

Distributional patterns of the Brazilian free-tailed bat *Tadarida brasiliensis* in the Peruvian territory

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The molossid bat *Tadarida brasiliensis* has a wide and apparently continuous distribution in South America. Although it has been reported in several localities of both versants of the Peruvian Andes, the potential distribution for this species has not been formally analyzed. Therefore, we describe its distributional pattern in the territory and provide comments about the possible influence of the Andes in its distribution. We gathered occurrence records from museums, acoustic surveys, literature, GBIF and Vertnet sources, and we selected localities to minimize spatial correlation. After defining a minimum-convex polygon of Peruvian records as background area, we use Maxent software with bioclimatic variables to construct species distribution models. Several models were evaluated using different metrics, and the model with the lowest AICc was selected. Then, the model was projected for Peruvian territory. *Tadarida brasiliensis* is reported for the first time in Cajamarca, Piura and Ica departments. The potential distribution model showed two disjunct suitable areas, one for the Pacific versant and other for the Amazonian versant of the Andes, but connected with moderate suitable conditions in the Huancabamba Depression region in northern Perú. Mean diurnal range and annual mean temperature were identified as the main limiting factors for the potential distribution of this species in this territory. *Tadarida brasiliensis* exhibits a discontinuous distribution in the Peruvian territory. In northern part, the Huancabamba depression zone has climatic conditions that may allow the east-west dispersal for this species. In central and southern parts, the higher crest of the Andes (> 4,500 m) has low suitable conditions due to the extreme climate. In the eastern, the lowland Amazonian forests has low suitability for this species, probably due to high temperatures. We suggest that the Andes could be acting a biogeographical barrier that limits the dispersal for this species, but population-genetic studies are needed to confirm this hypothesis. We identified that temperature is the main climatic factor that limit the dispersal of this bat. In conclusion, *T. brasiliensis* is mainly associated with desert and Andean slopes ecosystems in Perú, and we highlight the importance of incorporating acoustic records in the analysis of its distribution patterns.

El murciélago molósid *Tadarida brasiliensis* tiene una distribución amplia y aparentemente continua en América del Sur. Si bien se ha reportado en varias localidades de ambas vertientes de los Andes peruanos, la distribución potencial de esta especie no ha sido analizada formalmente. Por lo tanto, describimos el patrón de distribución de *T. brasiliensis* en el territorio peruano y brindamos comentarios sobre la posible influencia de los Andes en su distribución. Recopilamos registros de ocurrencia de museos, estudios acústicos, literatura, GBIF y Vertnet, y seleccionamos localidades para minimizar la correlación espacial. Después de definir un polígono mínimo convexo en base a los registros peruanos como área de calibración, usamos el software Maxent con variables bioclimáticas para construir modelos de distribución de especies. Se evaluaron varios modelos utilizando diferentes métricas y se seleccionó el modelo con el AICc más bajo. Luego, se proyectó este modelo en el territorio peruano. *Tadarida brasiliensis* es reportada por primera vez en los departamentos de Cajamarca, Piura e Ica. El modelo de distribución potencial mostró dos áreas adecuadas disjuntas, una para la vertiente del Pacífico y otra para la vertiente amazónica de los Andes, pero conectadas por las condiciones idóneas de la región de la Depresión de Huancabamba en el norte de Perú. El intervalo medio de temperatura diurna y la temperatura media anual fueron identificadas como los principales factores limitantes para la distribución potencial de esta especie en este territorio. *Tadarida brasiliensis* exhibe una distribución discontinua en el territorio peruano. En la parte norte, la zona de depresión de Huancabamba tiene condiciones climáticas que pueden permitir la dispersión este-oeste de esta especie. En las parte central y sur, los picos más altos de los Andes (> 4,500 m) tiene bajas condiciones adecuadas debido al clima extremo. En el este, los bosques amazónicos de las tierras bajas tienen baja idoneidad para esta especie, probablemente debido a las altas temperaturas. Sugerimos que los Andes podrían estar actuando como una barrera biogeográfica que limita la dispersión de esta especie, pero se necesitan estudios genéticos-poblacionales para confirmar esta hipótesis. Identificamos que la temperatura es el principal factor climático que limita la dispersión de este murciélago. En conclusión, *T. brasiliensis* se asocia principalmente con ecosistemas desérticos y de laderas andinas en el Perú, y destacamos la importancia de incorporar registros acústicos en el análisis de sus patrones de distribución.

Keywords: Andes; geographic barrier; maxent; potential distribution; suitability.

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Introduction

The Brazilian free-tailed bat *Tadarida brasiliensis* is a small-size insectivorous bat with one of the widest distributions in the western hemisphere (Wilkins 1989). It occurs in an extensive variety of habitats, ranging from deserts to montane humid forest (Eger 2007), with the ability to forage from the ground up to 3,000 m (McCracken et al. 2008).

In South America, only the subspecies *T. b. brasiliensis* is recognized (Schwartz 1955). Based on individuals from the east versant of the Andes and the subantarctic sub-region, Morales et al. (2018) suggest it apparently conforms to one genetic group. The potential distribution of the species showed it is strongly associated to the Andes (Escobar et al. 2015; Romero 2018), with few records in much of Amazonia

(Eger 2007), and presumably absent in lowland forest ecosystems (Wilkins 1989).

In the Peru, this species has been reported in the Equatorial dry forest, the coastal desert, the steppe, the Yungas and the lowland forests ecoregions (Pacheco *et al.* 2009). Due to the variety of occurrence records (Acha and Zapatel 1957; Solari *et al.* 2001; Zeballos *et al.* 2001; Mena and Williams 2002; Zelada *et al.* 2014; Aragón and Aguirre 2014), it is believed that this species presents a continuous distribution in this country (Eger 2007; Barquez 2018). However, the Andean Cordillera, is recognized as a great biogeographical barrier that limits the dispersal of many mammalian species, particularly in bats, between the Pacific and Amazonian versants and could drastically affect *T. brasiliensis* perceived distribution in the country (Koopman 1978; Patterson *et al.* 2012). To date, no analysis of the influence of the Andes, or how environmental conditions, influence the distribution patterns of *T. brasiliensis* in Perú has been conducted.

Species distribution models (SDMs) are frequently used for assessing the potential distribution of species (Razgour *et al.* 2016), based on occurrence records and the environmental characteristics of these localities (Franklin 2010). The main assumption of the models is that the climate of these localities represents part of the environmental component of the species' niche (Peterson and Soberón 2012), and therefore, it is possible to predict suitable areas for species presence. Determining most suitable areas could help us better understand possible geographical and environmental barriers for the species' distributions, and also provide information on its likely dispersal limitations (Barve *et al.* 2011).

The aim of this study is to describe the distribution patterns of *T. brasiliensis* in Perú using species distribution models and explore the possible influence of the Andes. Here, we test the hypothesis that *T. brasiliensis* has a continuous distribution in Perú, including the Andes mountain chain. Additionally, we report novel records in the territory and highlight priority research locations for this species.

Materials and Methods

Occurrence data. Occurrence data were selected from 139 records gathered from the following sources: the collection of mammals, Museo de Historia Natural de San Marcos (MUSM; $n = 51$) in Lima, bat acoustic surveys (this work, $n = 26$), literature (Acha and Zapatel 1957; Zeballos *et al.* 2001; Pari *et al.* 2015; Morales *et al.* 2018; Portugal 2018; $n = 30$), the Global Biodiversity Information Facility (GBIF 2019; download on July 8, 2019; $n = 11$), and Vertnet (Constable *et al.* 2010; download on August 7, 2019; $n = 22$). In order to avoid sampling bias caused by spatial correlation (Razgour *et al.* 2016), localities used as occurrence data were manually chosen such that no two localities were separated less than 25 km, which is the approximate mean displacement of *T. brasiliensis* for foraging flights from their roost (Allen *et al.* 2009). For GBIF and Vertnet sources, only records from scientific collections were considered to avoid

spatial bias in the distribution (Beck *et al.* 2014). The majority of the occurrence records (74 %) were dated after 1960. All records covered a temporal range from 1900 to 2019. See selected locality details in Appendix 1.

The acoustic surveys were performed in 23 localities distributed across eight departments of Perú: Ayacucho, Cajamarca, Ica, La Libertad, Lima, Piura, Puno and Tacna, from 2014 to 2019. Recordings were obtained by performing active monitoring in acoustic transects, using Pettersson ultrasonic detectors D240x and M500-384 plugged into digital recorders or mobile phone devices. Recording sessions were performed between 18:00 and 23:00 hrs, in rainless conditions, for one night per site (Kingston 2016). We selected pulses in which the search phase consists of a downward quasi-constant frequency component ranging from 30 kHz to 26 kHz, described as characteristic for this species (Gillam and McCracken 2007; Arias-Aguilar *et al.* 2018). The sound files are stored in the MUSM for further studies involving the development of an acoustic library for Perú.

Novel localities are reported using the political departments of Perú. For the biogeographical analyzes, we used the terrestrial ecoregions of the world (Olson *et al.* 2001) and the biogeographic regionalization of the Neotropical region (Morrone 2014).

Study area. Two types of geographical spaces were delimited: the background and the projection areas. The background area must offer a good coverage of the conditions within the species environmental tolerance (Anderson 2013), and at regional scales, using a specific area to model partial-niche produce more sensitive models (Razgour *et al.* 2016). Thus, we calculated a minimum-convex polygon based on our occurrence data (Brown 2014) and applied a buffer of 50 km. As projection area, we used the layer of the Peruvian territory obtained from Instituto Geográfico Nacional (IGN, www.idep.gob.pe), assuming that it represents an accessible area for this species (Barve *et al.* 2011) and considering that climatic conditions within this area were well represented by the background area (Anderson and Raza 2010). All the geospatial operations were done using ArcMap 10.5.1 (Esri 2016).

Environmental data. Bioclimatic data from the global interpolated climate database WorldClim 1.4 were used (Hijmans *et al.* 2005) with a grid resolution of 30 arc-seconds (~1 km). We downloaded 15 variables representing current climate, but removed Bio 8, Bio 9, Bio 18 and Bio 19 because they can have spatial abnormalities (Escobar *et al.* 2014). We masked these climatic rasters to the extent of the background area to generate background point. To avoid multicollinearity (Elith *et al.* 2011), a Spearman's correlation test between variables were performed using the R package fuzzySim 3.0, to select variables with correlation values lower than 0.85 (Syfert *et al.* 2013). Also, we selected variables considering their relevance to the representative Peruvian climate (Schwarb *et al.* 2011), as well as their rela-

tionships with the occurrence of *T. brasiliensis* (Duff and Morrell 2007; Hristov et al. 2010).

Distribution model. We constructed an SDM using the maximum entropy algorithm Maxent 3.4.1 (Phillips et al. 2018). The background area was used to calibrate the model, and then projected to the Peruvian territory. For calibration, different models were built with 10,000 random background points and evaluated with spatial cross validation. We explored different complexity settings for Maxent: regularization multipliers in intervals of 0.5, ranging from 1.0 to 5.0, and feature class combinations L, Q, H, LQ, LH, QH, LQH, LQHP, and LQHPT, where "L" is linear, "P" is product, "Q" is quadratic, "H" is hinge and "T" stands for threshold (Radosavljevic and Anderson 2014). We performed the evaluation process with the spatial cross validation procedure "checkerboard2" (aggregation factor = 4) using the R package ENMeval 0.3.0 (Muscarella et al. 2014) with R 3.5.3 (R Core Team 2019). We evaluated variable importance with Maxent's variable jackknife test (Phillips et al. 2006). Following Warren and Seifert (2011), the model selection was made based on the Akaike information criteria corrected for small samples (AICc) that provide a comparison of the most informative and parsimonious model (Razgour et al. 2016). We use the metrics of the model with lowest AICc value and projected it using the Maxent cloglog transformation. Model evaluation details can be found in Appendix 2 and model response curves in Appendix 3.

Results

We found that *T. brasiliensis* is found from sea level (MUSM 4,793, 5,368; Lima department) to 4105 m (ROM 93863, 93868; Junín department) in Perú. In the Pacific versant, the species was found up to 3,149 m (via ultrasonic record), whereas on the Amazonian versant most records are in the Andean piedmont (>1047 m), and only two records are reported in the lowland eastern humid forest of Perú at 360 m (MUSM 6045 194441; San Martín department). With acoustic surveys, we reported for the first time its presence in Cajamarca, Piura and Ica departments. We recognized the occurrence of *T. brasiliensis* in the Desert and the Puna provinces of the South America transition zone, in the Ecuadorian province of the Pacific Dominion, and in the Yungas, the Ucayali and the Rondônia provinces of the South Brazilian dominion.

We selected five variables as most ecologically relevant and not highly correlated (Table 1). Then, from 81 computed models using these variables, we chose the model with the lowest AICc obtained with following parameters: LQ as features class combination and 1 as regularization multiplier (AUCtrain: 0.7836, AUCtest: 0.7211, OR10: 0.0912, AICc: 1073.82, Δ AICc: 0). Based on the evaluation results (Appendix 2 and 4), we observed that in models with more parameters, the average AUCtest increase, which means that these models are stricter than the others. But we also observed that AUCdiff and the OR10 increase with more complexity, what is typically related to overfitting in these more complex

Table 1. Selected variables contribution. Selected bioclimatic variables and their contribution in the selected model.

Potential Distribution Model	Variables Contribution	
	Percent contribution	Permutation importance
Mean Diurnal Range (Bio 2)	57.4731	64.8406
Annual Mean Temperature (Bio 1)	18.4447	28.2832
Temperature Annual Range (Bio 7)	6.6362	6.8761
Precipitation Seasonality (Bio 15)	3.3811	0.000
Annual Precipitation (Bio 12)	14.0648	0.000

models. Our selected model presents less complexity but also the less overfitting in comparison with other models.

Bioclimatic variables with the greatest influence in the distribution of *T. brasiliensis* were mean diurnal range of temperature (Bio 02) and annual mean temperature (Bio 01), which contribute to 64.8 % and 28.3 % to the model, respectively. Response curves of each variable (Appendix 3) showed that annual temperatures between 15 to 20°C present predicted values over 0.5, while temperatures over 10°C in mean diurnal ranges reduce significantly the predicted values of occurrence. The jackknife test showed that the variable with the highest gain when used in isolation was annual mean temperature, while the one which decreased the gain the most when omitted was mean diurnal temperature.

The SDM showed a slightly disjunct distribution for *T. brasiliensis* in Perú, where two different core areas with high suitability values (> 0.5) were obtained (Figure 1). The first area corresponded to the coastline ecosystems in the Pacific versant of the Andes, included in the Desert and Xeric Shrublands biome, where higher predictive values seem to be restricted to the Sechura desert and Tumbes-Piura dry forest ecoregions. The other area corresponded to Andean slopes ecosystems in the Amazonian versant, where higher predictive values were detected above 1000 m, in the Yungas and wet Puna ecoregions. In northern Perú, a moderately suitable area in the Huancabamba Depression region, connects the western and eastern suitable areas. The higher part of the Andes (above 4500 m elevation) exhibited low environmental suitability (< 0.2) for this species. Similarly, the lower Amazonian forest had low environmental suitability (< 0.4).

Discussion

It was previously reported that *T. brasiliensis* has a broad and continuous distribution in Perú (Wilkins 1989; Eger 2007; Barquez et al. 2015); however, based on our model, we reject that hypothesis. Our correlative model predicted that this species has a largely discontinuous distribution in the country, where two disjunct areas with high suitability values could be identified: the Pacific and Amazonian versants, separated by the Andes. Contrary to the model presented by Escobar et al. (2015), we identified highly suitable environmental conditions in the coastal and Andean slopes ecosys-

tems. Furthermore, supporting [Wilkins \(1989\)](#), we found this species is mostly absent in lowland forest of the Amazonia.

Based on the localities of occurrence and the predictions of the model, we identified two areas in the Peruvian territory that have not been sampled enough or remain unassessed for this species: the Huancabamba depression zone and the eastern slopes of the central Peruvian Andes. In the Huancabamba depression zone, although the SDM showed moderate suitability (0.4 to 0.6), no specimens are known to occur in this zone or in the vicinity (less than 25 km). Thus, we consider that the Huancabamba depression zone remains poorly studied and requires increased focus on bat research priorities. On the other hand, the eastern slopes of the central Peruvian Andes –specially the zone between Junín and Pasco departments– where our model indicated moderate suitability (~ 0.6) is one the better surveyed areas in the country ([Mena 2010](#); [Arias et al. 2016](#)). We believe that *T. brasiliensis* has yet to be detected in this geographic area, because most surveys have only used mist nests, a methodology with only moderate efficiency when in collecting insectivorous bats ([Rydell et al. 2002](#)).

Despite the information gaps, we consider that our model efficiently represents the environmental niche of this species in Perú, in great part because our occurrence data covered a great part of the territory. We accomplished this, by incorporating ultrasonic records which increased data occurrence in about 41 % (Appendix 1); therefore, we support recent suggestions that acoustic surveys contribute and complement traditional methodologies in studying insectivorous bat species ([Hintze et al. 2019](#)).

Our model estimated only a moderate suitability index (~ 0.6) in the dry forests of the Huancabamba depression. Although this zone was proposed as an important biogeographical barrier for montane species ([Weigend 2004](#)), this region was also suggested as an east-west corridor that allow gene flow in *Sturnira erythromos* and likely other species ([Pacheco and Patterson 1992](#)). We currently lack occurrence data for *T. brasiliensis* in this region, but considering the low elevation of the Andean in this area ([Pacheco 2002](#)), we propose that the species likely uses the depression to connect populations on the eastern versant with those of the western versant of the Andes. Future biological inventories in the area will test this hypothesis.

On the other hand, in central and southern Perú, our model revealed broad separation in the suitable environmental conditions for the potential distribution of the species. Due to the topographic characteristics and the extreme climate conditions in the higher elevations ([Garreaud 2009](#)), the Andes are considered as important biogeographical barrier for several groups of mammals ([Patterson et al. 2012](#)). However, the role of the Andes as a biogeographic barrier for bats has seen little debate since the pioneering works of [Koopman \(1978\)](#) and [Pacheco and Patterson \(1992\)](#), but it has been argued that only few bat species are capable of inhabiting high elevations ([Patterson](#)

[et al. 1998](#)). Although *T. brasiliensis* has the ability to fly up to 3,000 m above the ground to forage ([McCracken et al. 2008](#)), our model suggest that this species is limited by extreme climatic conditions on the highest parts of the central and southern Andes, likely due to cold weather and permanent snow ([Garreaud 2009](#)). Additionally, we believe that biological factors could also influence its distribution in the higher elevations of the Andes ([Krauel et al. 2018](#)). For example, the diet of *T. brasiliensis* includes coleopterans, lepidopterans, hemipterans and dipterans ([Lee and McCracken 2002](#); [Alurralde and Díaz 2018](#)), but the diversity and abundance of these insects declines with increasing elevation ([Hodkinson 2005](#)). Therefore, reduced prey availability could make it difficult for this species to inhabit the higher Andes.

Furthermore, our model also revealed high suitable conditions restricted to the deserts and Lomas ecosystems of the Pacific versant (Figure 1). As in other western bat species in Perú, such as *Artibeus fraterculus* ([Patterson et al. 1992](#)) and *Glossophaga soricina* ([Webster 1993](#)), the homogeneous climatic conditions of this ecoregion ([Rundel et al. 1991](#)) could have allowed the latitudinal dispersal of *T. brasiliensis* close to the coastline ([Wiens and Donoghue 2004](#)). However, the biogeographical processes by which this species arrived to these ecoregions are still

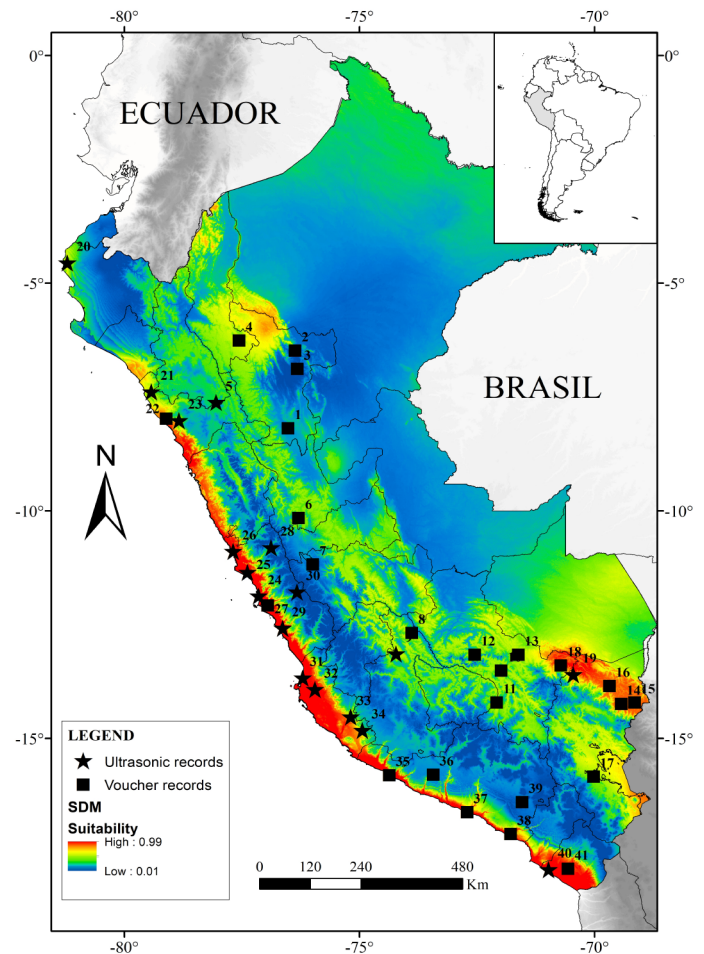


Figure 1. Selected localities and the potential distribution model (SDM) of *T. brasiliensis* in the Peruvian territory.

unknown (Lim 2009). We believe that the Huancabamba depression is closely related to the distributional patterns in South America, but population-level phylogenetic studies of the individuals from the central Andean mountains and Pacific versant are needed to test dispersal hypothesis.

Based on our model, it could be expected that individuals from the eastern and western versant have accumulated some degree of genetic variation. Genetic differentiation between individuals from different versants has been reported for other Neotropical bats, resulting in some cases in the validation or description of new species, such as *Lophostoma occidentale* (Velazco and Cadenillas 2011), *Sturnira bakeri* (Velazco and Patterson 2014), and *Artibeus aequatorialis* (Larsen et al. 2010). In North America, studies on intraspecific genetic variation for *T. brasiliensis* suggested that genetic structure is correlated with niche differentiation (Morales et al. 2016) and not with the currently recognized subspecies boundaries (Russell and McCracken 2005; Morales et al. 2016). Morales et al. (2018) found that individuals of *T. brasiliensis* from South America formed a unique population group based on the combined analysis of molecular and morphometric data; however, their study did not include representative data for populations from the Pacific versant of Perú or Ecuador. Thus, we highlight that a genetic survey for *T. brasiliensis* considering samples from both versants is badly needed.

In the Amazonian versant, our model reveals that lowland humid forests ecosystems present few suitable areas for the species (Figure 1). Although the distribution map of Wilkins (1989) seems to include a small part of Amazonia with this ecosystem, and Pacheco et al. (2009) stated the species was present in the lowland forest ecoregion (*sensu* Brack-Egg 1986), we found only two records in lowland forests (San Martín Department). In the apparent absence of east geographical barriers for bats in Perú (Proches 2006) and considering the ability of this bat to fly long distances (McCracken et al. 2008), the limitation of dispersal for *T. brasiliensis* in this ecosystem is probably related with climate conditions and/or biotic interactions (Peterson and Soberón 2012). The climate in lowland Amazonian forests is characterized by high precipitation and temperature (Vieira et al. 2004), with remarkable seasonal variation in the southeast (Jenkins 2009). Since our models revealed that the potential distribution of *T. brasiliensis* is highly influenced by mean diurnal range and annual mean temperature, and considering that ambient temperatures affect metabolic rates in bats (Reichard et al. 2010), it is likely that high temperatures in this ecosystem are one of the most important limiting factors for the species. Although it was documented that *T. brasiliensis* prefers temperatures between 22 to 32 °C to develop optimally (Herreid 1967), response curves of our model showed that suitable values of temperature vary between 15 to 20 °C in the Perú; higher temperatures may generate hyperthermia in this bat, limiting its dispersal and supporting what we stated.

Additionally, in the Amazonian forests, there are other

possible limiting factors. The high plant diversity (Cardoso et al. 2017) and dense coverage that characterize the lowland tropical forest (Nogueira et al. 2005; Nabe-Nielsen 2001) could limit the open-space flight of insectivorous bats such as *T. brasiliensis* (Fenton 1990; Kalko 1997). In addition, it is reported that this species usually roosts in caves or human dwellings (Allen et al. 2009), which are scarce in this type of forest (García-Rosell 1965; Kvist and Nebel 2000); thus, potential roosting sites may represent another factor that restricts the niche of *T. brasiliensis* in this territory.

In general, our model suggests *T. brasiliensis* is mainly associated with deserts and Andean slopes ecosystems (Figure 1). Further, a great number of locality records in South America and previous work on potential distributions support this pattern (Escobar et al. 2015). However, due to the difficulties in capturing *T. brasiliensis* with conventional methods (Rydell et al. 2002), we highlight the importance of incorporating acoustic records proceeding from reliable sources to increase the number of records and therefore to improve modelling precision, especially when certain Andean and Amazonian regions remain poorly studied. Notably, the ecological mechanisms associated with geographical dispersal in South America and potential speciation in widespread species, such as *T. brasiliensis*, has yet to be completely investigated (Pyron and Burbrink 2009).

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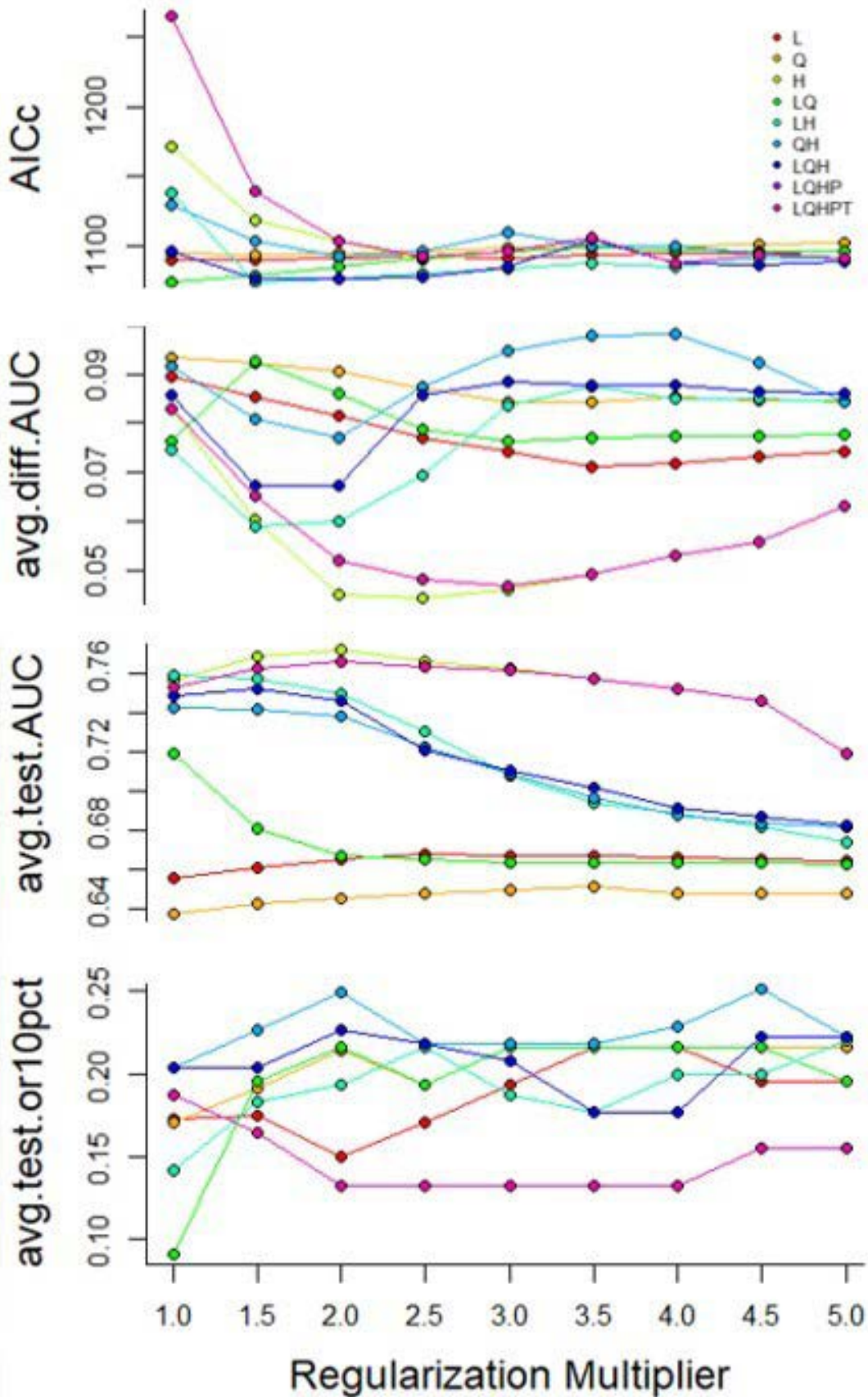
Appendix 1

Selected localities used for the SDM of *T. brasiliensis* in the Peruvian territory. Occurrence records were taken from the following institutions: Museo de Historia Natural de San Marcos (MUSM); Field Museum of Natural History (FMNH); Royal Ontario Museum (ROM); National Museum of Natural History (NMNH); American Museum of Natural History (AMNH). Records with an asterisk (*) are specimens examined by Morales *et al.* (2018). Acoustic records were obtained between 2014 to 2019 and remain stored in MUSM.

N°	Departament	Locality	Terrestrial ecoregions	Biogeographic Provinces	Coordinates	Year	Type of record
1	San Martín	Tocache, Qa San Francisco	Ucayali Moist Forest	Ucayali province	-08° 11' 21.3" S -76° 30' 51.4" W	1948	MUSM 6045
2	San Martín	Tarapoto	Ucayali Moist Forest	Ucayali province	-06° 28' 59.9" S -76° 22' 00.0" W	1954	Acha and Zapatel (1957)
3	San Martín	Río Ponasa	Ucayali Moist Forest	Ucayali province	-06° 53' 06.0" S -76° 19' 00.9" W	1954	Acha and Zapatel (1957)
4	Amazonas	Molinopampa	Peruvian Yungas	Ucayali province	-06° 15' 34.7" S -77° 33' 30.9" W	2011	MUSM 37049
5	Cajamarca	Cajabamba	Peruvian Yungas	Puna province	-07° 37' 20.6" S -78° 02' 49.5" W	2019	Ultrasonic call
6	Huánuco	Huacar	Peruvian Yungas	Yunga province	-10° 09' 24.9" S -76° 17' 34.6" W	1982	MUSM 5114-5119
7	Junín	Junín city	Central Andean Wet Puna	Puna province	-11° 10' 39.5" S -75° 59' 21.6" W	NA	ROM 93863, 93868*
8	Ayacucho	La Mar	Peruvian Yungas	Yunga province	-12° 41' 00.0" S -73° 52' 59.9" W	1941	GBIF (FMNH 52909)
9	Ayacucho	San Cristobal de Huamanga	Peruvian Yungas	Yunga province	-13° 08' 54.0" S -74° 13' 18.3" W	2019	Ultrasonic call
10	Cuzco	Santa Ana	Central Andean Wet Puna	Yunga province	-13° 30' 41.2" S -71° 58' 59.5" W	NA	NMNH 194443*
11	Cuzco	Chumbivilcas	Peruvian Yungas	Yunga province	-14° 12' 42.4" S -72° 04' 48.8" W	2009	MUSM 25965
12	Cuzco	Machu Picchu	Peruvian Yungas	Yunga province	-13° 09' 47.0" S -72° 32' 44.0" W	NA	NMNH 194440*
13	Cuzco	Paucartambo	Peruvian Yungas	Rondônia province	-13° 09' 43.9" S -71° 37' 10.9" W	2001	MUSM 19421, 19422
14	Puno	Sandia	Peruvian Yungas	Rondônia province	-14° 14' 41.9" S -69° 25' 51.9" W	1900	AMNH 16074*
15	Puno	Sandia	Bolivian Yungas	Rondônia province	-14° 12' 34.9" S -69° 08' 56.0" W	2009	MUSM 26758
16	Puno	Carabaya	Peruvian Yungas	Rondônia province	-13° 51' 00.0" S -69° 41' 00.0" W	1941	GBIF (FMNH 52968)
17	Puno	Carabaya	Central Andean Wet Puna	Yunga province	-15° 50' 21.6" S -70° 01' 09.8" W	1941	FMNH 52675*
18	Puno	Carabaya	Peruvian Yungas	Rondônia province	-13° 23' 59.9" S -70° 43' 00.0" W	1950	Vertnet (FMNH 68548)
19	Puno	Interoceánica	Peruvian Yungas	Rondônia province	-13° 36' 11.8" S -70° 27' 10.5" W	2018	Ultrasonic call
20	Piura	Talara	Tumbes-Piura Dry Forest	Ecuadorian province	-04° 33' 27.9" S -81° 12' 39.3" W	2017	Ultrasonic call
21	La Libertad	Cañoncillo	Sechura Desert	Desert province	-07° 23' 24.1" S -79° 25' 24.8" W	2018	Ultrasonic call
22	La Libertad	Loma Cerro Campana	Sechura Desert	Desert province	-07° 58' 30.0" S -79° 06' 30.0" W	2013	Zelada <i>et al.</i> (2014)
23	La Libertad	Menochuco	Sechura Desert	Desert province	-08° 01' 25.5" S -78° 50' 16.4" W	2018	Ultrasonic call
24	Lima	Humedales Ventanilla	Sechura Desert	Desert province	-11° 52' 37.5" S -77° 08' 41.4" W	2017	Ultrasonic call
25	Lima	Lomas de Lachay	Sechura Desert	Desert province	-11° 21' 27.9" S -77° 23' 00.5" W	2017	Ultrasonic call
26	Lima	Albuferas Medio Mundo	Sechura Desert	Desert province	-10° 53' 51.6" S -77° 41' 12.1" W	2014	Ultrasonic call
27	Lima	La Molina	Sechura Desert	Puna province	-12° 04' 50.1" S -76° 56' 52.0" W	2017	MUSM 47378
28	Lima	Churín	Sechura Desert	Desert province	-10° 48' 53.3" S -76° 52' 35.8" W	2019	Ultrasonic call
29	Lima	Azpitia	Sechura Desert	Desert province	-12° 35' 11.7" S -76° 37' 57.4" W	2017	Ultrasonic call
30	Lima	San Mateo	Central Andean Wet Puna	Desert province	-11° 47' 11.3" S -76° 19' 39.0" W	2019	Ultrasonic call
31	Ica	Humedales de Caucato	Sechura Desert	Desert province	-13° 40' 32.9" S -76° 12' 16.7" W	2019	Ultrasonic call
32	Ica	Villacuri	Sechura Desert	Desert province	-13° 55' 48.5" S -75° 56' 44.4" W	2019	Ultrasonic call
33	Ica	Plaza Palpa	Sechura Desert	Desert province	-14° 32' 01.1" S -75° 11' 06.5" W	2019	Ultrasonic call
34	Ica	Plaza Nazca	Sechura Desert	Desert province	-14° 49' 39.7" S -74° 56' 13.4" W	2019	Ultrasonic call
35	Arequipa	Atiquipa	Sechura Desert	Desert province	-15° 48' 30.0" S -74° 21' 46.0" W	NA	Zeballos <i>et al.</i> (2001)
36	Arequipa	Caravelí	Sechura Desert	Desert province	-15° 47' 50.3" S -73° 25' 42.8" W	NA	Pari <i>et al.</i> (2015)
37	Arequipa	Cueva Camaná	Sechura Desert	Desert province	-16° 37' 25.0" S -72° 42' 33.0" W	NA	Pari <i>et al.</i> (2015)
38	Arequipa	Valle de Tambo	Sechura Desert	Desert province	-17° 06' 09.9" S -71° 46' 55.8" W	NA	Zeballos <i>et al.</i> (2001)
39	Arequipa	Arequipa city	Sechura Desert	Desert province	-16° 23' 55.9" S -71° 32' 13.1" W	NA	Pari <i>et al.</i> (2015)
40	Tacna	Humedales de Ite	Sechura Desert	Desert province	-17° 53' 13.8" S -70° 58' 43.7" W	2014	Ultrasonic call
41	Tacna	Valle de Sama	Sechura Desert	Desert province	-17° 51' 54.0" S -70° 33' 43.0" W	2015	Portugal (2018)

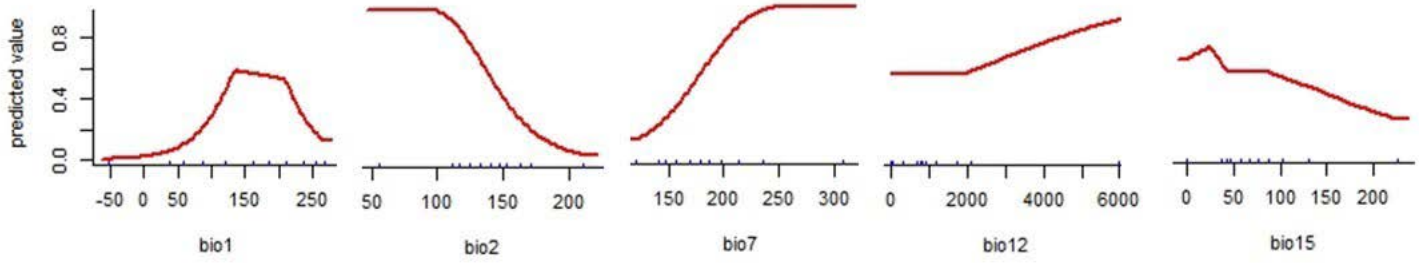
Appendix 2

Model evaluation details. The selection of the model was made using: delta AICc, average AUCdiff, omission rate at 10th percentile presence threshold, and average AUCtest. Evaluations were made with the “checkerboard2” spatial partition schema. The feature class combinations were: L: linear, P: product, Q: quadratic, H: hinge and T: threshold. The evaluation process was performed using ENMeval package version 0.3.0 (Muscarella *et al.* 2014).



Appendix 3

Response curves. Response curves obtained by the selected model for each selected variable are reported.



Appendix 4

Results of evaluation of the parameters. Results of evaluation of parameters performed in the R package ENMeval 0.3.0, considering the selected variables.

Features	Rm	train.AUC	avg.test.AUC	avg.diff.AUC	avg.test.orMTP	avg.test.or10pct	AICc	delta.AICc	Parameters
L	1	0.6785	0.6545	0.0901	0.0833	0.1727	1089.4835	15.6557	5
Q	1	0.6691	0.6344	0.0955	0.0833	0.1705	1092.1535	18.3257	4
H	1	0.8319	0.7642	0.0762	0.0477	0.1642	1171.2578	97.4301	24
LQ	1	0.7836	0.7211	0.0762	0.0686	0.0913	1073.8277	0.0000	6
LH	1	0.8208	0.7552	0.0785	0.0477	0.1831	1137.3702	63.5424	21
QH	1	0.8244	0.7419	0.0925	0.0477	0.2684	1100.4562	26.6285	16
LQH	1	0.8221	0.7472	0.0870	0.0477	0.2456	1095.2968	21.4690	15
LQHP	1	0.8265	0.7567	0.0792	0.0477	0.1642	1218.7652	144.9375	27
LQHPT	1	0.8265	0.7567	0.0792	0.0477	0.1642	1218.7652	144.9375	27
L	1.5	0.6785	0.6599	0.0867	0.0833	0.1746	1090.1189	16.2911	5
Q	1.5	0.6714	0.6403	0.0938	0.0833	0.1913	1093.0100	19.1823	4
H	1.5	0.8163	0.7747	0.0507	0.0477	0.1850	1112.6823	38.8545	16
LQ	1.5	0.7668	0.6805	0.0943	0.1083	0.1955	1078.2007	4.3729	6
LH	1.5	0.8011	0.7531	0.0628	0.0477	0.1831	1075.1797	1.3519	8
QH	1.5	0.8065	0.7405	0.0810	0.0477	0.2267	1109.3867	35.5590	16
LQH	1.5	0.8044	0.7474	0.0715	0.0477	0.2248	1081.0063	7.1785	10
LQHP	1.5	0.8066	0.7635	0.0562	0.0477	0.1623	1124.3387	50.5109	18
LQHPT	1.5	0.8066	0.7635	0.0562	0.0477	0.1623	1124.3387	50.5109	18
L	2	0.6772	0.6643	0.0841	0.0833	0.1496	1091.0507	17.2229	5
Q	2	0.6736	0.6441	0.0921	0.0833	0.2140	1094.3039	20.4761	4
H	2	0.8107	0.7690	0.0439	0.0477	0.1538	1104.7173	30.8896	14
LQ	2	0.7411	0.6667	0.0894	0.1083	0.2390	1083.7044	9.8766	6
LH	2	0.7937	0.7383	0.0657	0.0477	0.2248	1074.9997	1.1720	7
QH	2	0.8016	0.7287	0.0849	0.0477	0.2182	1113.2738	39.4460	16
LQH	2	0.7974	0.7321	0.0775	0.0477	0.2494	1077.9907	4.1630	8
LQHP	2	0.8039	0.7630	0.0492	0.0477	0.1538	1114.9026	41.0749	16
LQHPT	2	0.8039	0.7630	0.0492	0.0477	0.1538	1114.9026	41.0749	16
L	2.5	0.6765	0.6672	0.0808	0.0833	0.1496	1092.2950	18.4672	5
Q	2.5	0.6758	0.6470	0.0891	0.0833	0.1932	1096.0801	22.2524	4
H	2.5	0.8041	0.7611	0.0475	0.0477	0.1538	1090.4313	16.6035	10
LQ	2.5	0.7119	0.6645	0.0821	0.0833	0.1932	1090.2051	16.3773	6
LH	2.5	0.7858	0.7180	0.0761	0.0250	0.2078	1085.1064	11.2787	9
QH	2.5	0.7959	0.7111	0.0946	0.0477	0.2182	1097.7182	23.8905	12
LQH	2.5	0.7897	0.7070	0.0940	0.0477	0.2182	1081.8063	7.9786	8
LQHP	2.5	0.8056	0.7600	0.0487	0.0477	0.1538	1094.0688	20.2411	11
LQHPT	2.5	0.8056	0.7600	0.0487	0.0477	0.1538	1094.0688	20.2411	11
L	3	0.6759	0.6675	0.0772	0.1042	0.1705	1091.2385	17.4107	4
Q	3	0.6773	0.6495	0.0854	0.0852	0.2159	1098.4081	24.5803	4
H	3	0.8021	0.7564	0.0496	0.0477	0.1538	1085.9274	12.0996	8
LQ	3	0.6755	0.6633	0.0781	0.1269	0.2159	1097.6606	23.8329	6
LH	3	0.7798	0.6979	0.0819	0.0250	0.1557	1082.0946	8.2669	7
QH	3	0.7883	0.6982	0.0975	0.0705	0.2182	1101.6644	27.8366	12

Apendix 4 continuación...

Features	Rm	train.AUC	avg.test.AUC	avg.diff.AUC	avg.test.orMTP	avg.test.or10pct	AICc	delta.AICc	Parameters
LQH	3	0.7827	0.6983	0.0927	0.1102	0.1557	1093.0987	19.2710	10
LQHP	3	0.8021	0.7556	0.0501	0.0477	0.1538	1085.9274	12.0996	8
LQHPT	3	0.8021	0.7556	0.0501	0.0477	0.1538	1085.9274	12.0996	8
L	3.5	0.6759	0.6677	0.0723	0.1061	0.2159	1092.8782	19.0504	4
Q	3.5	0.6758	0.6509	0.0852	0.0625	0.2159	1098.6055	24.7777	3
H	3.5	0.8009	0.7513	0.0528	0.0477	0.1538	1091.6724	17.8446	9
LQ	3.5	0.6721	0.6640	0.0776	0.1061	0.1951	1097.7642	23.9365	5
LH	3.5	0.7718	0.6887	0.0797	0.1102	0.1992	1085.6237	11.7960	7
QH	3.5	0.7784	0.6924	0.0958	0.0705	0.1869	1130.5313	56.7036	17
LQH	3.5	0.7705	0.6904	0.0871	0.1102	0.1557	1097.9921	24.1644	10
LQHP	3.5	0.8009	0.7513	0.0528	0.0477	0.1538	1091.6724	17.8446	9
LQHPT	3.5	0.8009	0.7513	0.0528	0.0477	0.1538	1091.6724	17.8446	9
L	4	0.6736	0.6672	0.0725	0.0852	0.1951	1094.8511	21.0233	4
Q	4	0.6723	0.6487	0.0856	0.0625	0.2159	1101.4590	27.6312	3
H	4	0.7985	0.7408	0.0585	0.0477	0.1765	1101.8029	27.9752	11
LQ	4	0.6708	0.6640	0.0776	0.1269	0.1951	1096.9411	23.1134	4
LH	4	0.7516	0.6836	0.0797	0.1102	0.1765	1092.7787	18.9509	8
QH	4	0.7643	0.6843	0.0921	0.0790	0.1850	1113.4687	39.6410	13
LQH	4	0.7538	0.6852	0.0803	0.1330	0.1992	1091.2361	17.4084	7
LQHP	4	0.7985	0.7408	0.0585	0.0477	0.1765	1101.8029	27.9752	11
LQHPT	4	0.7985	0.7408	0.0585	0.0477	0.1765	1101.8029	27.9752	11
L	4.5	0.6701	0.6665	0.0734	0.0852	0.1951	1097.2066	23.3789	4
Q	4.5	0.6713	0.6486	0.0851	0.0625	0.2159	1100.4614	26.6336	2
H	4.5	0.7951	0.7263	0.0631	0.0477	0.1557	1101.3407	27.5129	10
LQ	4.5	0.6702	0.6642	0.0775	0.1269	0.2159	1095.4363	21.6086	3
LH	4.5	0.7222	0.6761	0.0820	0.1102	0.1992	1088.3320	14.5043	5
QH	4.5	0.7442	0.6787	0.0858	0.0790	0.1680	1098.5480	24.7202	8
LQH	4.5	0.7345	0.6792	0.0805	0.1102	0.1765	1087.7865	13.9588	5
LQHP	4.5	0.7951	0.7263	0.0631	0.0477	0.1557	1101.3407	27.5129	10
LQHPT	4.5	0.7951	0.7263	0.0631	0.0477	0.1557	1101.3407	27.5129	10
L	5	0.6692	0.6655	0.0745	0.0852	0.1951	1095.8348	22.0071	3
Q	5	0.6723	0.6488	0.0852	0.0625	0.2159	1101.5643	27.7365	2
H	5	0.7895	0.7060	0.0723	0.0477	0.1557	1101.9515	28.1238	9
LQ	5	0.6696	0.6639	0.0781	0.1061	0.2159	1096.4307	22.6029	3
LH	5	0.7099	0.6704	0.0833	0.1102	0.2201	1089.9782	16.1505	5
QH	5	0.7254	0.6729	0.0791	0.0477	0.1680	1095.2162	21.3884	6
LQH	5	0.7196	0.6725	0.0825	0.1102	0.1992	1089.9919	16.1642	5
LQHP	5	0.7895	0.7060	0.0723	0.0477	0.1557	1101.9515	28.1238	9
LQHPT	5	0.7895	0.7060	0.0723	0.0477	0.1557	1101.9515	28.1238	9