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Updated habitat suitability estimates and conservation implications for the short-tailed chinchilla *Chinchilla chinchilla* (Lichtenstein, 1830) (Rodentia: Chinchillidae)

Estimaciones actualizadas de la idoneidad de habitat e implicaciones para la conservación de la chinchilla de cola corta *Chinchilla chinchilla* (Lichtenstein, 1830) (Rodentia: Chinchillidae)

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Abstract: The short-tailed chinchilla (*Chinchilla chinchilla*) is a species classified as endangered throughout its distribution and for which neither a conservation nor management plan exists. Ecological niche models (ENMs) allow detection of potential areas of occurrence for species that are rare and/or of conservation interest. Here, we built and evaluated a suite of ENMs that incorporated new records for the species in Bolivia and removed those whose veracity could not be confirmed to provide an updated estimate of the extent of suitable habitat for *C. chinchilla*. Following model selection based on partial ROC, omission rate, and AICc, we then projected our top models across the historical distribution of *C. chinchilla* to identify locations of potentially suitable habitat. An ensemble of top models highlighted suitable habitat in Argentina, Bolivia, Chile, and Peru, with values of probability of suitable habitat up to 0.72. Together, these results demonstrate that suitable habitat still exists across the historical range of this species, provide insight into the climatic niche of this species, and highlight areas across the four countries for which future surveys of wild populations may be worthwhile.

Keywords: Andes. Ecological niche model. Maxent. Short-tailed chinchilla. South America

Resumen: La chinchilla de cola corta (*Chinchilla chinchilla*) es una especie clasificada como críticamente amenazada a lo largo de su distribución y para la cual no existen planes de manejo ni de conservación. Los modelos de nichos ecológicos (MNEs) permiten detectar áreas de probable ocurrencia para especies que son consideradas raras y/o de interés para la conservación. En este estudio, construimos y evaluamos un conjunto de MNEs que incorporaron nuevos registros para la especie en Bolivia y eliminaron aquellos cuya veracidad no pudo ser confirmada, para proporcionar una estimación actualizada de la extensión del hábitat adecuado para *C. chinchilla*. Después de seleccionar los mejores modelos basados en ROC parcial, tasa de omisión y AICc, los resultados de los mismos fueron proyectados a lo largo de la distribución histórica de *C. chinchilla* para identificar localidades con hábitat potencialmente adecuado. Un conjunto de los mejores modelos destacaron hábitat adecuado en Argentina, Bolivia, Chile y Perú, con valores de probabilidad de hasta 0.72. En conjunto, estos resultados demuestran que todavía existen hábitats idóneos en todo el rango histórico de la especie, proporcionan información sobre su nicho climático, y resaltan áreas en los cuatro países para las cuales valdría la pena organizar búsquedas de poblaciones silvestres en el futuro.

Palabras clave: Andes. Modelo de nicho ecológico. Maxent. Chinchilla de cola corta. Sur América.

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INTRODUCTION

Natural ecosystems are experiencing human-induced changes of significant magnitude over an unprecedently short timescale (Pimm *et al.*, 2014; Diaz *et al.*, 2019). These effects are being felt across the globe and are thought to be responsible for major changes to human welfare, ecosystem services, and wildlife populations (Hooper *et al.*, 2012; Faurby & Svenning, 2015; Rapacciuolo *et al.*, 2017). The most pernicious effects are those that have resulted in local extirpation or which have brought populations to the brink of extinction, as in the case of the short-tailed chinchilla *Chinchilla chinchilla* (Lichtenstein, 1830).

The short-tailed chinchilla is one of the most emblematic rodents native to the Andes. Overexploitation of wild chinchilla populations for their valuable pelts in the 19th and early 20th century was responsible for the species' population decline across its former range. Consequently, the short-tailed chinchilla was classified as Endangered by the International Union for Conservation of Nature (IUCN) (Roach & Kennerley, 2016), in Appendix I of the Convention on International Trade in Endangered Species (CITES), and as threatened or critically endangered in Peru, Bolivia, and Argentina (Valladares *et al.*, 2014a, 2018). Because of uncertainties about its historical distribution, the extent and stability of the full range of this species is currently unclear. Historically, the species was known from the coast and Andes of central Peru south through the highlands of west-central Bolivia (Anderson, S., 1997), northern Chile (Spotorno *et al.*, 2004), and adjacent northwestern Argentina (Osgood, 1943; Barquez *et al.*, 2006).

Chilean populations, thought to be extinct due to overexploitation by 1953 (Jiménez, 1996), were rediscovered in the highlands of northern Chile above 3,400 m (Spotorno *et al.*, 1998, 2004; Tirado *et al.*, 2012). In Peru, before most populations were exterminated by overexploitation, short-tailed chinchillas were reported as abundant, ranging from the coast near Lima to elevations over 3,300 m (Osgood, 1943 quoting from von Tschudi, 1845); similar observations about Bolivian populations in La Paz, Oruro, and Potosí departments were reported by Walle (1914). This author noted, however, that "the extinction of the species will only be a matter of time if measures are not taken to preserve it" (Walle, 1914, p. 371). Bolivian populations were thought to be extinct (Anderson, S., 1997; Salazar-Bravo *et al.*, 2002), but have since been rediscovered in the highlands of Potosí Department (Delgado *et al.*, 2018a, 2018b).

The conservation of endangered species requires accurate information about their distributions, so that conservation practitioners and decision-makers can best identify and safeguard habitats based on recognized priorities (Guisan *et al*., 2013; Sánchez-Mercado *et al*., 2014). Surveys for rare and threatened species are essential for monitoring populations and supporting conservation outcomes (Guisan *et al.*, 2006). However, knowing where to direct survey effort is often hampered by a paucity of data regarding species' distributions, biology, and ecology (Thompson, 2013). Ecological niche models (ENMs) provide an approach to mapping potentially suitable habitat to guide field surveys (Pearson *et al.*, 2007; Aizpurua *et al*., 2015) and have been used in this manner for a variety of taxa, including mammals (Anderson, R. & Martinez-Meyer, 2004; Gerstner *et al.*, 2018). The application of ENMs is appealing because it is efficient (*e.g.*, relative to random sampling; Guisan *et al.*, 2006), and research has demonstrated that the detection of rare species is greatly improved when surveys are guided by ENMs (*e.g.*, Raxworthy *et al*., 2003; Bourg *et al.*, 2005). ENMs employ quantitative methods that allow inferring ecological requirements of a species based on the conditions of areas where its presence is known, and then calculating the probability of habitat suitability in other areas (Wisz *et al*., 2008; Peterson *et al*., 2011). Thus, it is not surprising that in recent decades, ENMs have become a fundamental tool in ecology, conservation and natural resource management (Guillera-Arroita *et al*., 2015).

In the context of the short-tailed chinchilla, the only attempt at using ENMs to guide field work of conservation importance was presented by Copa Alvaro *et al.* (2014). These investigators developed an ENM of suitable areas for the potential presence of the species in Bolivia, based on anecdotal trapping records in the counry (provided by local interviewees), verified records of the presence of the species in Chile, and museum records from Argentina and Bolivia. The potential suitability map produced by these authors was fairly effective. In fact, independently from their work, our team verified the presence of wild populations of the species in a locality that their model identified with the second-highest suitability level (*i.e.*, between 52.4-66.8 percent; Delgado *et al.*, 2018b). Since the publication of Copa Alvaro *et al.* (2014), new information has emerged about the presence of the short-tailed chinchilla in Bolivia. For example, at least one wild population is now known to be present in the southern portion of the country and a critical review of historical and museum records of Bolivian origin demonstrated that the veracity of a locality used by Copa Alvaro *et al.* (2014) could not be confirmed (Delgado *et al.*, 2018b). In light of these changes in knowledge of the distribution of the short-tailed chinchilla in Bolivia, and in order to provide an updated map of habitat suitability for the species in Bolivia and neighboring countries, we developed a new model that includes the new records, removes those of dubious origin, and was constructed attending to best-practice standards and ecological principles that are known to affect the performance of these types of models (Barve *et al.*, 2011; Boria *et al.*, 2014; Cobos *et al.*, 2019; Araújo *et al.*, 2019).

MATERIALS AND METHODS

OCCURRENCE RECORDS

The localities used in this study are distributed across three countries in the region: Argentina, Bolivia, and Chile between -19° and -27° latitude. All locations are located on the western side of the Andes at altitudes between 3,500 and 5,000m (Table 1). We obtained the Argentinean localities from the Global Biodiversity Information Facility (GBIF) (Teta & Rodríguez, 2020) and the works of Ortiz *et al.* (2010), near the Socompa volcano, and Walker *et al.* (2007) in the northern region of Catamarca province. The Chilean localities come from environmental impact studies conducted by Salares de Atacama SCM (2011) and Minera Gold Fields Salares Norte Ltda. (2013), as well as records published by Lagos *et al.* (2012) and Valladares *et al.* (2012, 2014b). The location reported by Tirado *et al.* (2012) was not included because a specific coordinate could not be obtained. Bolivian occurrences were obtained from the map published by Copa Alvaro *et al.* (2014), as well as the record published by Delgado *et al.* (2018a), and from a skull found by Nuria Bernal (personal communication) in or near the Eduardo Avaroa Reserve. Based on discussion of the reported locations of *C. chinchilla* in Bolivia by Delgado *et al.* (2018b), we did not include the Cochabamba location associated with a specimen in the Museum of Vertebrate Zoology [MVZ M-97361] due to questions concerning the accuracy of its locality data. Similarly, we omitted a Peruvian locality from the Royal Ontario Museum [ROM 91301] because of uncertainty over the location and source of the record (Spotorno & Patton, 2015). Thus, we ultimately compiled 24 total localities for consideration in the modelling process.

However, sampling bias that produces geographic clusters of localities can artificially increase spatial autocorrelation of localities used in ENMs, potentially leading to model overfitting and inflated values of performance used for model evaluation (Veloz, 2009; Hijmans, 2012). Spatial filtering of occurrence data (*i.e.*, removing spatial clusters of occurrence records in a way that retains the greatest amount of information) can therefore improve predictions of ENMs by reducing overfitting and improving model performance (Anderson, R. & Raza, 2010; Boria *et al.*, 2014). Thus, we spatially filtered our data using SDMtoolbox version 2.2 (Brown *et al*., 2017) in ArcMap 10.6.1. Given environmental heterogeneity and likely degree of sampling bias in the region, we chose a thinning distance of 10 km, which has previously been used for Andean mammals (Gerstner *et al.*, 2018). Spatial filtering ultimately reduced the overall occurrence data set from the 24 described above to 19 localities (*i.e.*, two in Argentina, nine in Bolivia, and eight in Chile; Table 1), which we ultimately used in our modeling efforts.

Table 1. Occurrences records of *Chinchilla chinchilla* considered for modeling efforts.

Record	Country	Department/ Province	Elevation	Reference	Used
1	Argentina	Salta	3974	Teta & Rodríguez (2020)	No
2	Argentina	Salta	3946	Ortiz *et al.* (2010)	Yes
3	Argentina	Catamarca	4091	Walker *et al.* (2007)	Yes
4	Bolivia	Potosí	4400	Copa Alvaro *et al.* (2014)	Yes
5	Bolivia	Potosí	4268	Copa Alvaro *et al.* (2014)	Yes
6	Bolivia	Potosí	4531	Copa Alvaro *et al.* (2014)	Yes
7	Bolivia	Oruro	4484	Copa Alvaro *et al.* (2014)	Yes
8	Bolivia	Oruro	4048	Copa Alvaro *et al.* (2014)	Yes
9	Bolivia	Oruro	4531	Copa Alvaro *et al.* (2014)	Yes
10	Bolivia	Oruro	4825	Copa Alvaro *et al.* (2014)	Yes
11	Bolivia	Potosí	4363	Delgado *et al.* (2018a)	Yes
12	Bolivia	Potosí	4497	Nuria Bernal (personal communication)	Yes
13	Chile	Antofagasta	4939	Valladares *et al.* (2012)	Yes
14	Chile	Atacama	4732	Valladares *et al.* (2014b)	Yes
15	Chile	Atacama	3783	Valladares *et al.* (2014b)	Yes
16	Chile	Atacama	4007	Lagos *et al.* (2012)	Yes
17	Chile	Atacama	3979	Lagos *et al.* (2012)	Yes
18	Chile	Atacama	4143	Lagos *et al.* (2012)	No
19	Chile	Atacama	4057	Lagos *et al.* (2012)	No
20	Chile	Atacama	4386	Lagos *et al.* (2012)	Yes
21	Chile	Atacama	3985	Salares de Atacama SCM (2011)	Yes
22	Chile	Atacama	4661	Minera Gold Fields Salares Norte Ltda. (2013)	Yes
23	Chile	Atacama	4566	Minera Gold Fields Salares Norte Ltda. (2013)	No
24	Chile	Atacama	4383	Minera Gold Fields Salares Norte Ltda. (2013)	No

Furthermore, the choice of study extent can have a significant effect on model output. Including areas with suitable environments that lack records (*e.g.*, due to dispersal limitations or biotic interactions) can cause a model's algorithm to recognize spurious environmental differences and indicate these regions as unsuitable (Anderson, R. & Raza, 2010; Barve *et al.*, 2011). Thus, we defined a species-specific study region by creating circular buffers of 1° around each occurrence and merging each buffer into a single polygon. The resulting area was then used to define the region used for building candidate models.

ENVIRONMENTAL DATA

We considered 15 climatic variables from WorldClim (Fick & Hijmans, 2017) in our analyses at a resolution of ~1 km^2, excluding the four layers that combine precipitation and temperature into the same layer, due to spatial anomalies (Escobar *et al.*, 2014). We also considered land cover data for 2015 from the Climate Change Initiative Global Land Cover database (ESA, 2017). All environmental layers had the same extent and resolution. To reduce redundancy among environmental variables, we used correlation analyses on the 15 climatic variables for the study region by identifying variable pairs with correlations of r ≥ 0.8 and retaining the variable that we considered more biologically relevant for the species (Appendix 1). Ultimately, we included annual mean temperature (BIO1), isothermality (BIO3), temperature seasonality (BIO4), temperature annual range (BIO7), annual precipitation (BIO12), precipitation of driest month (BIO14), precipitation seasonality (BIO15) and land cover.

MODEL BUILDING

We modeled the potential distribution of *C. chinchilla* using Maxent, a presence-background model that uses a maximum entropy approach to estimate the most uniform distribution of a species' occurrence across the study area, minimally constrained by the provided environmental data (Phillips *et al.*, 2006). Importantly, Elith *et al*. (2011) showed that Maxent performs well with sparse datasets (*e.g.*, rare species). We randomly sampled 10,000 background localities from the study area.

Estimating optimal levels of model complexity is a challenging but necessary enterprise to generate realistic geographic predictions, especially for rare species (Galante *et al*., 2018; Gerstner *et al.*, 2018). Thus, we generated a suite of candidate models with different levels of complexity by varying two key parameters in Maxent: feature classes (FCs) and regularization multiplier (RM) (Phillips & Dudík, 2008; Elith *et al*., 2011; Anderson, R. & Gonzalez, 2011; Warren & Seifert, 2011). The FCs available in Maxent control the flexibility of the modeled response to each predictor variable, whereas the regularization multiplier determines the degree to which model complexity (*i.e.*, number of parameters) is penalized. We built a suite of 64 candidate models of varying complexity. Specifically, we considered linear (l), quadratic (q), product (p), and hinge (h) feature classes (l, h, q, lh, lq, lp, qp, lqp) and a range of regularization multipliers from 0.5-4.0 in 0.5 increments.

MODEL SELECTION

We assessed performance across the candidate models by using the common approach of randomly dividing the data into training and test sets, thus creating a semi-independent dataset for model evaluation (Guisan & Thuiller, 2005). We used 80% of the points to build the model and the remaining 20% for model validation. Model selection was based on recent advances in niche modeling and followed guidelines provided by Cobos *et al.* (2019). Specifically, we first removed non-significant candidate models based on partial ROC tests (Peterson *et al*., 2008), with 500 iterations and 50% of data for bootstrapping. We then filtered by omission rates (*E* = 5%; Anderson, R. *et al*., 2003) and model complexity (AICc; Warren & Seifert, 2011). Thus, best models were identified as those within 2 AICc units of the minimum from the significant, low-omission candidate models.

Following model selection, we created final models using the full set of occurrences and the selected parameterizations. We produced 10 replicates by bootstrap, with logistic outputs, and then transferred the final models to a larger study region bounded between -10.5° and -32.5° latitude (Figure 1), based on the historical distribution of the species (Valladares *et al*., 2018), in order to identify areas in the greater region worth surveying for the species (Raxworthy *et al*., 2003; Pearson *et al.*, 2007). We used the mobility-oriented parity and metric (MOP; Owens *et al*., 2013) to assess areas where strict extrapolation (*i.e.*, transfer areas with values outside the range of climates in the calibration area) occurs. All model building, selection, and extrapolation steps were performed in the kuenm package in R (Cobos *et al.*, 2019).

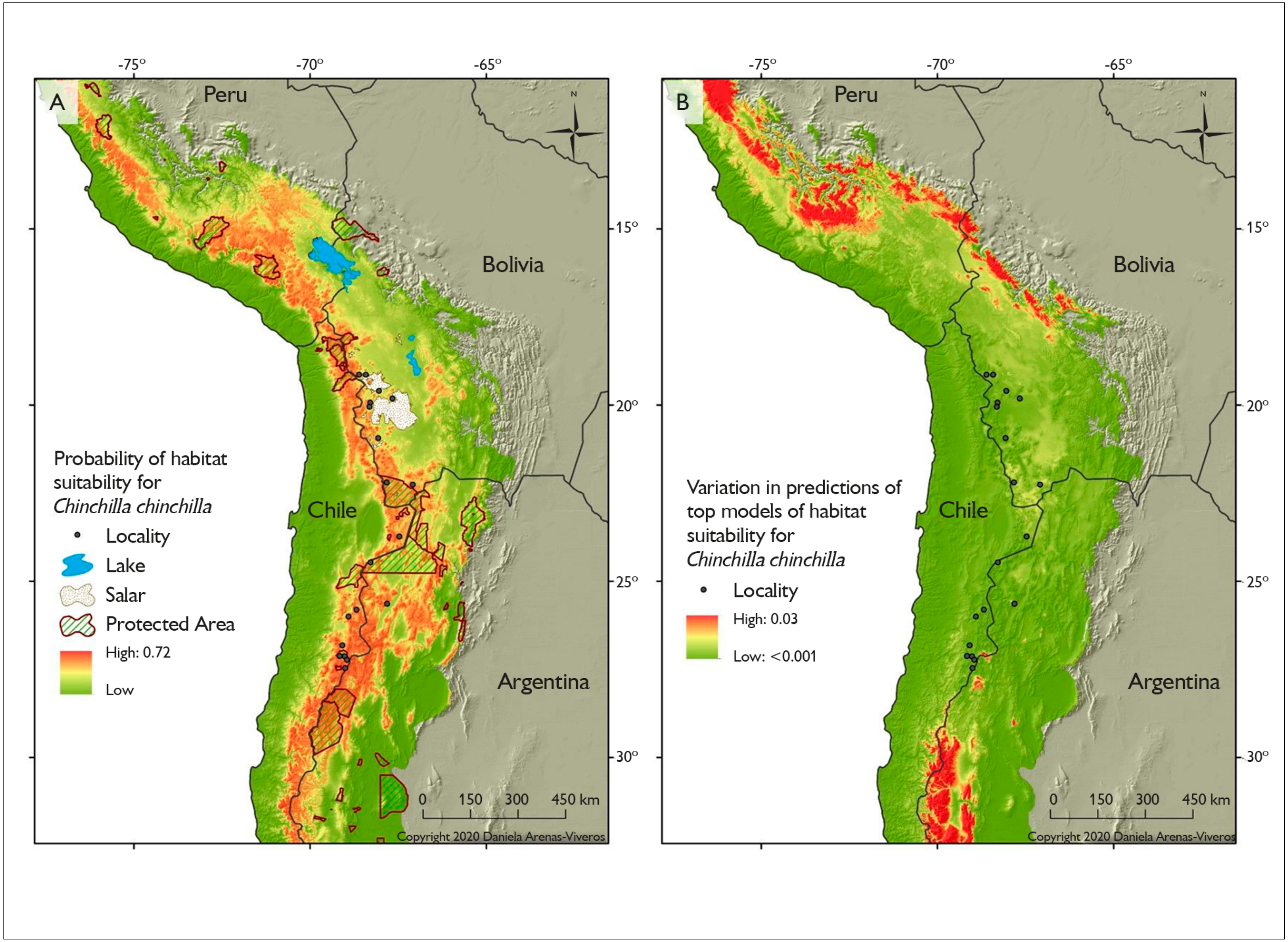

Figure 1. A) Geographical prediction of suitable habitat across the historical distribution of *C. chinchilla* based on the top models. Warmer colors (*e.g.*, red) represent areas with higher probability of habitat suitability, whereas cooler colors (*e.g.*, green) represent areas with lower probability; B) variation in habitat suitability predictions among the top models.

RESULTS

Model building in kuenm (Cobos *et al.*, 2019) resulted in 64 candidate models with different feature class and regularization multiplier combinations. Out of the 64 candidate models, 12 models satisfied all criteria (i.e., statistically significant and met the omission rate and AICc criteria; Table 2). Because we had multiple top models that satisfied all criteria, we used the average of all replicates across parameters to consolidate results for the species (Figure 1).

Table 2. Summary of the 64 models considered during the model building process. Following evaluation based on significance (*i.e.*, partial ROC), omission rate, and AICc criteria, 12 final models, in bold, were used for interpretation of habitat suitability across the historical range of the species. 'RM' refers to the regularization multiplier used, whereas 'FC' refers to the feature class (h: hinge, l: linear, p: product, q: quadratic).

(Continue)

RM	FC	Partial ROC	Omission rate	AICc	Delta AICc	Weight AICc	Number of parameters
2.0	**qp**	**0**	**0**	**474.39**	**0.00**	**0.73**	**3**
2.0	**lqp**	**0**	**0**	**474.39**	**0.00**	**0.43**	**3**
3.5	**lq**	**0**	**0**	**474.42**	**0.03**	**0.17**	**3**
3.5	**q**	**0**	**0**	**474.42**	**0.03**	**0.15**	**3**
2.5	**qp**	**0**	**0**	**474.61**	**0.22**	**0.28**	**2**
2.5	**lqp**	**0**	**0**	**474.61**	**0.22**	**0.22**	**2**
3.5	**qp**	**0**	**0**	**474.94**	**0.55**	**0.10**	**1**
3.5	**lqp**	**0**	**0**	**474.94**	**0.55**	**0.09**	**1**
4.0	**qp**	**0**	**0**	**475.53**	**1.14**	**0.06**	**1**
4.0	**lqp**	**0**	**0**	**475.53**	**1.14**	**0.06**	**1**
4.0	**lq**	**0**	**0**	**476.16**	**1.77**	**0.05**	**3**
4.0	**q**	**0**	**0**	**476.16**	**1.77**	**0.05**	**3**
3.0	qp	0	0	476.49	8.69	0.00	2
3.0	lqp	0	0	476.49	8.69	0.00	2
3.5	l	0	0	480.52	12.72	0.00	1
4.0	l	0	0	480.89	13.10	0.00	1
4.0	h	0	0	481.25	13.45	0.00	3
2.5	l	0	0	481.55	13.75	0.00	2
2.5	lp	0	0	481.77	13.97	0.00	2
3.0	lp	0	0	482.23	14.44	0.00	2
3.0	l	0	0	482.54	14.74	0.00	2
3.5	lp	0	0	482.79	14.99	0.00	2
2.0	l	0	0	483.25	15.45	0.00	3
4.0	lp	0	0	483.44	15.64	0.00	2
2.0	lp	0	0	484.15	16.35	0.00	3
4.0	lh	0	0	486.11	18.31	0.00	4
1.5	lp	0	0	486.14	18.34	0.00	4
1.5	q	0	0.25	467.80	0.00	0.02	3

Table 2. (Conclusion)

RM	FC	Partial ROC	Omission rate	AICc	Delta AICc	Weight AICc	Number of parameters
1.0	qp	0	0.25	468.42	0.62	0.02	3
1.0	lqp	0	0.25	468.42	0.62	0.02	3
2.0	lq	0	0.25	469.22	1.42	0.01	3
2.0	q	0	0.25	469.22	1.42	0.01	3
2.5	lq	0	0.25	470.84	3.04	0.01	3
2.5	q	0	0.25	470.84	3.04	0.01	3
1.5	lq	0	0.25	471.05	3.25	0.00	4
1.5	qp	0	0.25	471.20	3.40	0.00	3
1.5	lqp	0	0.25	471.20	3.40	0.00	3
3.0	lq	0	0.25	472.59	4.80	0.00	3
3.0	q	0	0.25	472.59	4.80	0.00	3
1.0	q	0	0.25	473.50	5.70	0.00	5
2.5	h	0	0.25	473.92	6.12	0.00	4
2.5	lh	0	0.25	473.92	6.12	0.00	4
3.0	h	0	0.25	474.60	6.80	0.00	3
3.0	lh	0	0.25	474.85	7.05	0.00	3
1.0	lq	0	0.25	475.84	8.04	0.00	6
3.5	h	0	0.25	477.82	10.02	0.00	3
0.5	lq	0	0.25	480.63	12.83	0.00	8
1.0	l	0	0.25	481.87	14.07	0.00	4
3.5	lh	0	0.25	481.99	14.19	0.00	4
1.5	l	0	0.25	484.33	16.54	0.00	4
0.5	l	0	0.25	487.38	19.58	0.00	7
2.0	h	0	0.25	488.33	20.53	0.00	8
2.0	lh	0	0.25	488.33	20.53	0.00	8
1.0	lp	0	0.25	491.30	23.50	0.00	6
0.5	lp	0	0.25	509.16	41.36	0.00	10
1.0	h	0	0.25	NA	NA	NA	22
1.0	lh	0	0.25	NA	NA	NA	20
1.5	h	0	0.25	NA	NA	NA	22
1.5	lh	0	0.25	NA	NA	NA	23
0.5	q	0	0.5	476.31	8.51	0.00	7
0.5	lqp	0	0.5	483.63	15.83	0.00	8
0.5	qp	0	0.5	484.11	16.31	0.00	8
0.5	h	0	0.5	NA	NA	NA	49
0.5	lh	0	0.5	NA	NA	NA	50

The ensemble of top models shows suitable habitat in all four countries from the historical range of *C. chinchilla* (*i.e.*, Argentina, Bolivia, Chile, and Peru; Figure 1A), with a probability of suitable habitat up to 0.72. Medium to high suitable habitat was constrained to areas above 3,000 m along the Andes, with areas as high as 5,000 m in Chile and Argentina considered suitable by our analyses (with the exception of the Altiplano region above 3,800 m). Importantly, there was generally low variation among model predictions, except for areas in the northern and southern portions of the study region (Figure 1B), which were both outside of the calibration area. Annual mean temperature (BIO1) consistently had the highest percent contribution and permutation importance across replicates of all top models. Furthermore, the ensemble indicated relatively high probability of suitable habitat across a number of protected areas within Chile, Bolivia, and Argentina (Figure 2).

DISCUSSION

Identifying potential distributions and areas of suitable habitat is essential for conservation and management planning for endangered species (Hoffman *et al.*, 2008). Ecological niche models can be useful for predicting the probability of habitat suitability across a region of interest (Peterson *et al*., 2011). This can, in turn, inform decisions about future biological surveys (Raxworthy *et al*., 2003) or highlight areas that may yield successful reintroductions (D'Elía *et al.*, 2015), albeit after considering a number of other important ecological factors. The short-tailed chinchilla was considered extinct in Bolivia until Delgado *et al.* (2018a) reported the existence of a population in areas neighboring the Laguna Colorada. Adding this record and the one reported by N. Bernal (personal communication), we developed a new estimate of the potential distribution of *C. chinchilla* that expands upon the work of Copa Alvaro *et al.* (2014) in Bolivia and provides estimates of suitable habitat across the historical range of *C. chinchilla*. Below, we discuss the implications of our findings.

GEOGRAPHIC DISTRIBUTION OF SUITABLE HABITAT

Our suite of models identified a number of areas of apparently suitable habitat. First, the area with the most extensive amount of predicted suitable habitat occurred along the Argentina-Chile border between -25° and -32° latitude (Figure 1A), although the area below -30° latitude was somewhat variable among models (Figure 1B). Moving north, areas of suitable habitat appear to follow the western range of the Andes into Peru. These results indicate several areas to prioritize for conducting new surveys for the species. For example, there were a number of areas in central Argentina (*e.g.*, Serrania de San Luis and Serrania de Cordoba) and southern Peru that had suitability values similar to that of areas where our group verified presence of wild chinchilla populations in Bolivia, suggesting that these areas should be high priority for future survey efforts. Furthermore, although *C. chinchilla* is believed to be extirpated from Peru (Pacheco, 2002), our model also highlighted areas of potentially suitable habitat in southern and western Peru. While we ultimately excluded a GBIF record from Peru (see Methods), we note that our model highlights Cerro de Pasco, which suggests that the record may be representative of a wild population.

The estimates from our modeling efforts may also signal important aspects of the ecology of the short-tailed chinchilla. In particular, we found that annual mean temperature (BIO1) was the most important predictor variable, even though we considered a number of temperature and precipitation variables that represented both average climatic conditions (*e.g.*, BIO1 and BIO12) as well as climatic variability (*e.g.*, BIO4 and BIO15). From a geographical perspective, we found that many high elevation areas, such as mountain peaks, were frequently predicted to be areas of suitable habitat. Together, this suggests a strong influence of average temperature, particularly over any measure of precipitation, on distribution patterns of this species. This is important given the susceptibility of montane mammals to climate change (Rubidge *et al*., 2012;

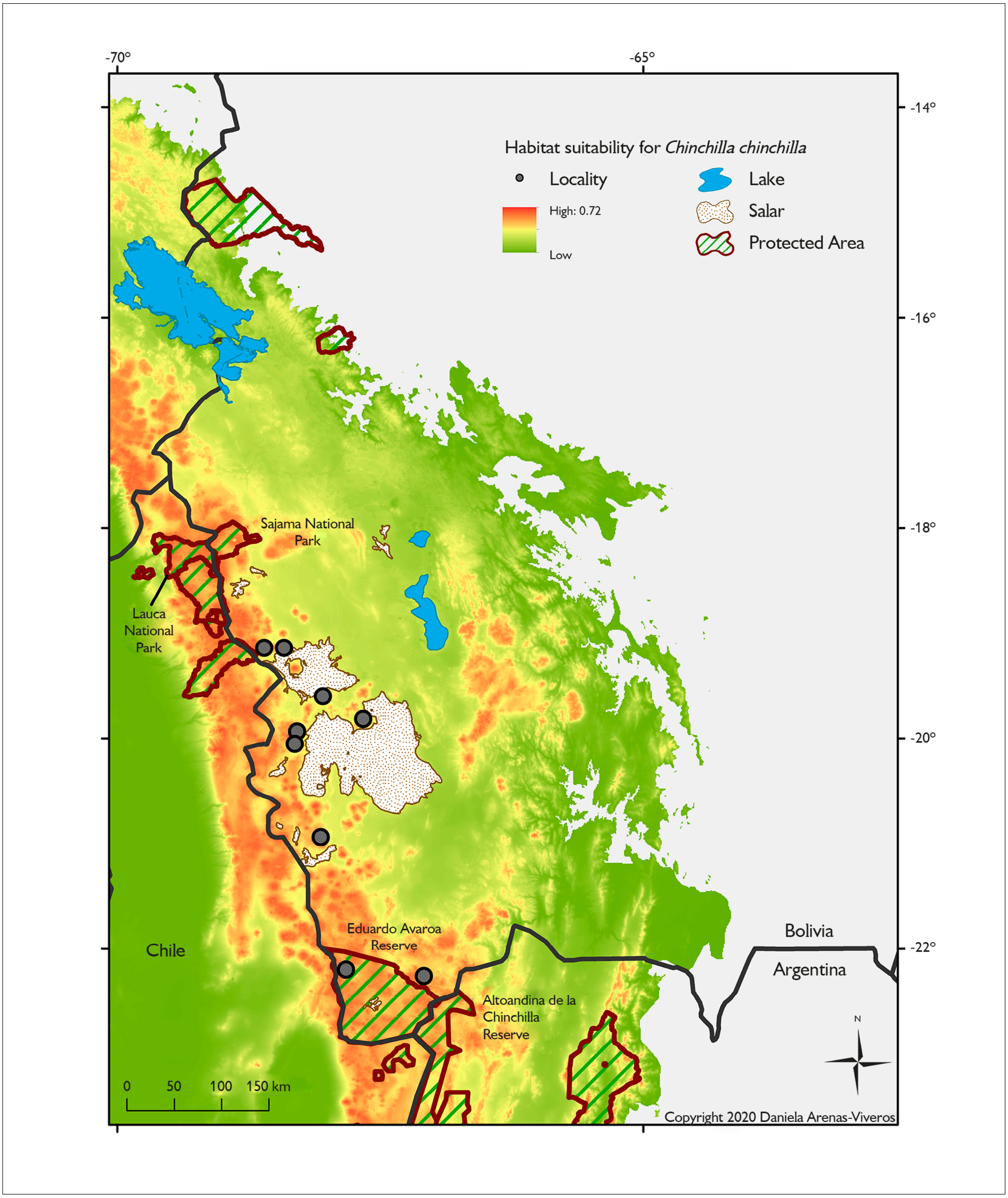

Figure 2. Habitat suitability predictions for *C. chinchilla* in Bolivia. Protected areas, including the Eduardo Avaroa Reserve (bottom left) are indicated with maroon outlines and green hashes.

McCain, 2019), and further demonstrates that climate change likely constitutes an added threat to this species as temperatures continue to increase. This suggests that the species could ultimately run out of suitable habitat over time if it is indeed tracking temperature changes by moving upslope. This discovery, in combination with the impact that overexploitation has had on wild populations, highlights the urgency for developing conservation and/or management plans for the short-tailed chinchilla.

COMPARISONS TO PRIOR DISTRIBUTIONAL ESTIMATES

There are a number of important discussion points concerning the results of our range-wide estimate compared to the estimate of suitable habitat in Bolivia by Copa Alvaro *et al.* (2014), which represents the most recent distributional estimate of any kind for this species. When comparing the potential distributions in Bolivia from the two models, there are important similarities and differences. One important difference is the lack, in our model, of highly suitable areas in the eastern cordillera in the departments of La Paz and Cochabamba (Figure 2). This difference is undoubtedly due to the decision to exclude a record from Cochabamba associated with a specimen in the Museum of Vertebrate Zoology; this supposed record represented the only locality for the species in the Puna Mesophytic province (figure 1 in Copa Alvaro *et al.*, 2014). That our model ensemble did not identify suitable habitat in this region provides further support that this record may be faulty. However, we did find high levels of agreement between the two studies in terms of suitable habitat within the Eduardo Avaroa Reserve (EAR) in southern Bolivia (Figure 2), which is not surprising given the two new records from this region following the publication of Copa Alvaro *et al.* (2014). Moreover, the high degree of agreement between the two studies with regard to suitable habitat in the EAR further demonstrates the need to conduct surveys for the species in this reserve, and also points to this reserve as a potentially important area from which to launch conservation initiatives for the species. Similarly, Sajama National Park, located in the Oruro department, is indicated as an area of suitable habitat for the species in Bolivia.

CONSERVATION OF WILD CHINCHILLA POPULATIONS

Given the conservation status of *C. chinchilla* and its history of being overharvested, protected areas across the region may represent important locations for future conservation efforts geared towards the species. Importantly, a series of protected areas are distributed across the historical distribution of this species, and many of them overlap with predicted areas of high suitability. Reserves along the Argentina-Chile border coincide with some of the largest expanses of predicted suitable habitat in our models. In addition, protected areas along country borders represent a unique opportunity for joint conservation initiatives. For example, Sajama National Park in Bolivia borders protected areas in Chile (*e.g.*, Lauca National Park), and the EAR shares a boundary with the *Reserva Provincial Alto Andina de la Chinchilla* in the Jujuy department in Argentina (Figure 2). These protected areas should be surveyed to confirm the species' presence and assess the status of any extant populations.

In 2014, Valladares and collaborators lamented that at the time of publication there was an almost complete lack of basic information on the biology of *C. chinchilla*. Unfortunately, this situation has changed very little in the intervening years. With the confirmation of the presence of wild populations in Bolivia and Chile, and the interest of several groups of dedicated biologists, this knowledge gap should start to close, at least with respect to these populations. As the second decade of the new millennium starts, it becomes imperative to agree upon a conservation and management plan for a species that is endangered, not only because of the isolation of its potential habitats, but also because of the low genetic diversity found in its populations (Spotorno *et al.*, 2004).

Our results highlight the need to conduct systematic sampling and to search for remaining populations in the historical distribution of *C. chinchilla*. While this work represents an updated, operational estimate of suitable habitat, more information is needed to effectively conserve habitat for this species. Additional records of this species will have multiple benefits, one of which will be to help improve the models analyzed herein and thus improve our capacity to predict areas where additional populations of *C. chinchilla* can be found. In that regard, we want to highlight the potential for citizen science to achieve new records across the region. For example, Gerstner *et al*. (2018) benefited immensely from nine additional records provided by citizens (i.e., an increase of 60% of the records used in the model) to update distributional estimates for the olinguito *Bassaricyon neblina* Helgen, Pinto, Kays, Hekgen, Tsuchiya, Quinn, Wilson & Maldonado, 2013. We believe that this is a route worth exploring with citizens and researchers across the four South American countries from which this species has been documented.

CONCLUSION

The present contribution represents updated habitat suitability estimates for the short-tailed chinchilla (*C. chinchilla*) across its historical range by including new records of the species from Bolivia. This new prediction presents areas of relatively high probability of habitat suitability in all four countries from the historical geographic range. The need for systematic sampling in areas with the potential for high habitat suitability in both historical and contemporary areas of the species' distribution is highlighted, as well as the potential for citizen science as a tool to uncover additional localities that will permit the construction of updated models that are better informed for estimating the potential distribution of this species.

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Appendix 1. Correlation matrix of candidate climate variables across the study region. Final variables were selected by retaining the variable that we considered more biologically relevant for the species among variable pairs with correlations ≥ 0.8. Selected climate variables for consideration during the modeling process included annual mean temperature (BIO1), isothermality (BIO3), temperature seasonality (BIO4), temperature annual range (BIO7), annual precipitation (BIO12), precipitation of driest month (BIO14), and precipitation seasonality (BIO15).

Variables	BIO1	BIO2	BIO3	BIO4	BIO5	BIO6	BIO7	BIO10	BIO11	BIO12	BIO13	BIO14	BIO15	BIO16
BIO1	-													
BIO2	-0.444	-												
BIO3	-0.443	0.704	-											
BIO4	-0.008	0.324	-0.387	-										
BIO5	0.868	0.038	-0.217	0.282	-									
BIO6	0.901	-0.758	-0.515	-0.296	0.571	-								
BIO7	-0.342	0.944	0.434	0.596	0.166	-0.714	-							
BIO10	0.995	-0.434	-0.496	0.080	0.881	0.880	-0.306	-						
BIO11	0.982	-0.509	-0.376	-0.195	0.793	0.945	-0.459	0.962	-					
BIO12	-0.292	0.325	0.055	0.303	-0.120	-0.406	0.385	-0.284	-0.344	-				
BIO13	-0.209	0.378	0.111	0.320	-0.013	-0.366	0.429	-0.206	-0.272	0.950	-			
BIO14	-0.428	-0.168	-0.058	-0.227	-0.542	-0.220	-0.198	-0.428	-0.359	0.267	0.060	-		
BIO15	-0.020	0.435	0.068	0.549	0.232	-0.273	0.526	0.006	-0.138	0.289	0.511	-0.486	-	
BIO16	-0.216	0.392	0.109	0.343	-0.012	-0.381	0.447	-0.211	-0.283	0.959	0.994	0.056	0.499	-
BIO17	-0.505	-0.142	0.005	-0.251	-0.618	-0.281	-0.189	-0.507	-0.432	0.223	-0.004	0.917	-0.573	-0.009