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Reevaluation of the Geographical Distribution of Bradypus tridactylus Linnaeus, 1758 and B. variegatus Schinz, 1825

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Reevaluation of the Geographical Distribution of *Bradypus tridactylus* Linnaeus, 1758 and *B. variegatus* Schinz, 1825

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Abstract

The confusing nomenclatural history of *Bradypus tridactylus* and *B. variegatus* has led to incorrect taxonomic attributions through time and, consequently, errors in range map inferences. In this note, we reevaluate the geographical distribution of *B. tridactylus* and *B. variegatus* based on museum specimens, field observations, and literature records of sloths. Our analyses revealed considerable range differences when compared to previous distribution inferences. For instance, *B. tridactylus* is restricted to the Guyana shield, and in Brazil it is only found north of the Amazon River and east of Negro River. Additional analysis using an Ecological Niche Modeling technique, and considering only bioclimatic and topographic variables, predicted that potential suitable areas for *B. tridactylus* are mostly limited by cold temperatures. However, when comparing our model to the present time distribution of forests we observed that the suitable area for *B. tridactylus* may be smaller than predicted by the model.

Keywords: Bradypus, ecological niche modeling, geographical distribution, sloths.

Introduction

The living three-toed sloths are classified in four species, *Bradypus pygmaeus* Anderson and Handley, 2001, *B. torquatus* Illiger, 1811, *B. tridactylus* Linnaeus, 1758, and *B. variegatus* Schinz, 1825. They only occur in the Neotropics, and most of them are exclusive to distinct biomes, except for *B. variegatus* that can be found from the forests of Nicaragua to the Atlantic Rainforest in southern Brazil (Hayssen, 2010). *Bradypus pygmaeus* and *B. torquatus* are considered endangered. The former is endemic to the Isla Escudo de Veraguas, Province of Bocas del Toro in Panama, while the latter only occurs in the Atlantic Forest of Brazil. *Bradypus tridactylus* is only found in the north-central region of South America (Anderson and Handley, 2001).

The pale-throated sloth *B. tridactylus* and the brown-throated sloth *B. variegatus* have a long and confusing nomenclatural history. *Bradypus tridactylus* was first named by Linnaeus (1758), and this is the currently used scientific name of the pale-throated sloth. Schinz referred to the brown-throated sloth when naming *B. variegatus* in the early 19th century (Schinz, 1825). However, in the following years the name "*B. tridactylus*" was attributed to the brown-throated sloth by different authors, the last being Ávila-Pires and Gouveia (1977). As a result, the name *B. tridactylus* referring to the brown-throated sloth has been adopted in many papers, especially those published before 1970. For instance, Vieira (1953) described the fauna observed in different localities of Alagoas state, northeastern Brazil, during two expeditions in 1951 and 1952. The author registered four brown-throated sloths, which he classified as *B. tridactylus*, following the valid nomenclature for that time. Only in the 1980's, the name *B. variegatus* was used again for the brown-throated sloth. Wetzel (1982) reviewed the nomenclature, described the synonymy, named *B. variegatus* as the brown-throated sloth, and recognized nine subspecies. For a detailed description of *B. tridactylus* and *B. variegatus* nomenclature see Hayssen (2009, 2010).

Despite the solved nomenclature, a recent study based on morphological criteria and molecular data revealed about 30% taxonomic misidentification between the pale and the brown-throated sloth in museum collections (Moraes-Barros *et al.*, in press). Part of these misidentifications can be explained by the lack of taxonomic updating in museum collection specimens. A critical outcome of these misidentifications and the confusing nomenclature is the inferred geographical distribution of *B. tridactylus* and *B. variegatus*. Based on this previous misidentification study (Moraes-Barros *et al.*, in press) and considering the need of an updated range map of these sloth species, we reevaluated the historical and recent specimen records, elaborated a corrected map of the geographic distributions of *B. tridactylus* and *B. variegatus*, and generated a predictive model of *B. tridactylus* distribution using an ecological niche modeling technique.

Methods

Range map

We used specimen records obtained from museum collections, field expeditions, and literature to elaborate a range map for *B. tridactylus* and *B. variegatus*. The data set of museum specimens consisted of morphologically reviewed sloths. We thus only used

records of specimens which could be undoubtedly identified. The criteria used to classify specimens are described in Anderson and Handley (2001). We included specimens described in Anderson and Handley (2001) and reviewed sloths from the following museums: IEPA – Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá, Amapá, Brazil; MN – Museu Nacional, Rio de Janeiro, RJ, Brazil; MPEG – Museu Paraense Emílio Goeldi, Belém, PA, Brazil; MVZ – Museum of Vertebrate Zoology, University of California, Berkeley, CA, USA; and MZUSP – Museu de Zoologia da Universidade de São Paulo, São Paulo, SP, Brazil. Data from field expeditions encompassed direct observations and individuals captured in order to collect biological samples for molecular biology studies. These expeditions were carried out from 2001 to 2009 and included members of our research group and coworkers. Data obtained from literature that represented localities distinct from those listed in museum collections were added to the final data set (Table 1). The use of data recovered from literature was particularly difficult. Because of the confusing taxonomic history of *B. tridactylus* and *B. variegatus*, we considered taxa names keeping in mind that the nomenclature differed over time. We therefore compared the described taxa name in each publication and updated it to the current valid name whenever needed. Some publications were not considered because their reported occurrences could not be confirmed.

Predictive model of geographical distribution — ecological niche modeling

We used Maxent v.3.3.1 (Phillips *et al.*, 2006; <http://www.cs.princeton.edu/~schapire/maxent>) to generate a predictive model of *B. tridactylus* distribution. Collection localities were compiled from Anderson and Handley (2001) and from sources given in Table 1. We used 19 bioclimatic parameters of current climate from the WorldClim dataset version 1.4 (Hijmans *et al.,* 2005) at 1 km resolution. These metrics are derived from monthly temperature and rainfall climatologies and represent biologically meaningful variables for characterizing species range (Nix, 1986). In addition to the bioclimatic variables, we also used a topographic variable derived from remote sensing data. Shuttle Radar Topography Mission (SRTM) digital elevation data at 90 m resolution were aggregated to 1 km resolution in order to be added as environmental predictor in the Maxent runs. Besides mean elevation, the standard deviation based on 90 m data was also included as an indicator of surface ruggedness.

We did not use forest cover data as environmental predictor due to the characteristics of our species data set. The majority of data is composed by historical records from several museums. According to the ecological niche modeling literature, museum records are very useful in many studies, including the case presented here, but in order to build a consistent model, the species occurrence period must match the period of the environmental variables (Graham *et al.*, 2004).

Results and Discussion

The collected data constitute a view of historical and present-time occurrence of the pale and the brown-throated sloths (Fig. 1, Table 1). Although data are available about where these sloths are found, few studies indicate were they do not occur. Some records obtained from museum specimens represent historical occurrences of species and localities that today are no longer suitable for sloths, mostly because of anthropogenic effects; an example is the State of Paraná in Brazil. There is only one record for *B. variegatus* in Paraná (Table 1) and today the species is considered extinct in this state due to deforestation (Mikich and Bérnils, 2004). A similar situation is found in northern Argentina, where records of *B. variegatus* date from the 1910's and 1920's (Onelli, 1913; Massoia, 1980; FMNH21672 – Field Museum of Natural History, Chicago, IL, USA). There are, however, no recent records of sloths from this country. As pointed out by Redford and Eisenberg (1992), the southern limit of this species' range is poorly known.

Some other localities still bear suitable habitats for sloths, as has been shown in recent studies in the remaining Atlantic Forest fragments of Pernambuco, Brazil (Silva Jr. and Pontes, 2008), northern Ecuador (Ríos, 2001), and southeastern Caracas region, Venezuela (Castillo and Sales, 2006). Nevertheless, information about the presence and absence of sloths at the present time is not complete and accurate. We therefore opted to present a range map that reflects the total distribution area, depicted from all recorded past and present occurrences (Fig. 1). We did not consider the fact that some localities within this total area may no longer be inhabited by sloths and discuss this point below.

The updated range map of *B. variegatus* shows that contrary to previous descriptions (Gardner, 2007; Hayssen, 2010), this species is found north of the Amazon and in northwestern Brazil, between the Negro and Branco rivers (Fig. 1). Similarly, there are differences between the previously inferred

distribution of *B. tridactylus* and the range map presented in Fig. 1. Most of this divergence is due to taxonomic misidentifications (Moraes-Barros *et al.*, in press). Its area of distribution is smaller than previously described, as the species does not occur south of the Amazon River, an area that Gardner (2007) had included in his range map of *B. tridactylus*. The pale-throated sloth is also absent west of the Negro River and southeastern Venezuela, which differs from the range map presented by Chiarello *et al.* (2008). Therefore, *B. tridactylus* is restricted to the Guiana shield region and is sympatric with *B. variegatus* only along the northern margin of the Amazon River (Fig. 1).

The range map presented in Fig. 1 provides only an estimated area of continuous distribution of these sloth species. To properly evaluate the present-time distribution and reveal possible isolated populations, recent records of species presence and absence are needed. This kind of study demands time and intensive field work. In the case of sloths their arboreal habits, slow movements, and time spent in the

canopy make direct observation difficult, thus limiting the recording of occurrences. Hence, as shown by Moreno and Plese (2006), Ecological Niche Modeling techniques can be used as a tool to determine the potential distribution of sloth species. These authors modeled the current distribution of *B. variegatus* in Colombia, highlighting suitable and non-suitable areas for the species. Phillips *et al.* (2006) used ecological niche modeling based on maximum entropy (Maxent) to generate predictive models of species distribution for two Neotropical mammals, *Microryzomys minutus* (Rodentia: Muridae) and *B. variegatus*. The modeled distribution of *B. variegatus* through the entire Neotropical region predicted suitable areas encompassing different biomes. Within Brazil, most of the suitable areas were predicted in the Amazon rainforest and Atlantic forest, although areas within the Cerrado biome were also considered suitable. In fact, there are recent records of *B. variegatus* in the Cerrado domain (Table 1), which indicates that forested regions within this biome should not be discarded as occurrence localities for this species.
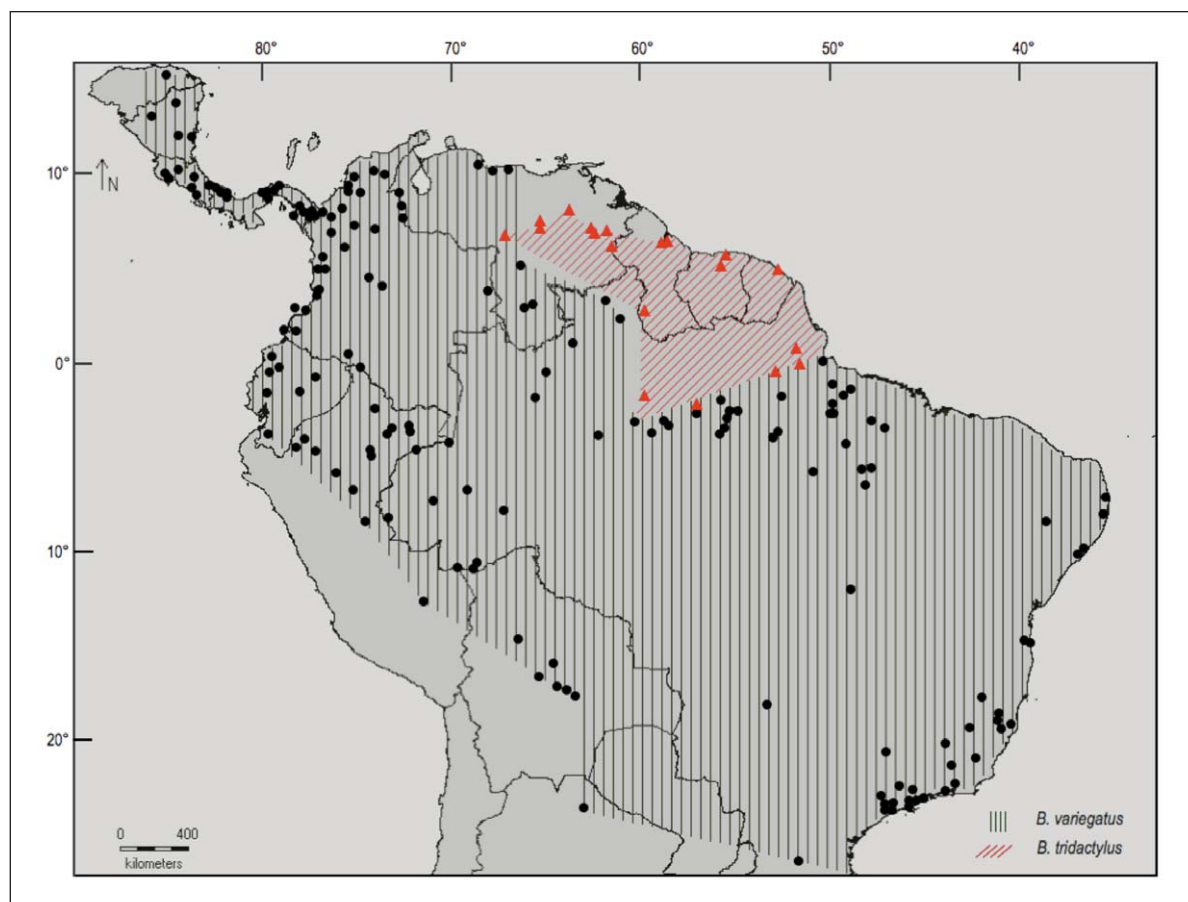

Figure 1. Reevaluated range map of *B. variegatus* and *B. tridactylus.* Black circles and red triangles represent occurrence records for *B. variegatus* and *B. tridactylus,* respectively. These records are described in Table 1.

Table 1. Description of **B. tridactylus** (**bold**) and *B. variegatus* localities used to infer geographic distribution, except for localities described in Anderson and Handley (2001). Species records are based on museum collections (museum acronyms) and literature (references). We also considered data from field studies carried out from 2001 to 2009, including direct observations (*) and individuals captured for blood or tissue sampling (biological samples deposited in Labec DNA and Tissue Collection).

Locality			Source of record - year	Species
Bolivia	Beni	Beni Biosphere Reserve	Roldan and Simonetti (2001)	*B. variegatus*
Brazil	Acre	Assis Brasil	Labec - 2009	*B. variegatus*
		Brasiléia	Labec - 2009	*B. variegatus*
		Rio Branco	Labec - 2009	*B. variegatus*
		Xapuri	Labec - 2009	*B. variegatus*
	Alagoas	Manimbu	MZUSP - 1952	*B. variegatus*
		São Miguel dos Campos	MZUSP - 1951	*B. variegatus*
		Mangabeiras	Vieira (1953)	*B. variegatus*
	Amapá	Estrada Campo Verde km 7, Porto Platou	MN	***B. tridactylus***
		RDS Rio Iratapuru, Lg. Baliza	IEPA - 2005	***B. tridactylus***
		Cachoeira de Santo Antônio, Rio Jari, Il. do Cemitério	MPEG	***B. tridactylus***
	Amazonas	Balbina	MZUSP - 1988	***B. tridactylus***
		Boca do Pauini	MZUSP - 1974	*B. variegatus*
		Estirão do Equador, Rio Javari	MPEG - 1960	*B. variegatus*
		Lago do Batista	MZUSP - 1937	*B. variegatus*
		Maraã	MZUSP - 1977	*B. variegatus*
		Rio Tootobi, Rio Demini	MPEG - 1981	*B. variegatus*
		Rio Juruá	MZUSP - 1902	*B. variegatus*
		Itacoatiara	MZUSP - 1937	*B. variegatus*
		Santa Cruz, Rio Eiru	MZUSP - 1936	*B. variegatus*
	Bahia	Ilhéus	Labec - 2006	*B. variegatus*
		Itabuna	Labec - 2006	*B. variegatus*
	Espírito Santo	Sooretama Biological Reserve	Chiarello (1999); Lara-Ruiz and Srbek-Araújo (2006)	*B. variegatus*
		Linhares Forest Reserve	Chiarello (1999)	*B. variegatus*
	Goiás	Surrounds of Parque Nacional de Emas	Fischer *et al.* (2004)	*B. variegatus*
	Maranhão	Imperatriz	MPEG - 1987	*B. variegatus*
		Miritiba	MZUSP - 1907	*B. variegatus*
		Res. Biol. Gurupi	Lopes and Ferrari (2000)	*B. variegatus*
	Minas Gerais	Passos	MN	*B. variegatus*
		Parque Florestal Estadual Rio Doce	Stallings *et al.* (1991)	*B. variegatus*
		Rio Novo	MN	*B. variegatus*
		Teófilo Otoni	Labec - 2006	*B. variegatus*
		Viçosa, Mata do Paraíso	Prado *et al.* (2008)	*B. variegatus*
	Pará	Abaeté	MN	*B. variegatus*
		Altamira	Labec - 2001	*B. variegatus*
		Belém, Castanhosinho, Igarapé	MPEG - 1957	*B. variegatus*
		Belém, Instituto Agronômico do Norte	MPEG - 1964	*B. variegatus*
		Belém	MPEG - 1957	*B. variegatus*
		Belterra	MN	*B. variegatus*
		Benevides, Retiro de Nazaré, Estância	MPEG - 1964	*B. variegatus*
		Cacoal	MPEG	*B. variegatus*
		Cametá	MZUSP - 1937	*B. variegatus*
		Castanhal	MPEG - 1958	*B. variegatus*
		Faro	MN	***B. tridactylus***
		Fordlandia	MZUSP - 1960	*B. variegatus*
		Igarapé Açu	MPEG - 1955	*B. variegatus*
		Igarapé Açu, Lazarópolis do Prata	MPEG - 1955	*B. variegatus*

Table 1, *continued.*

| Locality			Source of record - year	Species
Brazil *(cont.)*	Pará *(cont.)*	Ilha Caviana de Fora	Labec - 2004	*B. variegatus*
		Ipixuna, Rio Capim Grande	MPEG - 1994	*B. variegatus*
		Juruti	MPEG - 2006	*B. variegatus*
		Óbidos	MN	*B. variegatus*
		Paragominas, Faz. Cauxi	MPEG	*B. variegatus*
		Parauapebas - East Amazon Forest	Labec - 2007	*B. variegatus*
		Rio Tocantins, Tucuruí, Ilha Tocantins	MPEG - 1984	*B. variegatus*
		Rio Tocantins, Tucuruí, Vila Brabo	MPEG - 1984	*B. variegatus*
		Rio Xingu, Cachoeira do Espelho	MZUSP - 1986	*B. variegatus*
		Rod. Belém-Brasilia km 307	MPEG - 1960	*B. variegatus*
		Santarém, Ipanema	MN	*B. variegatus*
		Santarém, Santarém-Cuiabá km 16	MPEG - 1973	*B. variegatus*
		Taperinha	MPEG	*B. variegatus*
		Vigia, São Francisco	MPEG - 1955	*B. variegatus*
	Paraíba	João Pessoa	Dantas-Torres *et al.* (2010)	*B. variegatus*
	Paraná	Londrina	MZUSP - 1916	*B. variegatus*
	Pernambuco	Tapera	MZUSP - 1938	*B. variegatus*
		Recife and Carpina Forests	Amorim *et al.* (2004)	*B. variegatus*
		Zona da Floresta	Bezerra *et al.* (2008)	*B. variegatus*
	Rio de Janeiro	Barreiros	MN	*B. variegatus*
		Parati, Pedra Branca	MN	*B. variegatus*
		Teresópolis	MN	*B. variegatus*
		Teresópolis, Fazenda Boa Fé	MN	*B. variegatus*
	Roraima	Ilha de Maracá	Barnett and Cunha (1994)	*B. variegatus*
		Rio Mucajai, Rio Branco	MZUSP - 1962	*B. variegatus*
	São Paulo	Guaratinguetá	MZUSP - 1957	*B. variegatus*
		Guarulhos	Labec - 2001	*B. variegatus*
		Jundiaí	Labec - 2001	*B. variegatus*
		Praia da Boracéia	MZUSP - 1957	*B. variegatus*
		Rodovia Mogi-Dutra	Labec - 2002	*B. variegatus*
		Santos	MZUSP/Labec - 1918/2004	*B. variegatus*
		Serra da Cantareira	MZUSP/Labec - 1950/2006	*B. variegatus*
		Serra do Mar	Labec - 2004	*B. variegatus*
		São Paulo	Labec - 2009	*B. variegatus*
		São Sebastião	MZUSP/* - 1919/2008	*B. variegatus*
		Taboão da Serra	Labec - 2003	*B. variegatus*
		Ubatuba	MZUSP/* - 1905/2008	*B. variegatus*
	Tocantins	Araguatins	MZUSP - 1963	*B. variegatus*
		Near Angico and Santa Teresinha	* - 2009	*B. variegatus*
		Peixe	* - 2005	*B. variegatus*
Costa Rica	San Jose	Vicinity San Isidro Del General	MVZ - 1932	*B. variegatus*
	Limón	Pueblo Nuevo de Guácimo	Labec - 2005	*B. variegatus*
Peru	Huampami	Rio Cenepa	MVZ - 1978	*B. variegatus*
	Amazonas	La Poza, Rio Santiago, 180m	MVZ - 1979	*B. variegatus*
		Manu Biosphere Reserve	Solari *et al.* (2006)	*B. variegatus*
Venezuela		SE Caracas	Urbani and Bosque (2007)	*B. variegatus*
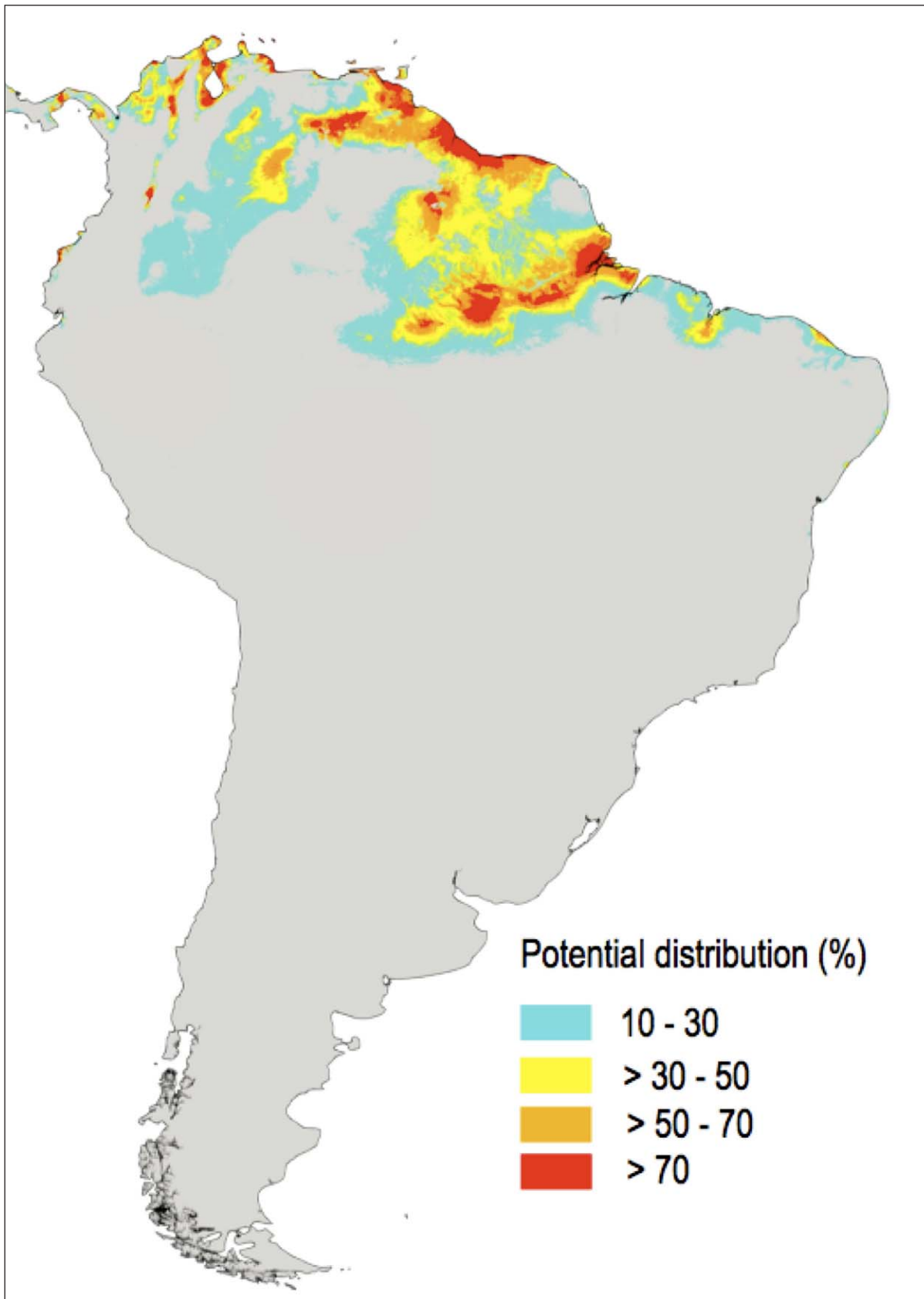
Figure 2. Predicted potential geographic distribution of *B. tridactylus* produced with 19 bioclimatic parameters and 2 topographic variables derived from remote sensing imagery. Colors represent habitat suitability and probability of the species' occurrence.

We followed Phillips *et al.* (2006) and generated a predictive model of *B. tridactylus* distribution. After running Maxent (Fig. 2), we observed that the environmental variables that presented the largest contributions to defining the potential areas of occurrence for *B. tridactylus* were minimum temperature of coldest month (64% of contribution), temperature seasonality (11%), mean temperature of coldest quarter (5%), and topography (5%). The climatic variables that limit *B. tridactylus* occurrence are all related to cold temperatures, which is supported by the fact that sloths are not fully homeothermic (Britton and Atkinson, 1938).

While the model behavior and results fit the data set and applied parameters (AUC = 0.98), it is important to mention that an inexistent gap is shown in Fig. 2 in the Amapá region (northern Brazil). This gap can be attributed to the environmental variable "minimum temperature of the coldest month" that is corrupted in that region. As mentioned before, the bioclimatic variables were obtained through the WorldClim dataset (Hijmans *et al.*, 2005), which is based on an interpolation of climate station data spread all over the world. As there are only a few stations in the Amapá region, interpolation will produce unprecise results. We believe that this might be the reason for the environmental layer being corrupted in that exact region.

As shown in Fig. 2, the model predicts the existence of a highly suitable area between Colombia and Venezuela. There are, however, no occurrence records for any of the sloth species from this region (see Fig. 1). This may be attributed to the lack of field efforts, and thus occurrence data, due to geopolitical issues. In our model, northern Venezuela was also predicted as suitable for *B. tridactylus.* Sloth occurrences in that region were, however, only recorded for *B. variegatus.* Important variables such as geographical barriers, competition, and preying are not considered in these models. The fact that environmental features of a particular area fit the attributes of the species' niche therefore does not necessarily mean that sloths indeed inhabit the area. Due to the arboreal habits of sloths, it is also important to include forest cover in these analyses. In a preliminary analysis, we superimposed a map of present-time forested areas to our predictive model. We observed that some areas predicted as suitable for *B. tridactylus* are no longer covered with forests, indicating that the total suitable region for this sloth's occurrence may be smaller than suggested by our model (data not shown).

In this study, we reevaluated the range of the brown and the pale-throated sloth. Although ecological niche models, such as Maxent, have been great assets in identifying potential areas of species occurrence and in supporting research in several fields, we wish to emphasize that they are tools that will never replace field efforts. In the case of sloths, predictive models can help defining areas for field investigations, and thus contribute to a better comprehension of the species. This is particularly interesting for *B. tridactylus* due to the lack of studies on population genetics and phylogeography, which have already been performed for *B. variegatus* (Moraes-Barros *et al.,* 2002, 2006, 2007).

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