



Distribution and new sightings of *Promops davisoni* Thomas, 1921 (Chiroptera: Molossidae) in the Atacama Desert, the driest place on Earth

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ABSTRACT

Davison's Mastiff Bat *Promops davisoni* is a poorly studied species, only present in Ecuador, Peru, and more recently in Chile, where its known geographic distribution is supported by very few records from the extreme north of the country. Using ultrasonic recordings, we reported new records of *P. davisoni* in northern Chile, extending its distribution range ca. 60 km southward to the Chaca and Camarones valleys in the province of Arica. Additionally, using Species Distribution Models, we predicted its potential distribution in the north of the country based on similar suitable habitats. The high number of recordings obtained in our study suggest a wide distribution and relative abundance of *P. davisoni* in the coastal valleys of the Arica province and surrounding urban areas, with a remarkable habitat diversity for populations of this species. In addition, our potential distribution models suggest its presence in other arid environments within the Atacama Desert. These data provide additional information on the current and potential distribution of *P. davisoni* and can be useful for further studies to better understand the biology and population dynamics of the species, as well as the design of conservation and management strategies.

1. Introduction

Promops Gervais, 1856, is a Neotropical molossid genus, widely distributed across Central and South America, represented by three species: *Promops centralis* Thomas, 1915, *Promops nasutus* (Spix 1823) and *Promops davisoni* Thomas, 1921 (Simmons and Cirranello, 2020). Koopman (1994) and Simmons (2005) treated *Promops davisoni* as a subspecies of *P. centralis*, but Gregorin and Chiquito (2010), based on morphological and morphometric analyses, recognized *davisoni* as a valid species, a recognition that was followed by (Lim, 2019). Davison's Mastiff Bat *Promops davisoni* is a rare and poorly known species, restricted to the north and central portion of the Pacific coast of South America. Bats of this species have been found in a variety of habitats including desert, dry forest, humid forest, and agricultural areas from

sea level up to about 1320 m (Lim, 2019), although data on the environmental factors influencing its occurrence are unknown. It feeds exclusively on insects that are captured in flight (Lim, 2019).

Until recently, *P. davisoni* was only recorded in western Ecuador and western Peru (Flores-Quispe et al., 2015). However, bat surveys using acoustic monitoring in arid environments of two coastal valleys and the capture of an individual at the Anzota caves, in the province of Arica, have recently revealed the first record of *P. davisoni* in Chile (Ossa et al., 2018). Like other molossid bats, *P. davisoni* forages in uncluttered airspace high above ground level, which makes it difficult to capture by using traditional methods such as mist nets or harp traps (MacSwiney et al., 2008; Schnitzler and Kalko, 2001; Silva and Bernard, 2017). In addition, known roost sites for this species are rock crevices in hard-to-reach cliff walls (Aragón and Aguirre, 2014; Flores-Quispe et al.,

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2015); therefore, acoustic surveys provide an efficient tool to record the presence of species where chances of live capture are low (MacSwiney et al., 2008; Schnitzler and Kalko, 2001; Silva and Bernard, 2017).

The known geographic distribution of *P. davisoni* in Chile is supported by very few records from the extreme north of the country (Ossa et al., 2018). Due to the few locality records and the lack of knowledge about key aspects of its biology and habitat requirements, *P. davisoni* was listed as Vulnerable by the Chilean legislation (Decreto Supremo N° 16/2020, MMA) and as Data Deficient by the International Union for Conservation of Nature (Solari, 2016). This lack of information hinders the development of effective conservation and management plans for this species. Changes in climate and land-use are listed as the major threats for many bat species globally (Frick et al., 2020; Sherwin et al., 2013). Most climate models suggest that the temperature in the arid and semi-arid zones of northern Chile will increase, in addition to the increased frequency, duration, and severity of drought as a result of climate change (Bambach et al., 2019). Additionally, northern Chile is expected to undergo extreme land-use change over the coming decades as a result of the growing population (INE, 2018). These anthropogenic pressures and global change may result in conditions too harsh for populations of *P. davisoni* to persist and is a threat to the long-term survival of the species. Within this context, an analysis of the distribution and environmental association of this rare species is crucial for the conservation of its populations in the national territory.

In the present study, we update occurrence data of *P. davisoni* presenting new records based on recent acoustic surveys conducted in the extreme north of Chile. We used these data in combination with

environmental variables to generate Species Distribution Models (SDMs) for this species and evaluate suitable habitats within the Arica province and the rest of the Atacama Desert, as well as to identify the environmental factors associated with its distribution.

2. Materials and methods

2.1. Study area

The study area was the Arica province (Fig. 1), one of two provinces of Chile's northernmost region, Arica and Parinacota. The province is bordered on the north by the Tacna province of Peru, the south by the Tamarugal province in the Tarapacá Region, the east by the Parinacota province and the west by the Pacific Ocean. Its capital is the port city of Arica. Located within the Atacama Desert ecoregion, the Arica province is characterized by a cold desert climate according to the Köppen climate classification, with a mean annual rainfall of 1,1 mm concentrated between June and September. Temperatures range from 13° to 22 °C all year (Luebert and Plischoff, 2017). Vegetation formations of the Azapa, Lluta, Chaca, and Camarones valleys consist of thorny forests and scrubland, composed primarily of *Geoffroea decorticans* and *Prosopis alba*, surrounded by large areas of absolute desert (Luebert and Plischoff, 2017). The Azapa and Lluta valleys are strongly influenced by human activity, mostly by agriculture (e.g., crops of alfalfa, corn, olive, avocado, guava, mango) and rural villages.

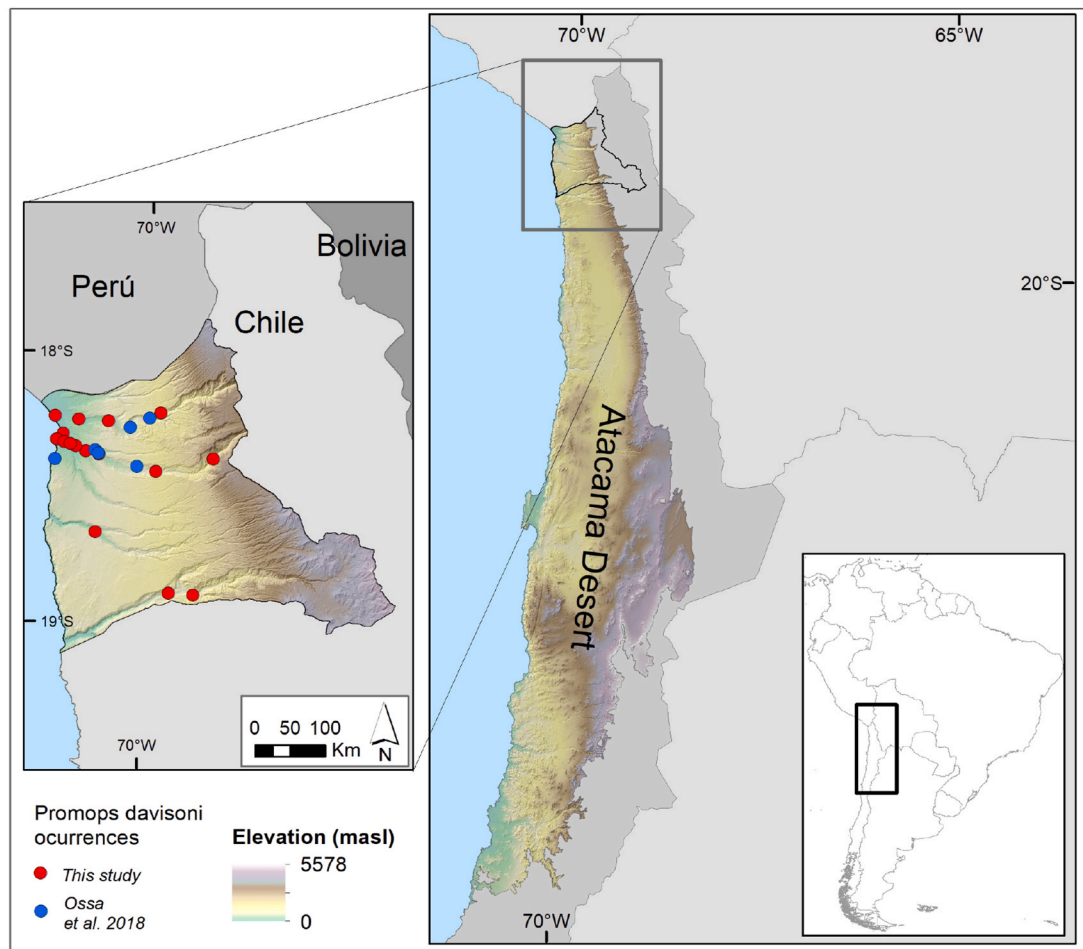


Fig. 1. Distribution map of records for *Promops davisoni* in the Arica province, northern Chile. The blue circles represent published records from Ossa et al. (2018) and red circles represent new records. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.2. Bat survey and species identification

Samplings were carried out at sixteen locations, including four sites in city of Arica and twelve distributed in four coastal valleys (Lluta, Azapa, Chaca, and Camarones) between September 2017 and February 2021 (Fig. 1; Table 1). Sampling sites in the Azapa and Lluta valleys were different from those surveyed by Ossa et al. (2018), and those in the Camarones and Chaca valleys, and Arica city, represent new study areas. Sampling locations were selected to cover the most representative land uses of the study area, including both natural and anthropized habitats at low and medium elevations (approximately 20–1680 m a.s.l.). At each sampling site, one automatic ultrasound recorder Song Meter SM4BAT FS with an external omnidirectional SMM-U1 ultrasonic microphone (Wildlife Acoustics, Inc., Maynard, MA, USA) was used. Detectors were placed at an approximate height of 4.5 m above ground level in uncluttered flyways and were programmed to record bat activity passively and continuously throughout the night from sunset (between 19:37 and 20:14 h) to sunrise (between 07:34 and 07:36 h), for at least two consecutive nights per sampling location.

Digitally recorded echolocation sequences were displayed and processed in BatSound 2.1 acoustic analysis software (Pettersson Elektronik AB, Upsala, Sweden). Sampling frequency of recordings was set to 384 kHz. From each echolocation sequence, defined as a recording file of 15 s maximum containing two or more pulses emitted by a bat, only search-phase pulses with a good signal-to-noise ratio were used in species identification. Each pulse was manually identified and assigned to *P. davisoni* after comparing the parameters of our recorded calls with reference calls of this species from Ossa et al. (2018) and Ugarte-Núñez (2020). Echolocation calls in this species are characterized by two types of pulses. The most common is a pulse with a short frequency modulated (FM) component at the beginning of the signal followed by an upward

convex quasi-constant frequency component (QCF), with a peak frequency between 32 and 34 kHz, occasionally interspersed with a second downward FM pulse with a QCF main component, with a peak frequency around 38 kHz and a broader bandwidth. The following parameters were used in the acoustic classification: duration (time between start and end of a pulse, measured in ms in the oscillogram), initial and final frequencies (measured in kHz in the spectrogram), bandwidth (difference between initial and final frequencies), the slope of frequency modulation (difference in kHz between the initial and final frequencies of the call divided by call duration) and peak frequency (frequency in kHz corresponding to the maximal intensity in the power spectrum). In each call sequence, we measured the interpulse interval (IPI) from the beginning of a call to the start of the next call. For each habitat sampled, the percentage of activity was calculated by counting the number of standardized echolocation passes per hour of sampling and dividing it by the total sum of passes recorded in all habitats.

2.3. Species distribution models

To identify suitable areas for the presence of *P. davisoni* in the Atacama Desert, a species distribution modelling (SDM) approach for species with low numbers of occurrence records was applied. The ensemble small models modelling (ESM) method (Breiner et al., 2015, 2018) is an SDM technique that allows obtaining statistically robust habitat suitability models from a low number of observed occurrence records, from combinations of bivariate models. It has been proven that this method is able to characterize reliable suitability models with even less than 25 occurrence records (Breiner et al., 2015). This is appropriate for the number of occurrence records collected in this study (22 unique records), which included the six localities reported by Ossa et al. (2018) and the sixteen new localities added by us. ESMs have been successfully tested for the identification of areas of suitability for different taxonomic groups. We ran the ESM analysis implemented in the ecospat package (Di Cola et al., 2017) in R 4.1.1 (R Core Team 2021).

As a first step, an ESM was calibrated in the province of Arica, the area where the records known to date for *P. davisoni* have been collected. Subsequently, the calibrated model was projected for the entire area of the Atacama Desert. For the Atacama Desert delimitation was considered for the hyper-arid bioclimate zone of northern Chile (Luebert and Plischoff, 2017). To calibrate and project the ESM model, five explanatory variables that are known to be relevant for the distribution of bat species (Razgour et al., 2016) were selected: elevation, slope, topographic position index, land use and temperature. Rainfall is a rare event in the Atacama Desert (Luebert and Plischoff, 2017); therefore, annual precipitation would not be a good predictor and it was not included as an explanatory variable in our study. Elevation and slope were obtained from a 90-m SRTM elevation model (Jarvis et al., 2008). This same elevation model was used to calculate the topographic position index (De Reu et al., 2013), using the Topographic tools set (Dilts, 2015) in ArcGIS ArcMap 10.8 software (ESRI, 2019). Land use was obtained from the Corporación Nacional Forestal (CONAF) land use cadastral updates after sampling the sites, selecting the sub-use category by region, and transforming it to raster format. These land uses included urban areas, scrubland (areas dominated by bush or arboreal species that do not exceed 2 m in height), arborescent scrub (areas dominated by arboreal species of more than 2 m in height), agricultural lands, bared ground, and herbaceous vegetation on riverbanks. Finally, a downscaling of a climatic surface of mean annual temperature was performed. The original resolution of 1 km was transformed to the analysis resolution of 90 m with the resample tool in ArcGIS ArcMap 10.8, using the bilinear method. All variables for both calibration and projection were worked at a resolution of 90 m. The final ESM projection assembly was obtained by calibrating three modelling techniques (GLM, GBM, and Maxent) with the five variables (see Fig. A1 in the Supplementary data). For each ESM run, the presences were partitioned into 80 and 20 for calibration and evaluation. Defining 1000 random pseudo-absences in the calibrated

Table 1
Sampling locations where *P. davisoni* was acoustically recorded in our study.

Locality	Coordinates	Altitude (m.a.s.l.)	Land use
Lluta Valley	18°24'38.0"S	364	Agricultural
	70°08'01.85"W		
	18°22'48.0"S	965	Agricultural (corn)
	69°56'34.79"W		
Arica City	18°24'28.98"S	162	Herbaceous vegetation on riverbanks
	70°14'27.94"W		
	18°27'33.6"S	28	Urban
	70°17'50.09"W		
	18°28'44.5"S	28	Urban
	70°19'11.84"W		
	18°29'17.80"S	62	Urban
	70°17'32.69"W		
Azapa Valley	18°23'56.80"S	18	Urban
	70°19'49.85"W		
	18°29'37.4"S	100	Urban
	70°16'14.09"W		
	18°30'51.3"S	223	Agricultural (olives)
	70°12'19.84"W		
	18°35'02.3"S	837	Agricultural (mango, guava)
	69°57'21.60"W		
	18°31'42.91"S 70°	313	Agricultural (olives)
	9°55.76"W		
Chaca Valley	18°30'4.54"S	138	Agricultural (olives)
	70°14'58.91"W		
	18°32'3.70"S	1678	Scrubland (dominated by bush or arboreal species that do not exceed 2 m in height)
	69°44'54.85"W		
	18°48'10.12"S	291	Arborescent scrub (dominated by arboreal species of more than 2 m in height)
	70°10'17.00"W		
Camarones Valley	19°00'54.0"S	848	Scrubland
	69°48'25.20"W		
	19° 0'39.63"S	651	Herbaceous vegetation on riverbanks
	69°53'49.19"W		

and projected area, the prediction ensemble was obtained by averaging 10 runs weighted according to the AUC values. Finally, the final projected ESM was transformed to binary format using the minimum predicted area as a criterion (Engler et al., 2004), selecting a 30% cutoff value from the intercept locations.

3. Results

Our acoustic surveys revealed the presence of *P. davisoni* across all sampling locations, with a total of 413 echolocation sequences detected (Fig. 2).

The land use type where echolocation sequences of *P. davisoni* were detected in our study included urbanized areas, agricultural crops (e.g., corn, olives, mango, guava), scrubland composed of *Pluchea chingoyo* (Chilca), *Schinus areia* (Pimiento) and *Atriplex atacamensis* (Cachiyuyo), *Aphyllocladus denticulatus* and *Tessaria* sp, herbaceous vegetation on riverbanks dominated by *Schoenoplectus pungens*, *Tessaria* sp, and *Typha domingensis* (Totora), and arborescent scrub composed of *Pluchea chingoyo* (Chilca), *Acacia macracantha* (Huarango), *Geoffroea decorticans* (Chañar), *Tessaria* sp, and *Schinus areia* (Pimiento). Scrublands concentrated 57% of the total echolocation sequences recorded, followed by urban areas (27%), agricultural lands (8%), herbaceous vegetation on riverbanks (7%), and arborescent scrub (1%). Other bat species recorded during the acoustic surveys were the Brazilian free-tailed bat *Tadarida brasiliensis*, Kalinowski's Mastiff bat *Mormopterus kalinowskii*, the Atacama *Myotis atacamensis*, and the small big-eared brown bat *Histiotus montanus*.

The ensemble model suitability suggests that *P. davisoni* has a wide distribution along the coastal valleys of the Arica province (Fig. 3). Additionally, ensemble model suitability showed a patchy distribution of *P. davisoni* in the rest of the Atacama Desert, with moderately suitable habitats along the coast, interior valleys and ravines in the Tarapacá and Atacama regions, including the Camiña (Tana), Copiapó and El Huasco valleys, and the coastal zone of the Antofagasta region (Fig. 3). The ranking of the contribution of each variable and each technique to the final assemblage are presented in Tables 2 and 3, and the weights of each bivariate model to construct the final assemblage are presented in the Table A1 of the Supplementary Data. The variables that contributed best to the final assemblage were land use and mean annual temperature, with 22% and 20% respectively.

4. Discussion

Using acoustic survey data, we reported new records of the Davison's Mastiff Bat *P. davisoni* in the extreme north of Chile and modeled its potential distribution in the Atacama Desert. Before this study, *P. davisoni* had not been reported in the Chaca and Camarones valleys. These sampling locations are located a distance between 30 and 60 km southward from the record in the Azapa valley (Ossa et al., 2018), thus representing the southernmost records of the species across its

geographic distribution range.

The results of our distribution model and the new records from Chaca and Camarones valleys suggest a wide distribution of *P. davisoni* in the coastal valleys of the Arica province and surrounding urban areas. Additionally, our potential distribution models suggest its presence in other arid environments within the Atacama Desert, with moderately suitable habitats along the coast and interior valleys which correspond to zones of high temperature (Luebert and Pliscoff, 2017). This finding is not surprising considering the similarity among bioclimatic and vegetation formations in these three regions (Luebert and Pliscoff, 2017), and could also be explained by the eco-morphology and habitat preferences of this species. Davison's Mastiff Bat is well adapted to forage in open spaces high above ground level, because of their high wing loading and high aspect ratio (Norberg and Rayner, 1987), which confer high speed flight making visits to these isolated valleys energetically cheap. Further surveys along the potential distribution localities would help to confirm the presence of *P. davisoni* in the Tarapacá, Antofagasta, and Atacama regions and to better understand its distributional pattern in our country.

Davison's Mastiff bats were detected in a variety of habitats in our study, from scrubland with xerophytic vegetation to agricultural and urban areas. Using capture with mist nets, Flores-Quispe et al. (2015) also reported individuals of *P. davisoni* flying over an agricultural reservoir in the Valley of Locumba in the department of Tacna, southern Peru. Artificial ponds in agricultural areas often promote an abundance and diversity of nocturnal insects, particularly in drought-prone regions like northern Chile (Lisón and Calvo, 2014; Loumassine et al., 2020; Stahlschmidt et al., 2012). The occurrence of *P. davisoni* in agricultural areas likely is a result of a combination of relatively high prey availability and the ability of these bats to forage in open spaces. The second highest detection of *P. davisoni* in our study was recorded within urban landscapes, suggesting that this elusive bat species may be a city dweller as occurring with other species of molossid bats that appear to benefit from urbanization and selectively forage in anthropized areas (Scanlon and Petit, 2008; Taylor et al., 2019; Threlfall et al., 2011; Voigt et al., 2016). Streetlights in urban areas may benefit bats by fostering a high concentration of insects (Avila-Flores and Brock Fenton, 2005; Eisenbeis, 2006; Jung and Kalko, 2010; Rydell, 2006). Likewise, bats have been observed using buildings in urban areas as roosting and foraging sites, temporary shelters, and for reproduction, and hibernation (Hourigan et al., 2006; Rodríguez-Aguilar et al., 2017; Voigt et al., 2016). To our knowledge, this appears to be the first record of *P. davisoni* foraging in this habitat (Lim, 2019). Currently, there are no direct threats to *P. davisoni*, which in part reflects our lack of knowledge about the biology and ecology of the species (Solari, 2016). Northern Chile is an area that is expected to undergo dramatic changes in the coming decades. The human population of Chile is expected to grow by nearly 15% by 2050 (INE, 2018), and the landscape is expected to turn mostly into agricultural and urbanized areas. Living and foraging in urban and agricultural landscapes may expose *P. davisoni* to potential threats such as the destruction and disturbance of their roosts, decreasing insect prey abundance and exposure to pesticides (Frick et al., 2020), and its effects may be even more important given that they are understudied. Bats have long been the victims of negative public opinion and are intentionally killed in fear that they are a source of zoonotic disease transmission such as rabies, and more recently the coronavirus disease (COVID-19) (Fenton et al., 2020; Lu et al., 2021; O'Shea et al., 2016; Schneeberger and Voigt, 2016). As the population grows and urban boundaries expand, bat-human conflicts become more common and could represent an important threat to populations of *P. davisoni* as they increasingly adapt to these human-dominated habitats. Additionally, scenarios for northern Chile predict that temperatures will increase as a result of climate change (Bambach et al., 2019); this is a relevant point since in our model the annual average temperature appeared as the second most relevant variable in the ensemble model. Rising temperatures is a direct cause of the water shortages and greater aridity, and this is likely to impact the

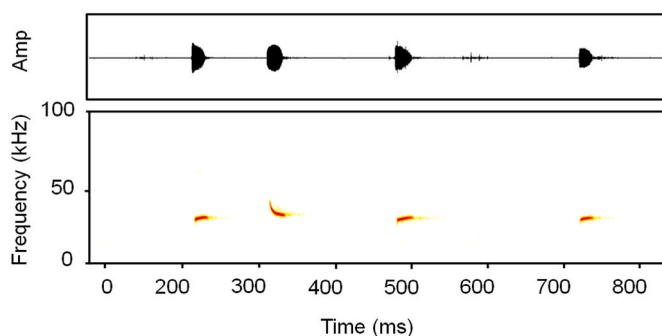


Fig. 2. Sonogram of the echolocation calls of *Promops davisoni* showing a typical sequence of calls recorded in our study.

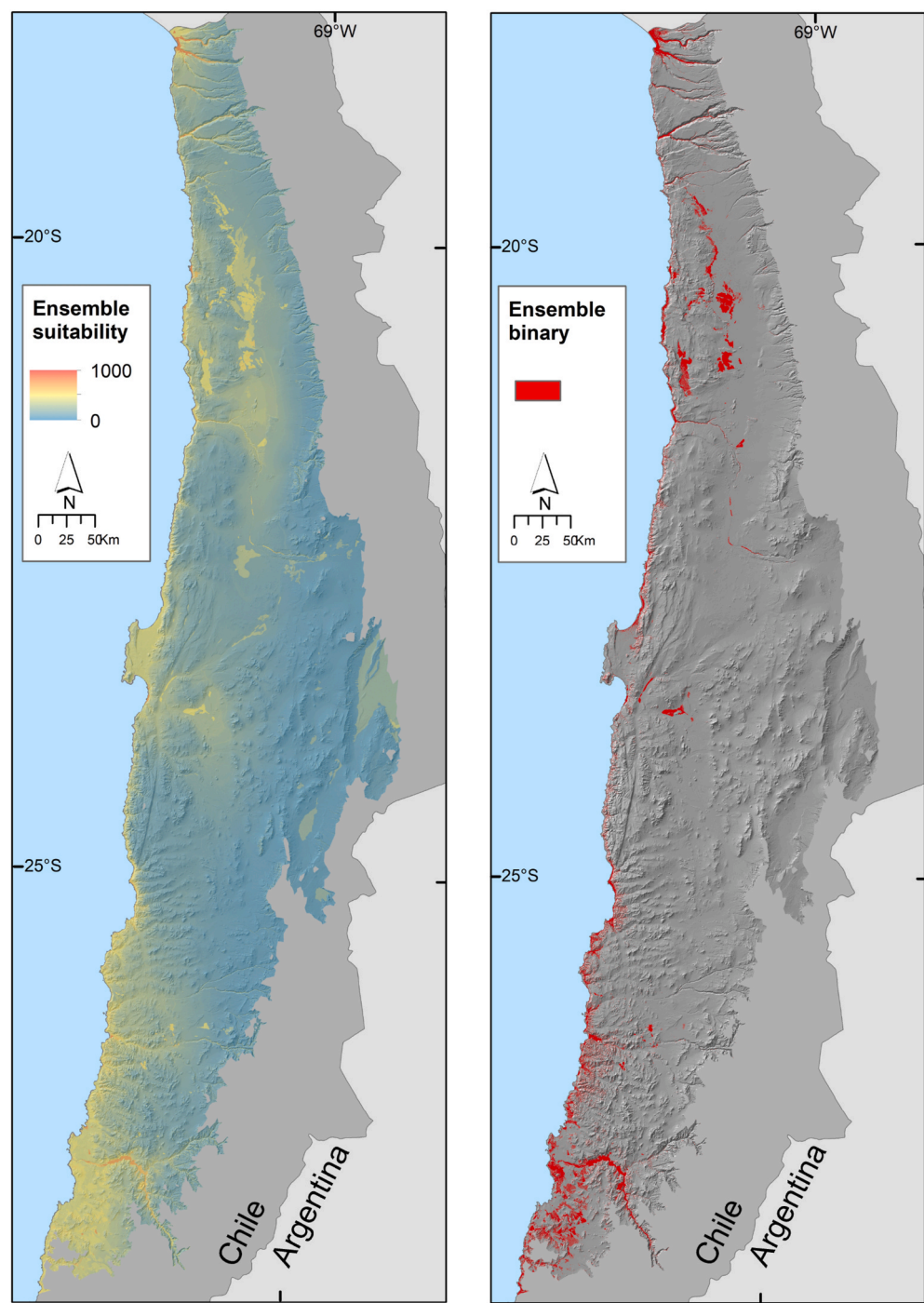


Fig. 3. Ensemble model suitability (left panel) and Ensemble binary model (right panel) for *Promops davisoni* in the Atacama Desert, northern Chile.

Table 2
Variable contribution for each modelling technique (GBM, GLM, MAXENT) used in bivariate models and final ensemble (Ensemble) projections.

Variable	GBM	GLM	MAXENT	Ensamble
Elevation	0,162996578	0,211441872	0,209419577	0,195433624
Slope	0,219163815	0,180754625	0,186055091	0,194699924
Temperature	0,174230025	0,217260811	0,215014757	0,202889249
Topographic position index	0,193497991	0,182898444	0,190051648	0,188675997
Land use	0,250111591	0,207644248	0,199458928	0,218301206

ecosystem and cause a reduction in biodiversity (Marquet et al., 2019), potentially forcing this and other arid-dwelling species to shift or contract their ranges, as has been observed in other arid and semiarid zones around the world (Piccioli et al., 2021). All these emerging threats increase the urgency for understanding the biology and population dynamics of the poorly known *P. davisoni*, for which further longer-term studies will be needed. The results from this study can be used to help predict how the Davison’s Mastiff bat will respond to these projected changes.

CRedit authorship contribution statement

Annia Rodríguez-San Pedro: Writing – original draft,

Table 3

Models' performance for each technique runs and final ensemble.

Model run	Threshold	Specificity	Kappa	AUC	TSS	SomersD	MPA	Boyce
RUN1_GBM	130	0,839	0,171	0,941	0,839	0,882	0,186	0,551
RUN1_GLM	630	0,915	0,297	0,96	0,915	0,92	0,688	0,817
RUN1_MAXENT	290	0,899	0,261	0,959	0,899	0,917	0,379	0,749
RUN1_EF	360	0,91	0,284	0,957	0,91	0,915	0,424	0,729

Conceptualization, Methodology, Investigation, Formal analysis. **Juan Luis Allendes:** Data collection, Investigation, Writing – review & editing. **Clemente A. Beltrán:** Investigation, Writing – review & editing. **Marcelo Mayorga:** Investigation, Writing – review & editing. **Patricio Pliscoff:** Writing – original draft, Methodology, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jaridenv.2021.104660>.

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