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Research Article

Hiding in a Cool Climatic Niche in the Tropics? An Assessment of the Ecological Biogeography of Hairy Long-Nosed Armadillos (*Dasypus pilosus*)

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Abstract

The hairy long-nosed armadillo (*Dasypus pilosus*) is endemic to the Andes in Peru and rarely studied, thus more investigations are needed. To gain a better understanding of this species' distribution and to facilitate future surveys and conservation management, we compiled available information on specimens of *D. pilosus*, provided an ecological biogeography perspective of these specimens, and estimated suitable areas for *D. pilosus* using ecological niche modeling. We compiled 25 specimen records from six departments in Peru and extracted the climatic and elevation conditions for records with coordinates. We concluded that *D. pilosus* may occupy relatively high elevation sites, hiding in a relatively cool climatic niche at tropical latitude. We suggested possible upper and lower temperature limits for *D. pilosus* and lower precipitation limit for the genus *Dasypus*. The ecological niche model estimated that about half of the International Union for Conservation of Nature (IUCN) range map was not suitable for *D. pilosus* and predicted additional suitable areas outside the IUCN range map in Amazonas and Cajamarca departments, Peru. We recommend that future field surveys or conservation management efforts prioritize regions associated with suitable areas predicted by our model and with species' available records (e.g., Río Abiseo).

Keywords

Andes, *Dasypus bellus*, *Dasypus kappleri*, *Dasypus novemcinctus*, ecological niche modeling, Maxent

The hairy long-nosed armadillo is a poorly studied species that is endemic to Peruvian Andes (Castro et al., 2015; Superina & Abba, 2014; Superina, Pagnutti, & Abba, 2014; Wetzel, 1985). The species' generic affinity has been debated (Castro et al., 2015; Gibb et al., 2016) and here we adopted the nomenclature more frequently used in the literature so far, which is *Dasypus* (*Cryptophractus*) *pilosus*. *Dasypus pilosus* has long reddish tan to reddish gray hair concealing the carapace, which makes it unique among *Dasypus* species (Castro et al., 2015; Wetzel & Mondolfi, 1979). The species is known to occur on the high, moist eastern slopes of the Andes in cloud forest and subparamo habitats (Wetzel, 1982; Wetzel, Gardner, Redford, & Eisenberg, 2007). Xenarthrans are generally understudied (Superina & Loughry, 2015), but information on *D. pilosus* in particular is scarce: according to Castro et al. (2015), only 18 publications (including book chapters) from 1856 to 2007, most focused on taxonomy and morphology, or even more conservative estimates of one publication according to Loughry, Superina, McDonough, and Abba (2015) and three according to Superina, Pagnutti, and Abba (2014). The ecology, population status, threats, and even the geographic distribution of *D. pilosus* are largely unknown. The International Union for Conservation of Nature (IUCN) has changed the status

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of the species from vulnerable to data deficient (Superina & Abba, 2014), and Superina et al. (2014) recommended prioritization of investigations on *D. pilosus* among armadillo species.

In lieu of new data collections, museum specimens are a good resource to study a species' distribution. With the recent and rapid digitization of museum specimens and establishment of electronic databases, specimen information is becoming easily accessible through the Internet (e.g., http://vertnet.org/). Castro et al. (2015) compiled a comprehensive list of specimens available and provided a detailed analysis of morphology and phylogeny for *D. pilosus*; however, the important perspective of ecological biogeography has been overlooked. Generally speaking, ecological biogeography attempts to explain biodiversity and distribution patterns in relation to ecological factors (Lomolino, Riddle, Whittaker, & Brown, 2010). One major focus of ecological biogeography is the study of species' geographic distributions and ecological (abiotic) niches (Hutchinson, 1957; Soberón, 2007). Besides the digitized museum specimens, ecological biogeography also greatly relies on geographic information systems (GIS), especially the digitalized maps of various environmental conditions (e.g., climate and elevation). With location data (latitude and longitude) of specimens, one can directly detect the associated environmental requirements. Ecological niche modeling (ENM), or species distribution modeling, is used frequently in ecological biogeography (Peterson et al., 2011). ENM uses species' occurrence data and environmental layers to estimate potential distributions, which are frequently used for conservation purposes (Bond, Thomson, & Reich, 2014; Feng, Lin, Qiao, & Ji, 2015; Fois, Fenu, Cuena Lombraña, Cogoni, & Bacchetta, 2015; Loiselle et al., 2003; Menon, Choudhury, Khan, & Peterson, 2010).

In this study, we aimed to gain a better understanding of the distribution of *D. pilosus* based on previously collected museum specimens and methods in ecological biogeography. Specifically, we aimed to investigate three questions. First, how many specimens of *D. pilosus* have been collected thus far? Second, what ecological information is associated with the collected specimens and does this information match the current literature? Third, where should future surveys focus in order to find this species? Three objectives stemmed from the proposed questions: (a) compiling available information of *D. pilosus* specimens; (b) interpreting the information of specimens from the perspective of ecological biogeography and comparing our interpretation with current understanding of the species' ecology; and (c) assessing the potential distribution of *D. pilosus* within its range based on known occurrences and relevant environmental variables to formulate priorities for future surveys or conservation management.

Method

Compiling Species Presence Data

We searched for information of museum specimens and observations through online databases (VertNet, http://vertnet.org/, Retrieved April 1, 2016; GBIF, http://www.gbif.org/, Retrieved September 3, 2016; iNaturalist, http://www.inaturalist.org/, accessed September 3, 2016). We also acquired information on specimens from the primary literature (Castro et al., 2015; Gardner, 2007; Wetzel, 1982, 1985; Wetzel & Mondolfi, 1979). The databases and literature overlapped in documenting several specimens; but when conflicting information occurred or when obvious doubts were raised (e.g., locality description), we used the following decreasing order of authority: literature, museum databases, external experts' opinions, and our own judgments. Our searches of databases and the literature yielded only museum specimen records. We georeferenced records with adequate locality descriptions using GeoNames WMS Viewer (http://geonames.nga.mil/namesviewer/default.asp), Google Maps, or local park maps. When available, we recorded the following information: museum, specimen ID, year collected, country, Peruvian administrative Levels 1–3 (department, province, and district), locality of collection site, latitude, longitude, elevation, and other information such as specimen preparation type and sex. Some records did not have information of administrative units of Peru or had such information but without specifying the level. Therefore, we located the administrative units or protected areas based on specimen coordinates and maps of administrative units of Peru (Retrieved from http://www.diva-gis.org/data on July 1, 2016) and protected areas (International Union for Conservation of Nature and United Nations Environment Programme's World Conservation Monitoring Centre, 2016).

Overlaying Specimens With Environmental Layers

We compiled a list of 25 unique specimens, 21 of which had geographic coordinates (Table 1). Aiming to gain a better understanding of the species' environmental requirements, we overlaid the georeferenced specimens with three environmental layers: annual mean temperature, annual precipitation, and elevation, retrieved from worldclim.org (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at the resolution of 2.5 arc min. We expected the three variables to represent the general, basic information of *D. pilosus* biogeography.

Ecological Niche Modeling

To estimate the species' potential distribution, we built an ecological niche model in Maxent algorithm (Phillips, Dudík, & Schapire, 2004) using the georeferenced

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Table 1. Compiled Information of Hairy Long-Nosed Armadillo (*Dasypus pilosus*) Specimens.

msID	Specimen ID	Year	Source	Country	Department	Province	District or protected area	Locality	Preparations	Sex	Elevation from tag	Extracted elevation
1	NHM-27.11.1.235	n/a	Castro et al. (2015); Wetzel and Mondolfi (1979)	Peru	Junín	Tarma	Acobamba	Acobamba, Junín	Skin	n/a	2,440 m	3,553 m
2	NHM-94.10.1.13	n/a	Castro et al. (2015); Wetzel and Mondolfi (1979)	Peru	Junín	Jauja	Monobamba	Maraynoic, Junin	Skin and Skull	n/a	n/a	3,492 m
3	MSB-49990	1980	VertNet retrieved April 2016	Peru	Huánuco	Huánuco	Chinchao	6 km NE Acomayo, 9300 feet	Skin	Female	2835 m	2,996 m
4	LSU-14352	1968	VertNet retrieved April 2016; Castro et al. (2015)	Peru	Huánuco	Huánuco	Chinchao	E slope Cordillera Carpish, Carretera Central, Huánuco	Skin	n/a	n/a	2,509 m
5	LSU-14353	1968	VertNet retrieved April 2016, Castro et al. (2015); Wetzel and Mondolfi (1979)	Peru	Huánuco	Huánuco	Chinchao	E slope Cordillera Carpish, Carretera Central, Huánuco	Skin	n/a	n/a	2,509 m
6	LSU-19240	1974	VertNet retrieved April 2016; Castro et al. (2015)	Peru	Huánuco	Huánuco	Chinchao	Bosque Taprag above Acomayo, Huánuco	Skin and skull	Female	n/a	2,509 m
7	LSU-19241	1974	VertNet retrieved 2016 April, Castro et al. (2015)	Peru	Huánuco	Huánuco	Chinchao	Bosque Taprag above Acomayo, Huánuco	Skin and skull	n/a	n/a	2,509 m
8	LSU-19242	1974	VertNet retrieved April 2016; Castro et al. (2015)	Peru	Huánuco	Huánuco	Chinchao	Bosque Taprag above Acomayo, Huánuco	Skin	n/a	n/a	2,509 m
9	LSU-19243	1974	VertNet retrieved April 2016; Castro et al. (2015)	Peru	Huánuco	Huánuco	Chinchao	Bosque Zapatagocha above Acomayo, Huánuco	Skin and skull	n/a	n/a	2,509 m
10	LSU-21888	1978	VertNet retrieved April 2016; Castro et al. (2015); Wetzel (1982)	Peru	Amazonas	Bagua	Aramango (Cordillera Colán or Chayu Naín)	Cordillera Colán, NE La Peca, Amazonas, Peru	Skin and partial skeleton	Male	3,201 m	2,831 m
11	LSU-18435	1973	VertNet retrieved April 2016; Castro et al. (2015)	Peru	Huánuco	Huánuco	Chinchao	Bosque Zapatagocha, Huánuco, Peru	Skin	n/a	n/a	2,509 m
12[a]	NMW-222	1833	Castro et al. 2015; Wetzel and Mondolfi (1979)	Peru	n/a	n/a	n/a	Unknown locality; bought in 1833 from an animal dealer in London	Mounted skin	n/a	n/a	n/a
13[a]	IRSNB-291536/319	1846	Castro et al. (2015); Wetzel and Mondolfi (1979)	Peru	La Libertad	Santiago de Chuco	Santiago de Chuco	Unknown locality. Suggested as Santiago, Piura, Peru by Fechkop and Yepes (1949)	Mounted skin without tail	n/a	n/a	n/a

(continued)

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Table 1. Continued

msID	Specimen ID	Year	Source	Country	Department	Province	District or protected area	Locality	Preparations	Sex	Elevation from tag	Extracted elevation
14	MUSM-CT1312	2013	Castro et al. (2015)	Peru	Amazonas	Luya	Tingo (Huiquilla)	Yurac Rume	Skin	n/a	n/a	2,846 m
15	MUSM-ING633	1999–2009[b]	Castro et al. (2015)	Peru	San Martín	Mariscal Cáceres	Huicungo	Concesión para la Conservación Alto Huayabamba	Skin	n/a	n/a	3,121 m
16	MUSM-2056	1974	Castro et al. (2015); Wetzel and Mondolfi (1979)	Peru	Huánuco	Huánuco	Chinchao	Zapatogocha, Acomayo	Skull and skin	Male	3,000 m	2,509 m
17	MUSM-7499	n/a	Castro et al. 2015	Peru	San Martín	Mariscal Cáceres	Huicungo (Río Abiseo)	Parque Nacional Río Abiseo	Skin	n/a	n/a	2,264 m
18[a]	MUSM-7500	n/a	Castro et al. (2015)	n/a	n/a	n/a	n/a	Unknown locality	Skull	n/a	n/a	n/a
19	MUSM-7501	1989	Castro et al. (2015)	Peru	San Martín	Mariscal Cáceres	Huicungo (Río Abiseo)	La Playa, ca 28 km NE Pataz, Las Papayas, vegetación ribereña	Skull and skin	Male	n/a	2,627 m
20	MUSM-7502	n/a	Castro et al. (2015)	Peru	San Martín	Mariscal Cáceres	Huicungo (Río Abiseo)	Parque Nacional Río Abiseo	Skull and skin	Female	n/a	2,264 m
21	MUSM-7503	1990	Castro et al. (2015)	Peru	San Martín	Mariscal Cáceres	Huicungo	NE Pataz, Las Papayas	Skull and skin	Male	n/a	2,468 m
22	MUSM-7504	1989	Castro et al. (2015)	Peru	San Martín	Mariscal Cáceres	Huicungo (Río Abiseo)	Río Colorado, Bosque en zona inundable, entre el mirador y la playa	Skull and skin	Female	2,950 m	3,486,m
23	MUSM-7505	1989	Castro et al. (2015)	Peru	San Martín	Mariscal Cáceres	Huicungo (Río Abiseo)	Río Colorado, entre el mirador y la playa, ca 28 km NE Pataz	Skull and skin	Female	2,930 m	3,486 m
24	MUSM-24214	n/a	Castro et al. (2015)	Peru	Pasco	Oxapampa	Huancabamba (Yanachaga-Chemillén)	Santa Barbara	Disarticulated carapace	n/a	3,400 m	2,539 m
25[a]	MUSM-26/27	n/a	Castro et al. (2015); Wetzel (1985)	n/a	n/a	n/a	n/a	"Guayaquil," no nation	Mounted skin	n/a	n/a	n/a

Note. The column "msID" corresponds to the specimen ID plotted in Figures 1 and 3. "n/a" means data not available or not applicable. The detailed coordinates are not shown for the purpose of protecting the species. NHM = The Natural History Museum, London, United Kingdom; MSB = Mammal Collection, Museum of Southwestern Biology, University of New Mexico, Albuquerque, USA; LSU = Louisiana State University, Museum of Zoology, Baton Rouge, USA; NMW = Naturhistorisches Museum Wien, Vienna, Austria; IRSNB = Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MUSM = Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru.

[a]Coordinate not available or not applicable.

[b]Exact collection year unknown.

specimen records and a set of environmental variables (19 bioclimatic variables; Hijmans et al., 2005) at the resolution of 2.5 arc min. Maxent calculates the probability of presence by minimizing the relative entropy between the probability densities of occurrences and the training background in the environmental space (Elith et al., 2006, 2011). Maxent is also known for its robust performance with few occurrences (Phillips & Dudik, 2008), which fits the situation of this study.

To avoid the issue of sampling bias, we only kept one record per pixel, thus the records retained (12 of the 21) were spatially unique. To consider the dispersal ability in our model (Soberón & Peterson, 2005), we restricted the training area to a two-decimal degree (approximately 220 km at equator) buffer around all spatially unique records, within which we selected 10,000 background points as pseudo-absences for model training. To avoid the influence of predictor collinearity and potential model overfitting, we eliminated bioclimatic variables based on their contributions to the full model and the correlation matrix, following Feng, Anacleto, and Papeş (2016). First, we built a Maxent model with all spatially unique presences (12) and all bioclimatic variables (19) using linear and quadratic features and default regularization value, according to an empirical study (Phillips & Dudik, 2008). Then, we eliminated highly correlated ($|r| \geq .7$) variables while retaining those with high contribution and removing those with no contribution to the accuracy gain of the first Maxent model. This procedure led to selection of three bioclimatic variables (BIO6, minimum temperature of the coldest month; BIO15, precipitation seasonality; BIO16, precipitation of the wettest quarter), which were used to train the final model.

To evaluate the performance of the model obtained with the three selected environmental variables, we split the occurrences into four sets with the ''checkerboard2'' method (Muscarella et al., 2014) and used alternatively three sets as training and the fourth one as testing. The advantage of ''checkerboard2'' over random split is that the former can lessen the influence of spatial autocorrelation and thus leads to more robust evaluation index (Muscarella et al., 2014). We calculated two evaluation indices: partial area under the receiver operating characteristic curve (pAUC; Peterson, Papeş, & Soberon, 2008) at the threshold of 5% training omission rate (5% of training presences predicted as absences) and true skill statistic (TSS; Allouche, Tsoar, & Kadmon, 2006) at the threshold of 0% training omission rate. Compared with the traditional AUC, the pAUC evaluates the model performance at high sensitivity levels (percentage of correctly predicted presences), in our case from 0.95 to 1, thus it is more appropriate for ENM that usually adopts threshold approaches (Peterson et al., 2008); a value of $\text{pAUC} > 1$ indicates model performance better than random. The TSS considers both sensitivity (percentage of correctly predicted presence) and specificity (percentage of correctly predicted absence) and its value ranges from -1 to 1, while a value > 0 indicates that the model performs better than random (Allouche et al., 2006).

We projected the model to the extent of area surrounding the IUCN range map of *D. pilosus*. We thresholded the raw prediction of continuous suitability values to binary format (suitable vs. unsuitable) based on the minimum training threshold (0% training omission rate), which identifies suitable areas at least as good as known occurrences (Pearson, Raxworthy, Nakamura, & Peterson, 2007). To identify possible limiting factors of *D. pilosus* distribution, we ran the multivariate environmental similarity surface analysis (MESS; Elith, Kearney, & Phillips, 2010) within the predicted absence or unsuitable area using the three climatic variables involved in ENM training (BIO6, BIO15, and BIO16) and specimens' coordinates as the reference group. This procedure identifies the most different environmental conditions that exceeded the conditions associated with specimens' coordinates in the area predicted unsuitable.

Relating Distribution Information With Protected Areas

To provide information for possible future field surveys and conservation management, we overlaid the specimens' coordinates and area predicted suitable with the map of protected areas (IUCN and UNEP-WCMC, 2016) in Peru. We calculated the frequency of specimens and the size of areas predicted suitable associated with each protected area.

Results

We compiled a data set with 25 records of *D. pilosus* specimens (Table 1 and Figure 1). The oldest specimen dates to 1833 (NMW-222). In the latter half of the 20th century, *D. pilosus* was repeatedly collected in the Andes in Peru and the newest specimen was collected in 2013 from Yurac Rume (Huiquilla private conservation area, Tingo district, Luya province, Amazonas department, Peru). The specimens generally occurred in five protected areas and seven surrounding districts (Level-3 administrative unit) in six departments (Level-1 administrative unit).

The tags of five specimens had the elevation of the collection sites, ranging from 2,440 to 3,400 m (Table 1). The elevation derived from specimens with geographic coordinates ranged from 2,264 to 3,553 m (Table 1). The geographic coordinates of the specimens were

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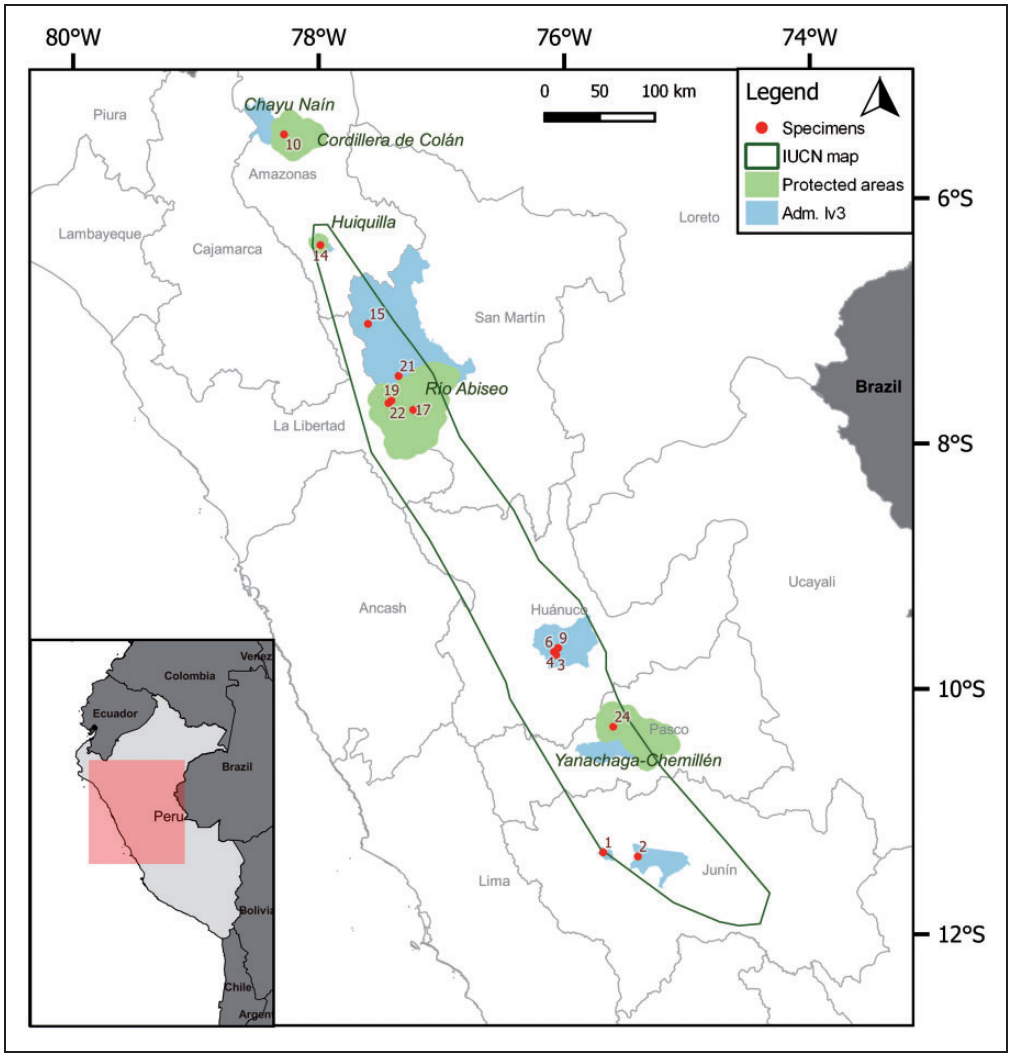


Figure 1. An overview of the distribution of *Dasypus pilosus*. The red circles represent the geographic coordinates of specimens. Numbers correspond to specimens listed in Table 1. The green open polygon represents the International Union for Conservation of Nature range map. The green-shaded polygons represent protected areas (names also in green) with specimen records. The blue-shaded polygons represent Level-3 administrative units (district) with specimen records.

representative of temperate climate, with annual mean temperature (BIO1 variable) of 8.9–16.7°C and annual precipitation (BIO12 variable) of 623–1,253 mm. Compared with annual mean temperature and annual precipitation of surrounding background (two decimal degrees buffer area), the known locations for this species appear to represent a narrow two-dimensional environmental space (Figure 2). We also mapped the differences in two climatic dimensions between the specimens and the projected area to illustrate possible regional climatic limits for this species (Figure 3).

The performance of Maxent model was better than random, according to pAUC of 1.85 ± 0.01 (mean $\pm$ *SD*) and TSS of 0.20 ± 0.01. The predicted potential distribution had a northwest to southeast extent along the Andes (Figure 4(a)). Within the IUCN range map, only 49% was predicted suitable for *D. pilosus*. Outside the IUCN range map, a considerable portion of Department of Cajamarca was predicted as suitable but was disconnected from the main potentially suitable area by a narrow gap of low elevation. Based on the MESS analysis, the majority of the unsuitable area exceeded the range of temperature of the coldest month (BIO6) associated with specimens' geographic coordinates (Figure 4(b)).

Among the protected areas in Peru, 33 were predicted partly or completely suitable for *D. pilosus* (Figure 4(a) and Table A1). Of the 33 protected areas, 5 had at least one *D. pilosus* record, while Río Abiseo had the most (5; Table A1).

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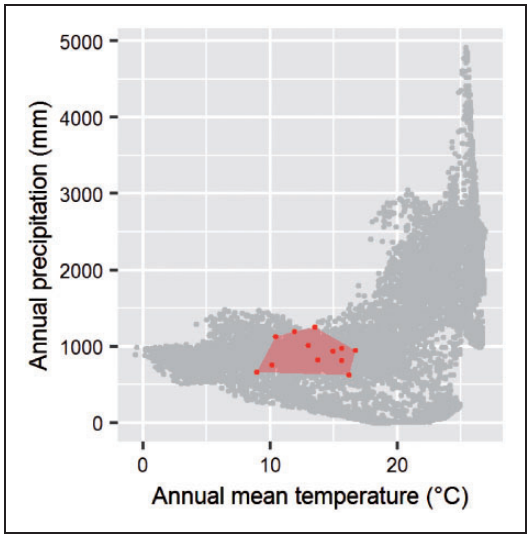


Figure 2. Illustration of climatic requirements for *Dasypus pilosus* in two-dimensional environmental space. The red points represent the climatic conditions associated with the geographic coordinates of specimens. The gray points represent climatic conditions associated with the pixels surrounding specimens in two decimal degree buffers. The red polygon is the convex hull of the specimens, illustrating the possible boundary of the precipitation and temperature requirements of *D. pilosus*.

Discussion

We compiled information for only 25 specimens of *D. pilosus*; however, this is the most comprehensive catalog of collected specimens of *D. pilosus*. The IUCN status of *D. pilosus* is "data deficient" (Superina & Abba, 2014), but we presume that *D. pilosus* is not extinct given the recent specimen collected in 2013 (MUSM-CT1312) and the observation record in 2009 (Abba & Superina, 2010). The species may be rare or have a low abundance, but considering the longtime span of the collecting history (from 1833 to 2013, 181 years), the small number of specimens (25) indicates that limited effort has been invested in studying *D. pilosus*. Thus, our work provides more support for the proposal of Superina et al. (2014) to prioritize *D. pilosus* in scientific studies, and we hope our work will promote more investigations of *D. pilosus*.

Compiling locality information broadened our understanding of the distribution of *D. pilosus*. The species has been found in the Peruvian departments of San Martín, La Libertad, Huánuco, and Junín, but uncertainty was associated with the 2009 observation in Huiquilla, Amazonas (A. M. Abba, personal communication, November 14, 2016; Abba & Superina, 2010; but see Wetzel, 1982). However, we found that two specimens of *D. pilosus* (LSU-21888 and MUSM-CT1312) have been collected from department of Amazonas, and LSU-21888 was collected well beyond the IUCN range map (Superina & Abba, 2014; Figure 1). In addition to these records, a considerable portion of southern Amazonas was predicted suitable by our Maxent model, supporting the possibility of *D. pilosus* presence in Amazonas. Besides locations in previously reported departments in the literature (Abba & Superina, 2010; Wetzel, 1982, 1985; Wetzel & Mondolfi, 1979), we also found a specimen (MUSM-24214) collected from Santa Barbara, a mountain in the department of Pasco. Based on the new distribution information for *D. pilosus*, we suggest a revision of the IUCN range map.

By associating climate variables to geographic coordinates of specimens, we gained a deeper understanding of environmental requirements for *D. pilosus*. Elevation recorded on the specimen labels ranged from 2,440 to 3,400 m and the values extracted with the geographic coordinates of specimens ranged from 2,264 to 3,553 m. The two sources of elevation are not identical because the extracted values represent the average elevation of surrounding pixels while the elevation recorded on specimen labels may represent the elevation of the collection site, though not well documented. However, the elevation ranges of the two sources generally described similar patterns. The compiled elevation information generally matched the description of the upper elevation limit for *D. pilosus* distribution (3,000–3,200 m; Abba & Superina, 2010; Wetzel, 1982) but not the lower elevation (500 m; Abba & Superina, 2010). Furthermore, low elevation is generally associated with warmer climatic conditions, thus the species' distribution at lower elevation contradicts our finding of temperature requirements for *D. pilosus*. Thus, we note that revisions of current assumptions of the elevation range for *D. pilosus* are needed.

The derived temperature requirements of the species, based on the specimen geographic coordinates, showed an intermediate climate profile within the surrounding area (Figures 2 and 3(a)). The areas predicted unsuitable were most different from georeferenced localities for *D. pilosus* in terms of coldest temperature (Figure 4(b)). The range of temperature values associated with the specimens corresponded to a narrow geographic area, thus we propose that *D. pilosus* is restricted to (or selecting) a temperate to relatively cool niche in the Neotropics. The elongated shape of the *D. pilosus* distribution could be explained by the upper and lower thermal limits of the species. The distribution of Dasypodidae taxa is directly affected by their physiological characteristics (i.e., low body temperature, low basal metabolism, and high thermal conductance; McNab, 1980). A limitation on distribution related to temperature seems likely for *D. pilosus*, similar to the limitation of the distribution of *D. novemcinctus* by cold temperature in the northern portion of its range (Feng & Papeş, 2015; Taulman & Robbins, 2014). The dense fur of *D. pilosus* may extend

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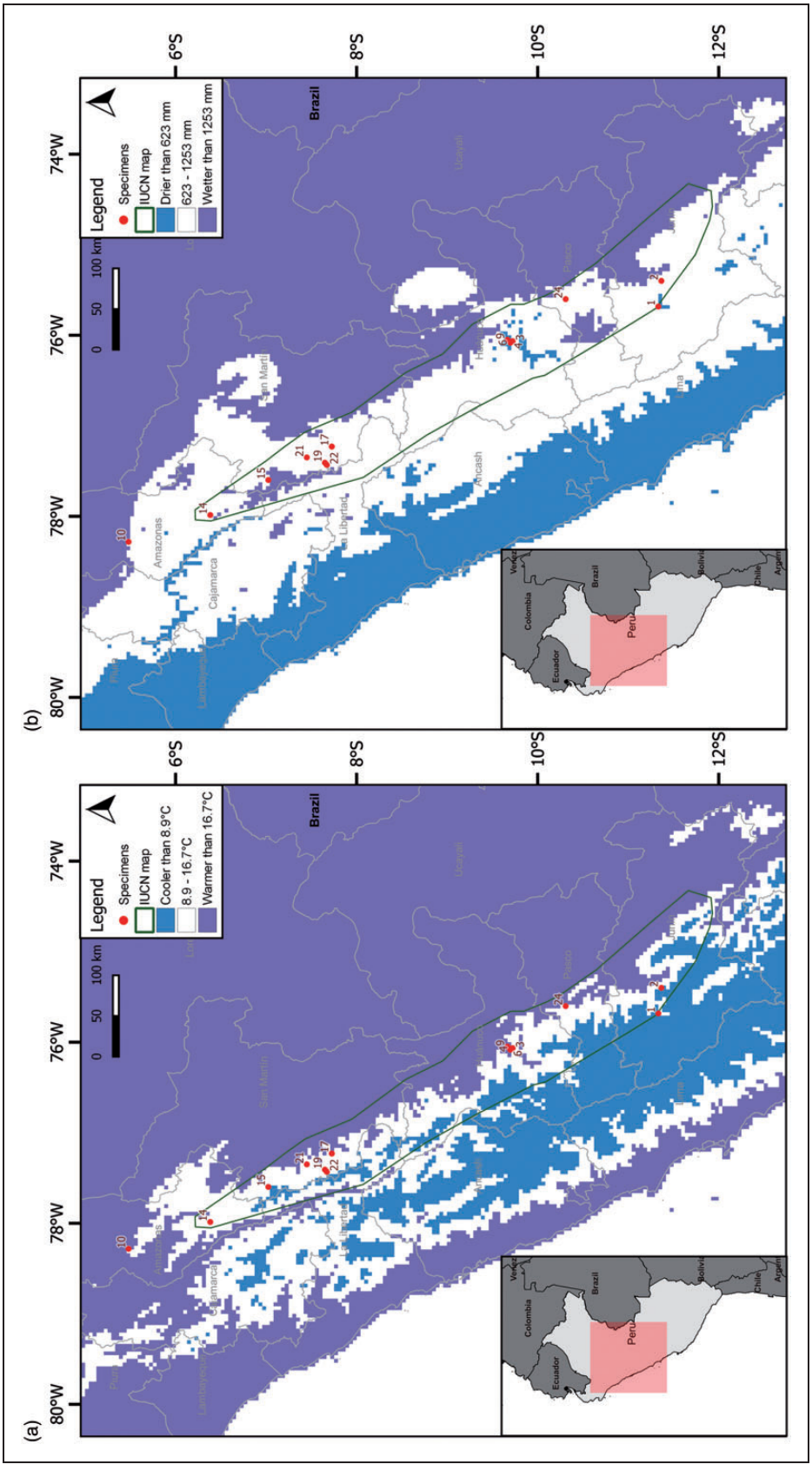


Figure 3. Illustration of climatic requirements for *Dasypus pilosus* in geographic space. The red circles represent the geographic coordinates of specimens. The green polygon represents the International Union for Conservation of Nature range map. In the white area, the annual mean temperature (Panel a) or annual precipitation (Panel b) are within the limit of conditions associated with the specimens. In the blue area, the annual mean temperature (Panel a) or annual precipitation (Panel b) are lower than those associated with the specimens. In the purple area, the conditions are higher than those associated with the specimens.

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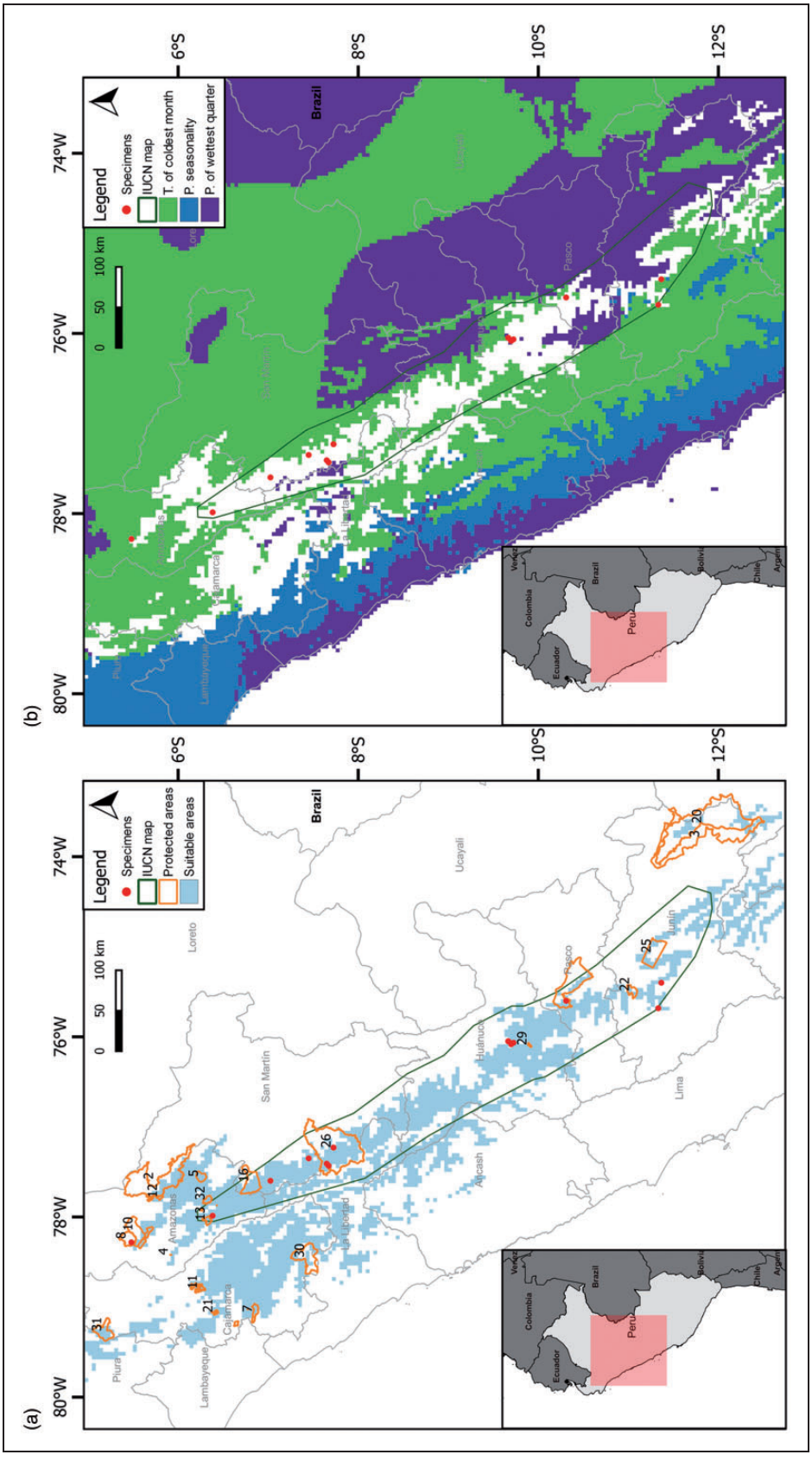


Figure 4. The suitable area for *Dasypus pilosus*, estimated with ecological niche modeling and climatic dissimilarity analysis. The red circles represent the geographic coordinates of specimens. The green polygon represents the International Union for Conservation of Nature range map. In Panel a, the area predicted suitable by the ecological niche model is represented by the blue color, whereas the orange polygons, with numeral labels (Table A1), represent protected areas either completely or partly suitable for *D. pilosus*. The multivariate environmental similarity surface analysis calculates the climatic similarity between target localities (area predicted unsuitable) and a group of reference points (coordinates of specimens) based on the three variables used in ecological niche modeling training (i.e., BIO6, minimum temperature of the coldest month; BIO15, precipitation seasonality; BIO16, precipitation of the wettest quarter). The most dissimilar variable of each target locality is shown in Panel b.

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its cold temperature tolerance; however, this tolerance is probably still narrow in light of the South American origin of armadillos (Leigh, O'Dea, & Vermeij, 2014), making the species more likely to be warm adapted than cold adapted (Superina & Loughry, 2012). Krmpotic et al. (2015) found less adipose tissue in the osteoderms of Dasypodinae than in those of Euphractinae, which may contribute to the high thermal conductance of Dasypodinae and therefore limited cold tolerance. In contrast, McNab (1980) explained the necessity of high thermal conductance to prevent overheating of armadillos in burrows. Therefore, the dense fur may pose an upper thermal limit on *D. pilosus* by hindering heat dissipation, given that the species' distribution appears to be restricted to a temperate regime, excluding the surrounding tropical climatic conditions.

The precipitation requirements derived from specimens used in the current study showed a plausible minimum limit (623 mm; Figures 2 and 3(b)). A minimum moisture limit was proposed for *D. novemcinctus* (380 mm [Taulman & Robbins, 1996, 2014] or 500 mm [Humphrey, 1974]) as necessary for maintaining a vegetative litter layer with prey items. The same rule seems to fit *D. pilosus* as well, given the species' suspected dietary requirements of ants and termites (Castro et al., 2015). Interestingly, two other *Dasypus* species (*D. kappleri* and the extinct *D. bellus*) have been shown to follow the precipitation limit of 500 mm (Feng, Anacleto, & Papeş, 2016). This suggests the possibility that, along with temperature, the distribution of *Dasypus* taxa is limited by low precipitation which in turn limits prey availability, given the shared adaptation to mymecophagy/insectivory among the species of *Dasypus* (Wetzel et al., 2007).

The predicted distribution of *D. pilosus* did not match the IUCN range map (Figure 1). A considerable portion (51%) of the IUCN range map was predicted as unsuitable, probably because of temperature regimes that are either too cold or too hot (Figures 2–4). Additional suitable areas were predicted outside the expert range map. The potential distribution presented here was based on a limited number of specimens of *D. pilosus*; however, all known specimens were included in the model and we considered the model prediction preliminary but valid. Previous methodological studies have found that Maxent algorithm is robust to low number of presences (from 5 to 25; Hernandez, Graham, Master, & Albert, 2006; Pearson et al., 2007; Wisz et al., 2008), and with the same number of presences, Maxent model is accurate for narrowly distributed species (Hernandez et al., 2006; van Proosdij, Sosef, Wieringa, & Raes, 2016). Additionally, applications of ENM have successfully guided field surveys in discovering rare species, and in several cases, these were based on low number of presences (3 presences of a mammal species in Jackson and Robertson, 2011; 8 presences of a plant species in Fois, Fenu, Cuena Lombraña, Cogoni, and Bacchetta, 2015; and 14 presences of a tree species in Menon et al., 2010). The Maxent model in our study was based on 12 presences (representing 21 specimen records), a sample size within the range of those that have led to useful models. Also, *D. pilosus* has a relatively narrow distribution (Abba & Superina, 2010; Wetzel et al., 2007) and the 12 presences were spread latitudinally throughout the IUCN range map (Figure 1). The theoretical and practical experiences from previous studies suggest that our prediction could guide future field surveys in a meaningful way (Fois et al., 2015; Hernandez et al., 2006; Jackson & Robertson, 2011; Menon et al., 2010; van Proosdij et al., 2016). Based on the geographic information we assessed, we suggest that future surveys or conservation management for *D. pilosus* should give priority to areas predicted suitable within existing protected areas (Table A1), especially those that have records of specimens (e.g., Río Abiseo). However, after more information is collected, we expect that an updated model could provide a refined potential distribution and guide field survey more efficiently.

Given the reality that the ecology of *D. pilosus* is unknown, it is worth emphasizing descriptions associated with two specimens. First, MUSM-7504 was a female with four embryos, suggesting that this species might exhibit polyembryony with identical quadruplets, like *D. novemcinctus* (McBee & Baker, 1982). Second, MSB-49990 was a juvenile caught on a ridge top, in a hole with three other individuals, indicating that *D. pilosus* may inhabit high elevations and build burrows, like other *Dasypus* armadillos (Sawyer, Brinkman, Walker, Covington, & Stienstraw, 2012; Trovati, 2015). Also, since MSB-49990 was a juvenile sharing the burrow with three other individuals, it is possible that they were from the same litter. Because *Dasypus* taxa generally show monozygotic polyembryony (Wetzel, 1982), and they generally do not share burrows except as young litter mates (McBee & Baker, 1982; McDonough & Loughry, 2008; Vizcaíno & Loughry, 2008), the two specimens provide evidence for reproduction through polyembryony with identical quadruplets in *D. pilosus* as well.

Implications for Conservation

The IUCN status of *D. pilosus* has been changed from vulnerable to data deficient (Superina & Abba, 2014), thus we suspect that there is little or no specific conservation effort on *D. pilosus*, probably because of the lack of knowledge for this species. Therefore, we argue that a first step for conservation of *D. pilosus* is to learn more about it. Our study improves the current state of knowledge of *D. pilosus* from three perspectives. First, we synthesized the most comprehensive *D. pilosus* specimen data set to date, and we expect this will facilitate future

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studies of *D. pilosus*. Second, we analyzed elevation and climatic requirements of *D. pilosus* and proposed that the narrow temperature tolerance of *D. pilosus* is the reason for its restricted distribution. Third, we provided maps of known locations of specimens and predicted potential distribution, together with protected areas in its range. The maps may facilitate future field surveys and conservation efforts. Our study exemplifies the potential of ecological biogeography tools (e.g., GIS and ENM) for use in gaining knowledge of species' distribution and ecology, especially for endangered or lesser studied species.

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Appendix

Table A1. Summary of Protected Areas in Peru that are Potentially Suitable for *Dasypus pilosus*.

mapID	WDPAID	Name	Type	Total area (km^2)	Percentage of suitable area	Number of specimens collected
1	555555639	Abra Patricia–Alto Nieva	Private conservation area	14.16	33.33	0
2	20183	Alto Mayo	Protection forest	1,820.00	26.51	0
3	303318	Ashaninka	Communal reserve	1,844.68	6.90	0
4	555555691	Berlin	Private conservation area	0.59	50.00	0
5	555555684	Bosque de Palmeras de la Comunidad Campesina Taulia Molinopampa	Private conservation area	109.21	100.00	0
6	555555640	Bosque Nublado	Private conservation area	33.54	50.00	0
7	555544103	Bosques Nublados de Udima Sector Centro	Wildlife refuge	121.83	60.00	0
8	555544088	Chayu Naín	Communal reserve	235.98	15.38	1
9	555555664	Copallín	Private conservation area	115.49	100.00	0
10	20179	Cordillera de Colán	National sanctuary	392.16	22.22	1
11	261	Cutervo	National park	82.14	100.00	0
12	555555660	Hierba Buena—Allpayacu	Private conservation area	22.82	100.00	0
13	555555669	Huaylla Belén—Colcamar	Private conservation area	63.38	100.00	0
14	555555631	Huiquilla	Private conservation area	11.41	100.00	1
15	555555674	Japu—Bosque Ukumari Llaqta	Private conservation area	186.96	40.00	0
16	555555687	Los Chilchos	Private conservation area	460.00	66.67	0
17	257	Manu	National park	17,162.95	4.10	0
18	20186	Megantoni	National sanctuary	2,158.69	14.55	0
19	555555670	Milpuj—La Heredad	Private conservation area	0.17	100.00	0
20	303323	Otishi	National park	3,059.73	20.67	0
21	20184	Pagaibamba	Protection forest	20.78	100.00	0
22	30034	Pampa Hermosa	National sanctuary	115.44	66.67	0
23	68137	Paracas	Ramsar Site, Wetland of International Importance	3,350.00	28.74	0
24	555555672	Pillco Grande—Bosque de Pumataki	Private conservation area	2.72	50.00	0
25	20181	Pui Pui	Protection forest	600.00	55.56	0
26	7461	Río Abiseo	National park	2,745.20	54.33	5
27	555555634	San Antonio	Private conservation area	3.57	33.33	0
28	555555596	San Fernando	National reserve	1,547.16	44.44	0
29	555555663	San Marcos	Private conservation area	9.86	100.00	0
30	30060	Sunchubamba	Hunting preserve	597.35	46.43	0
31	20178	Tabaconas Namballe	National sanctuary	321.25	73.33	0
32	555555647	Tilacancha	Private conservation area	68.00	100.00	0
33	12213	Yanachaga–Chemillén	National park	1,220.00	29.63	1

Note. The list of protected areas was compiled from IUCN and UNEP-WCMC (2016). The column "WDPAID" represents the protected area original identifier from IUCN and UNEP-WCMC (2016). The column "mapID" corresponds to the ID plotted in Figure 4(a).

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