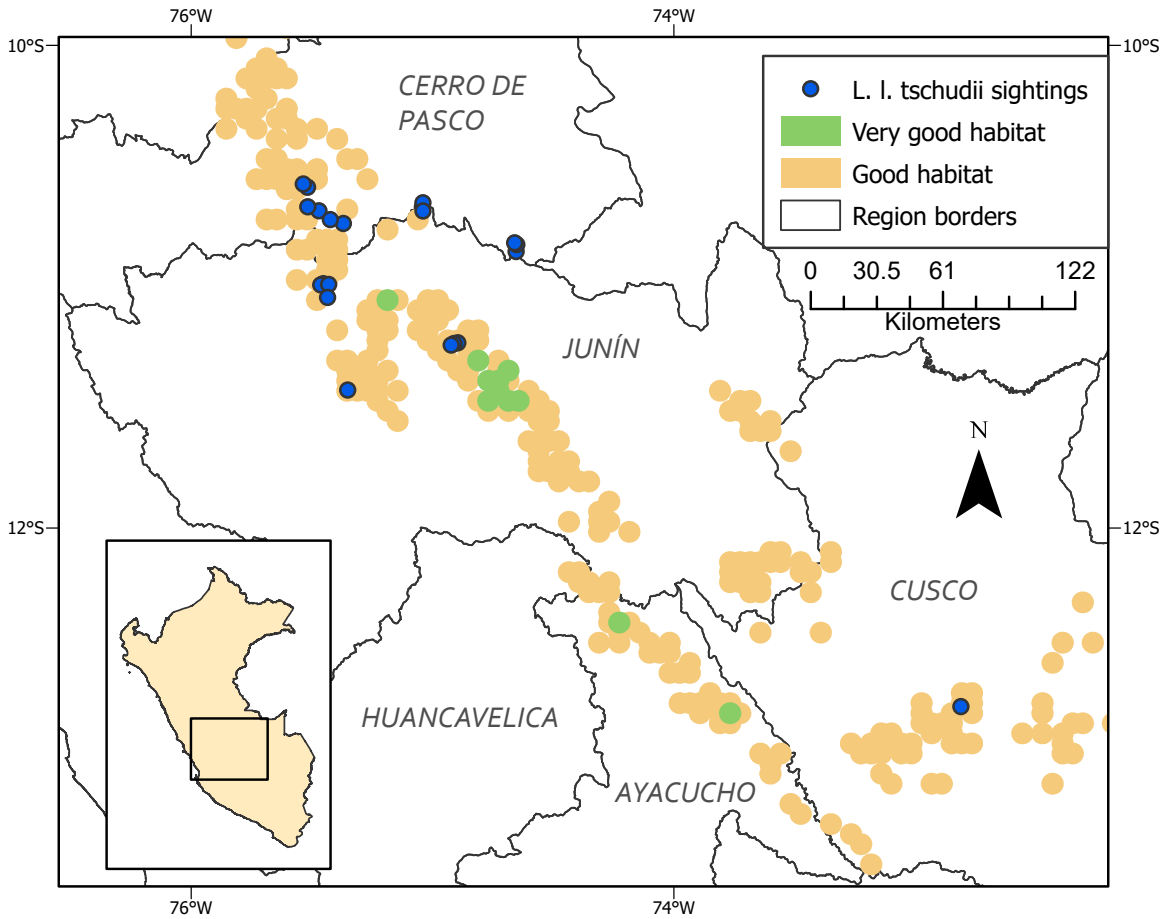

Fig 6 *L. l. tschudii* occurrences compared to suitable habitat predicted by the MaxEnt model. *L. flavicauda* and *L. l. tschudii* were never found occurring at the same site.

The lack of *Lagothrix* sightings in Ayacucho does not conclusively confirm absence, especially in areas where our survey efforts were limited by security issues. Almost 60% of the areas visited in this region were cultivated for coca (for cocaine production), while the remaining were small forest patches. More continuous forests did exist, but these were beyond the local jurisdictions, and controlled by armed guerrilla groups involved in drug trafficking, which we did not enter, either due to lack of permission or for our safety and that of our guides. Local informants indicated the presence of "large monkeys," in these forests, and that they are rarely seen in the smaller patches. Informants also indicated that these monkeys were more common in previous

364 years, but that hunting by indigenous Ashaninka groups in the area diminished their numbers. This,
365 with further increases in hunting in combination with deforestation due to coca cultivation likely
366 contribute to the species' rarity. In the patches we were able to survey in these areas we only
367 recorded the smaller bodied *Saguinus*, *Saimiri*, and *Cebus*. Finally, some of those interviewed in
368 the Union Mantara and Vizcatán areas in Junín claimed, based on photographs, to have seen *L.*
369 *flavicauda* in high elevation areas controlled by guerrilla groups. In particular, they pointed out
370 the area bordered by the Río Montaro as a place where *L. flavicauda* has definitely been seen.
371 During interviews, local people who had previously ceased coca cultivation in favour of coffee
372 and cacao indicated a recent return to coca in the area due to low market prices for legal crops.
373 This trend could have implications for future surveys and conservation actions.

374 Both of our models showed a strong negative correlation between *L. flavicauda* presence
375 and precipitation seasonality, consistent with the results of a study by Shanee (2016) in the northern
376 distribution of the species. This may be due to the phenology of arboreal food sources on which *L.*
377 *flavicauda* depends. Though the species has been found to use a variety of food resources and plant
378 parts, studies have shown seasonal shifts in feeding behaviour and dietary components (Shanee
379 2014; Shanee and Shanee 2011b). Andean species of *Cercropia*, for example, whose fruits and
380 leaves are commonly consumed by *L. flavicauda* (Shanee 2014), experience annual reproductive
381 changes due to climatic seasonality (Zalamea *et al.* 2011). Moreover, *L. flavicauda* have
382 commonly been observed consuming *Ficus* spp. fruit (Leo Luna 1980; Shanee 2014; Almeyda-
383 Zambrano *et al.* 2019), which have inter- and intra-specific asynchronous fruiting; together with
384 abundant production, this accounts for the genus' importance for many frugivores (Bronstein *et*
385 *al*. 1990; Kattan and Valenzuela 2013). Overall, while modelling with bioclimatic variables can

386 aid in determining areas with suitable niche conditions, these models do not provide clear
387 explanations for a given species' presence or absence.

388 Changing environmental conditions due to current and future climate change, in
389 combination with increasing anthropogenic impacts in the TABH are predicted to decrease
390 climatic niche availability and, in turn, species richness of plants (Ramirez-Villegas *et al.* 2014).
391 These changes will likely lead to further habitat loss and population reductions in *L. flavicauda*
392 and other primate species (e.g., Shanee 2016). Research suggests that the southern Peruvian Andes
393 are experiencing a slight decrease in precipitation along with significant increases in surface
394 temperatures (Vuille *et al.* 2003). Monthly rainfall projections based on fourth report of IPCC
395 climate change models suggest a significant future increase in rainfall seasonality in the tropical
396 Andes (Lavado Casimiro *et al.* 2011). Our models suggest that precipitation and seasonality are
397 among the most important predictors of *L. flavicauda* presence, therefore such changes could have
398 dire consequences for the species. This is especially true as lower-altitude species migrate to
399 occupy higher elevations with climate change, increasing competition for resources (Fisher 2011).
400 Future scenarios are further complicated by the fragmentation of habitats and intervening barriers
401 to dispersal (Sales *et al.* 2019), which would limit *L flavicauda's* ability to colonize new areas.

402 The buffer used to estimate areas as "Low" suitability based on proximity to human
403 settlement is meant to reflect hunting pressure on *L. flavicauda* (Buckingham and Shanee 2009).
404 Biodemographic hunting models have been created comparing human population and
405 demographic data with primate population density to demonstrate the deleterious impact of
406 hunting on primate "prey" species (Levi *et al.* 2011). Although hunting is known to be one of the
407 greatest threats to *L. flavicauda* (Shanee 2012), the assumption that there is high hunting pressure
408 closer to human settlements can be problematic due to differing practices among communities.

409 Conversely, in areas where community conservation initiatives have been enacted, such as the
410 community of Yambrasbamba in Amazonas, hunting of the species has been largely eliminated
411 and populations of *L. flavicauda* have increased (Shanee *et al.* 2015). In addition to hunting,
412 different regions in Peru have varying wildlife trafficking trends and pathways in which primates
413 are often trafficked as pets or tourist attractions, with large-bodied primates being the most
414 common victims (Shanee *et al.* 2017). Given this, using pressures from human hunting and
415 trafficking activity as variables in models like this may require more detailed surveying of local
416 practices to get a more nuanced representation of localized anthropogenic pressures.

417 While both models showed high statistical accuracies in their predictions, our MaxEnt
418 model performed better. While the GLM was more conservative in the predicted amount of
419 suitable habitat in the southern regions, there was a large amount of overlap in predictions between
420 both models. As with all models, ours are only as accurate as the data used. We were limited by
421 the relatively low number of localities compared to many other primate habitat suitability models
422 (Liu *et al.* 2019). Regardless, our model predictions and survey results should encourage the
423 continuation of surveys in southern Peru to increase presence data and model accuracy for the
424 species.

425 Overlaying the PA network and the MaxEnt predictions showed that ~75% of suitable
426 habitat is currently unprotected, with most protection being in the northern regions of the species'
427 range (Fig. 5c). This is much lower than that of a gap analysis performed in 2009 (Buckingham
428 and Shanee 2009), likely due to the recent growth of private and communal protected areas, as
429 well as increases in state parks in the northern regions of the *L. flavicauda* range (Shanee et al.
430 2017; Shanee 2018; Shanee et al. 2020). Peru has 18.8% of its land covered by the current PA
431 network, with 91.7% being within governmental PAs and 8.3% in private or communal PAs

(Shanee *et al.* 2020). While national PAs generally cover larger areas, they operate at a regional scale and rarely give rights or leadership roles to local people (Shanee *et al.* 2017; Horwich *et al.* 2012). The use of protected areas is key for the conservation of *L. flavicauda*, but new state protected areas can require large areas, free of other land uses, and can take years to formally create. Private and communal PAs, on the other hand, have proven effective for conservation in the regions of Amazonas and San Martin where relatively high human population densities limit opportunities for large state-run PAs (Horwich *et al.* 2012; Shanee *et al.* 2020). In these areas, local people are the primary decision makers and enforce their own regulations, ensuring that the methods of protection are in line with the values of their community. The promotion of communally and privately managed protected areas, particularly in key corridor areas, and education across landscapes can provide much needed protection (Shanee *et al*. 2015). Further, conservation concessions cover a great amount of suitable habitat in San Martín (Fig. 5). The inclusion of the conservation concessions caused the proportion of Very Good habitat within protected areas to increase from 34.63% to 38.1 %.

In the southern portion of the species range, our analysis illustrated that only the small areas of Pampa Hermosa and Pui Pui cover an area with some suitable *L. flavicauda* habitat near the southern most populations. As such, the development of PA and community conservation initiatives in the species' southern distribution are urgently needed, though successful conservation actions in the areas highlighted here will depend on an understanding of the socioeconomic and political situation to be able to garner local support (Chazdon *et al.* 2009).

Monitoring distributions, gene flow, and habitat suitability is critical to the conservation of *L. flavicauda*. Future research should use genetic assessments of diversity between the southern and northern populations of *L.* flavicauda to determine if gene flow is occurring. Patterns of

environmental variables should also be analysed between populations to better understand factors that facilitate migration between populations, and how they could be constrained with climate change and increasing human development (Sales *et al.* 2019). Using landscape genetic methods could also determine what landscape and/or ecological features strongly facilitate or hinder gene flow between populations and be used in planning new PAs or corridors (Olah *et al.* 2016).

Further investigation of the home ranges, and resource and land use of *L. flavicauda* will allow for better interpretation of the importance of SDM predictor variables. Differences in these attributes between the northern populations and the newly-discovered Junín populations will specifically indicate the necessary factors a habitat needs to sustain viable populations. This should involve working with local communities near and within the protected areas containing suitable habitat in the south, with a particular focus on environmental education as our experience suggests a lack of understanding of the importance of animals and ecosystem function within many local immigrant (i.e., non-indigenous) communities. The presence of drug traffickers and armed groups limited which sites we could visit, particularly in the area of Vizcatán in southern Junín, thus this area remains un-surveyed, a situation which needs to be urgently rectified once conditions allow. Further successful surveys will increase the number of presence and absence points for the species, will allow for more accurate analyses of their environmental needs, and encourage the initiation of conservation efforts in these areas to continue the growth of both state and private/community led efforts for *L. flavicauda*. This will also increase the likelihood of finding other high-altitude primate species localities and help us understand their distributions and conservation needs.

Acknowledgements

We thank the local communities we visited for allowing us to survey their surrounding forests and for their guidance in finding the monkeys. This work was funded by Boston University, and by Neotropical Primate Conservation thanks to grants from Primate Society of Great Britain, American Society of Primatologists, International Primatological Society, and Primate Conservation inc. Field work was carried out under Peruvian research permits (N° 173-2016-SERFOR-DGGSPFFS, and addendums 213-2016, 350-2017, and 389-2019). We also thank Dr. Suchi Gopal, who provided guidance in the performance of GIS analyses.

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