CONTRIBUTIONS

Integrating current range-wide occurrence data with species distribution models to map the potential distribution of Baird's Tapir

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Abstract

Identifying species distributions is fundamental to understanding their ecology and guiding conservation and management strategies. We compiled 756 unique range-wide Baird's tapir (*Tapirus bairdii*) detections via camera trapping of track/sign surveys in eight countries. We then estimated the distribution of suitable tapir habitat within a Maxent-modeling framework. Though there are some clear areas of over- and underpredicted habitat, the resultant models allowed us to significantly update the potential distribution map of Baird's tapir. We estimate that 39.4% of the available area is suitable for tapirs, but only 27.2% of that habitat occurs in protected areas. We discuss the areas that comprise suitable tapir habitat, and identify global and local threats in each country. **Keywords**: Climate, Distribution, Habitat Suitability, Maxent, Model.

Data Availability: Data is shared under a creative commons BY license. Data which are already published or publicly available are listed in Table 1. Data for Honduras is not yet publicly available (contact the authors). The presence data used in these models can be found at https://zenodo.org/record/18557.

Introduction

Species distribution patterns are dynamic traits that reflect the species' relationships with biotic and abiotic variables, their evolutionary histories, and their responses to disturbance (Elith & Leathwick 2009). Therefore, identification of such range-wide

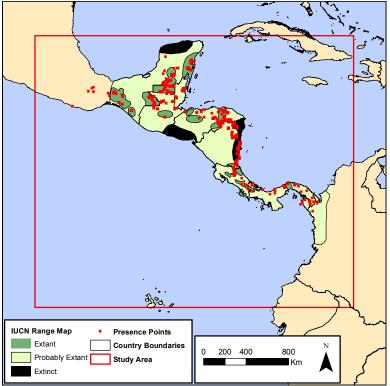


Figure 1: IUCN range map of Baird's Tapir. Locations of presence data used in the SDM, and study area extent are also included on this map.

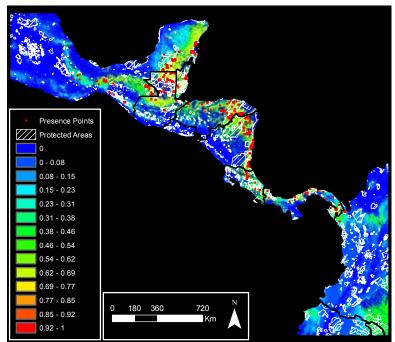


Figure 2: Maxent logistic output (values range from 0 to 1).

patterns is fundamental to the understanding of species ecology and to guide conservation initiatives, assessments and management strategies. The analysis of distribution patterns is particularly critical for species subjected to pressure from human activities

(e.g., habitat loss, hunting pressure) that may limit or reduce suitable habitat. Among all mammals, tropical large-bodied herbivores include some of the groups most threatened by human impact (e.g., Perissodactyla: rhinoceros, wild horses and tapirs; Baille et al. 2010). Yet, in comparison with large predators (e.g., felids) large herbivores usually draw less attention in terms of the urgency of their conservation despite the fact that the loss of large-bodied herbivore mammals causes a significant impoverishment of local mammal communities, and can lead to the disappearance of entire evolutionary lineages (e.g., Perissodactyla). Furthermore, extirpation of populations of largebodied herbivores, or even their marked decrease, can cause the interruption of the variate ecological roles these fauna play in their natural habitats (Dirzo et al. 2014; Ripple et al. 2015). The activities of large-bodied herbivores indirectly and directly affect the occurrence and abundance of coexisting species in their natural ecosystems. For example, by continuously browsing, trampling, defecating and urinating, large-bodied herbivores generate habitat heterogeneity that provides the opportunity for some species to establish (Ripple et al. 2015). Likewise, it has been shown that the experimental removal (mimicking defaunation) of large-bodied herbivores (tapirs included) from the tropical rain forest understory significantly affects seedling survival and recruitment patterns, resulting in increased seedling density, but decreased seedling diversity (Camargo-Sanabria et al. 2015).

The Baird's tapir (*Tapirus bairdii*) was originally distributed almost continuously from southern Mexico to northern Colombia and Ecuador (Alston, 1882; Matola et al., 1997). However, due to the compounding impacts of habitat alteration and hunting, the original distribution has been reduced by >50% and fragmented over the past three decades (Castellanos et al., 2008). The endangered status of Baird's tapirs, among other threatened large mammals such as jaguars (Panthera onca) and white-lipped peccaries (Tayassu pecari), has stimulated the establishment of the Mesoamerican Biological Corridor to enhance and ensure suitable habitat for connecting populations among spatially discrete protected areas (Miller et al., 2001). The endangered status of Baird's tapirs has also sparked many recent surveys and demographic studies in multiple countries across the entire range within and outside of protected areas (Gonzalez-Maya et al., 2012; Jordan & Urquhart, 2013; Mendoza et

al., 2013; Meyer *et al.*, 2013; Cove *et al.*, 2014). Surveys using new technologies such as camera traps have advanced our current understanding of local tapir distribution and even led to the rediscovery of populations previously believed to be extinct, for example, along the Caribbean coast of Nicaragua

Table 1: Presence data contribution by source and country.

Source	# of presences	Geographic coverage		
Garcia <i>et al.</i> (2009)	_	Guatemala		
Chris Jordan	167	Nicaragua		
Mendoza et al. (2013)	129	Mexico		
National Action Plan for Tapirs in Honduras	125	125 Honduras		
TEAM	47 Costa Rica			
Ninon Meyer	32	Panama		
Georgina O'Farrill	29	Mexico		
Celso Poot	28	Belize		
Cove <i>et al.</i> (2014)	11	Costa Rica		
Jan Schipper/José F. González-Maya	7	Costa Rica		
Cody Schank	7	Nicaragua		
Diego Lizcano	4	Colombia		
	Total = 756			

Table 2: Environmental predictor variables used in the SDM.

Variable Code	Variable Description
ALT	Elevation
BIO1	Annual Mean Temperature
BIO4	Temperature Seasonality (standard deviation *100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO12	Annual Precipitation
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

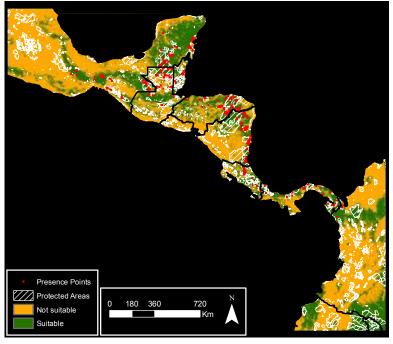


Figure 3:Threshold applied to Maxent output to produce a binary presence-absence map.

(Jordan & Urquhart, 2013). Yet, these new important datasets have not been compiled and analyzed on a range-wide scale, meaning that many of the previous distribution maps are either outdated or limited to only a portion of the original extent (e.g. regionally restricted, Mendoza et al., 2013). Here, we compiled data across all of the Mesoamerican countries (except El Salvador, where the species is reported as extinct) to estimate the current distribution of T. bairdii using the most recent

range-wide occurrence data within a species distribution modeling framework.

Materials and Methods

The emergence of modeling algorithms based on occurrence data have greatly improved our ability to describe distribution patterns of tropical species, for which accurate information on its presence (i.e., georeferenced records) can often be particularly limited (Cayuela et al. 2009). These modeling approaches use geo-referenced presence data and GIS layers describing spatial variation

in environmental variables (usually climatic) to identify the corresponding space in which the probability of species occurrence is heightened. Freely available software, such as Maxent, are used in these modeling procedures and achieve high predictive accuracy in creating maps of suitable habitat (Phillips & Dudik, 2008).

Our study area consists of a rectangular grid covering the entirety of the known distribution of Baird's tapir (101° to 74° W and 1° S to 22° N, at a resolution of 1 km2; ; Figure 1). The presence data used in this modeling exercise were compiled by IUCN/SSC Tapir Specialist Group (TSG) Country Coordinators and additional collaborators and sources (Table 1). The data set includes a total of 756 unique locations of tapir detections (camera trap and track/sign) across all range countries. Most observations cover the years 2000 to present, though there are a handful of records from the 1990s. We modeled the distribution of Baird's tapir with Maxent (Phillips & Dudik, 2008) using 10 climatic variables and elevation (Hijmans et al., 2005; Table 2) as predictor layers in the SDM (following Mendoza et al., 2013). The predictor Table 3: Suitable habitat for Baird's tapir by country, as predicted by the SDM. The second to last column is the percent of suitable habitat in each country that is protected, determined using data downloaded from protected planet.net (IUCN & UNEP-WCMC 2014). The last column shows the percent of suitable habitat contributed by each country across the study area, excluding Colombia because of its large area and probably small contribution to actual tapir habitat.

Country	Total Area (km2	Suitable Area (km2)	Suitable Area (%)	Suitable Protected (km2)	Suitable Protected (%)	Contribution (w/o Colombia)
Belize	21,591.68	15,928.29	73.77%	7,092.60	44.53%	3.37%
Colombia*	440,973.30	136,687.85	31.00%	24,253.81	17.74%	
Costa Rica	51,071.16	33,924.31	66.43%	11,895.11	35.06%	7.18%
El Salvador**	20,352.49	2,516.86	12.37%	458.05	18.20%	0.53%
Guatemala	109,151.03	57,070.46	52.29%	24,212.39	42.43%	12.09%
Honduras	111,916.88	60,624.57	54.17%	17,402.60	28.71%	12.84%
Mexico*	588,054.49	200,442.46	34.09%	32,156.10	16.04%	42.45%
Nicaragua	128,124.62	53,096.82	41.44%	29,289.86	55.16%	11.24%
Panama	73,645.89	48,632.14	66.04%	18,659.18	38.37%	10.30%
Total	1,544,881.55	608,923.75	39.42%	165,419.71	27.17%	
Total (w/o Colombia)		472,235.90				

*study area does not include all of country

**tapir are considered extinct in El Salvador

layers were masked so that islands were excluded from the analysis. We used a bias grid (Elith *et al.*, 2010; Clements *et al.*, 2012) to control for the effect of sampling bias in our presence data. We also selected the response curves and jackknife options to examine the effect of individual predictors (Supplement). All other Maxent settings were left at their defaults (including output = logistic). We then used a forest cover layer (Hansen *et al.*, 2013) to mask out all cells with less than 50% forest cover (Figure 2). Finally, we created a binary map (presence/absence) using model prevalence as a threshold (Liu *et al.*, 2005) (Figure 3; Supplement - detailed maps).

Results and Discussion

The resulting model estimated an area under the curve (AUC) of 0.881, predicting suitable habitat for Baird's tapir within all range countries with a discontinuous distribution that includes: the Sierra Madre and Pacific coast of Mexico; the volcanic chain in the Pacific slope of Mexico and Guatemala; the Yucatán Peninsula in Mexico, Guatemala and Belize; Atlantic coasts of Guatemala, Honduras and Nicaragua; and the Atlantic and Pacific coasts of Costa Rica, Panama and Colombia. Main habitat strongholds include forest remnants in the Sierra Sur of Mexico; the Selva Maya region in Mexico, Guatemala, and Belize; the Moskitia region in Honduras and Nicaragua; Atlantic coasts of Nicaragua, Costa Rica, and Panama; the Darien region in Panama and Colombia; and areas in the Pacific coast region of Ecuador..

The resulting binary map predicts 39.4% of the land surface in the study area as suitable habitat for tapirs (Table 3). However, the actual distribution of the species is much smaller, partly because the above estimate includes portions of the study area which fall outside of the known distributional limits of the species (especially true for Colombia and Ecuador - see Discussion). In addition, a relatively low threshold was chosen for the binary map, which could overestimate the amount of suitable habitat, however, this habitat suitability map could be further refined using expert knowledge. Furthermore, some of the habitat fragments classified as suitable are substantially smaller than commonly cited estimates of Baird's tapir home range (i.e., 2.32 square km in Costa Rica; Foerster 1998) or farther from larger connected forests or protected areas than expected tapir dispersal distances (i.e., 1.5 km for T. terrestris in Brazil; Medici 2010) questioning the ecological value of these patches for the species survival. Therefore, many suitable patches in our model results are likely too small and/ or too far from larger contiguous forest (e.g., protected areas) to sustain a viable population of tapirs over the long-term. More accessible, fragmented areas classified as suitable may also be less likely to harbor tapir populations due to high hunting rates (Peres 2001). Taking the above factors into consideration, the suitability map produced here can be further refined to represent the true distribution of the species by explicitly integrating expert opinion regarding viable populations, tapir movement ecology, and local on-theground knowledge.

Across the study area, only 27.2% of suitable habitat occurs in protected areas (Table 3). However, the "protected" status of these areas does not necessarily indicate that they serve as a refugia for tapirs. Protected areas are all managed differently depending on the country, their protection, or legal status (e.g., national park, forest reserve, indigenous lands, etc.), the local municipality where they are located, and the state of national policies and funding for reserve staff and guards (Hockings, 2003). Nicaragua, for example, has the highest proportion of tapir habitat under protection (55.2%), however the country has recently experienced extensive habitat destruction within protected area boundaries (Watsa, 2014). Hunting is also perceived to be a problem in some notable protected areas (e.g., La Amistad Bi-national Park in Costa Rica and Panama -- Castellanos et al., 2008), yet there remains

very limited tapir hunting in some unprotected areas where ecotourism and conservation education have succeeded in transforming local communities' views on tapirs, particularly in Costa Rica (Cove et al., 2014). Variables with the greatest percentage contribution to the model were temperature seasonality (33.9%), precipitation seasonality (31.5%), precipitation of the driest quarter (9.7%) and maximum temperature of the warmest month (9.1%), explaining about of 84% of the potential distribution. The response plots suggest that tapirs prefer habitats with both low temperature and precipitation seasonality, and intermediate range of maximum temperature in the warmest month (not too hot, neither too cold). The association of tapir's preferred habitat and low seasonal variation in temperature and precipitation suggests tapir populations could suffer high impact given current climate change scenarios for the region. Some of the most critical regions are those with low precipitation during the driest quarter such as the Selva Maya, where climate change may become a relevant threat to wild populations (Anderson et al., 2008; García et al., 2012). However, tapirs do occur in some tropical dry forests (see below in Costa Rica section), and studying these populations has the potential to contribute to our understanding of how tapirs mitigate and adapt to dry climates, and thus help in making tapir populations more resilient to the predicted impacts of climate change.

Below, we discuss the individual countries and their contributions to habitat for the Baird's tapir.

Mexico

The suitable tapir habitat identified by this study is mostly in agreement with the suitable habitat described by Mendoza et al. (2013) for the Mexican portion of the Mesoamerican biological corridor and its vicinity. Recent fieldwork conducted by Botello et al. (2014) and Naranjo et al. (2015) confirmed the presence of Baird's tapir in the areas identified by Mendoza et al. (2013), which are also included in this model. Modeled suitable habitat is predominantly located in areas where potential vegetation, according to Rzedowski (1998), are: tropical rainforest, semievergreen tropical rainforest, montane forest, pine and oak forest. To a lesser extent, suitable tapir habitat is located in areas of deciduous tropical forest and wetland. Scarce coincidence of potential tapir habitat with tropical dry forest areas contrasts with observed presence of Baird's tapir in that type of forest in more southern countries (e.g., Costa Rica). This situation might be related to lower annual precipitation in the dry forests of Mexico, which can reduce abundance of food resources and cause physiological stress.

It is evident that there are some areas for which this study predicts suitable habitat where tapirs certainly do not occur, most strikingly central Mexico. This overprediction results from: (1) including areas for which no historic or contemporary records of tapirs exist to support the species' presence (e.g., western limit of the state of Guerrero and northern limit of Veracruz, Puebla and Hidalgo); and (2) from including areas where tapir originally occurred but are now thought to be locally extinct due to human impact (e.g., Los Tuxtlas, Veracruz). In the first case, overprediction seems to be related to the occurrence of montane forest and pine-oak forest, which is somewhat similar to the forest where the species occurs in more southern locations. Yet, overall, model predictions are in agreement with regional studies indicating that main tapir strongholds occur in the states of Chiapas, Oaxaca, Campeche and Quintana Roo (Naranjo 2009). Despite the likelihood of overprediction, evidence indicates that Mexico supports $\sim 20\%$ of the remaining Baird's tapirs, making the country critical for the long-term survival of the species. A large portion of predicted suitable tapir habitat is within protected area boundaries ($\sim 16\%$, Table 3). However, deforestation in southern Mexico (Mendoza et al., 2013) and the decrease in availability of water resources due to climate change (O'Farrill et al., 2014) are likely to isolate main tapir strongholds by reducing habitat connectivity.

Belize

ocally known as mountain cow in Belize, T. bairdii Lis the country's national animal. With more than 60% forest cover (Cherringtion et al., 2010), and a wide network of terrestrial protected areas, tapirs are known to occur in all six districts of Belize. Our model suggests that \sim 74% of Belize's territory is suitable tapir habitat, including areas in all six districts. These findings support earlier work by Waters and Ulloa (2007) that documented the species' presence widely throughout the country, including outside protected areas. The two largest blocks of contiguous suitable habitat for tapirs are the Rio Bravo Conservation and Management Area in northwestern Belize, which is contiguous to the tri-national Maya Forest; and the Chiquibul/Maya Mountain Massif in southwestern Belize. The model also shows that the Central Belize Corridor, comprised primarily of privately owned unprotected lands, likely provides connectivity between these two larger tracts of forest, highlighting the importance of encouraging conservation on private property in Belize.

Urban expansion is the greatest threat to tapirs in Central Belize (Belize District). Central Belize is comprised primarily of lowland savanna, wetlands, and lowland broadleaf forests. Our model highlights this area as unsuitable habitat for the species; however work by Poot (2014) documented high incidence of tapir vehicle collisions in this human dominated landscape. Current monitoring efforts confirm regular presence of the species throughout this particular region, including wetlands and mangrove habitat (Poot unpublished). Conversion of large tracts of forest for sugar and grain production over the past three years in western Belize (Cayo District) will undoubtedly put additional pressures on the species' available habitat. Future conservation action should include groundtruthing the species presence at the national level, both inside and outside of protected areas, which will assist in future management decisions and policy by providing quantitative empirical data to inform decisions.

Guatemala

The results from this model are consistent with information presented by García et al. (2011), who indicated that the most extensive, continuous tract of suitable habitat for tapirs in Guatemala is the northeastern region of the country, primarily within the Maya Biosphere Reserve in the tri-national Maya Forest. The Sierra del Lacandón National Park (the area of connectivity with Mexico) and Sierra de las Minas Biosphere Reserve (the last primary cloud forest area) are two additional important regions for tapirs, given the high percentage of suitable habitat. In the central and eastern region there are numerous small patches of suitable habitat where the species still occurs; despite being isolated remnants, the importance of the genetic variability of those populations must be considered in future action planning. Although the model shows suitable habitat in the Pacific lowlands, the species is considered to be locally extinct (Saunders et al., 1950). Our results reveal suitable habitat for some sites where the species occurred in the 1900s, including the volcanic chain in the Pacific region; however forest fragmentation and reduction, and hunting have almost certainly resulted in the extirpation of the species from these regions.

Honduras

Our model shows that suitable habitat for Baird's tapirs in Honduras is located in lowland tropical forest in the east of the country (mainly the Honduran Moskitia), and cloud forest along the Atlantic coast. Both pine forest and dry forest habitats appear as areas of low suitability. We are unaware of any tapir report from pine forest in Honduras; and the most recent anecdotal records of tapirs in dry forest date back to the 1960's. Unsuitable habitat includes agricultural and urban areas. To a lesser extent the model also indicates suitable habitat in southwestern Honduras, although the occurrence and status of tapir populations in this region is unknown.

Pristine cloud forest remains in southwestern Honduras, but these areas have been historically surrounded by pine forest or pine-oak forest assumed to be poor habitat for tapirs; different from the cloud forest in the Atlantic which transitions into lowland broadleaf tropical forest (Anderson & Bonta, 2002). Nonetheless, few surveys have been carried out in southwestern Honduras cloud forests, thus our model points to this part of the country as an important area to search for tapirs in the future.

The tract of forest shared between eastern Honduras and northern Nicaragua is the second largest area of continuous tapir habitat in the study area. However, this trans-frontier biosphere reserve is being rapidly deforested for pasture lands. The model indicates continuous suitable tapir habitat from the Panama Canal to central Honduras where the Aguan Valley, dominated by agricultural landscape, rises as a barrier; this barrier continues to the south across pine forest, pine-oak forest and human dominated landscapes.

Previous work estimated that 38.5% of all forest in Honduras is inside protected areas (ICF-GIZ, 2014), nonetheless the model shows that only 28.71% of the tapir's suitable habitat is under some protection category. The creation of protected areas has not aligned well with the critical areas for Baird's tapir conservation; a program for tapir and wildlife conservation at a large scale is needed to ensure the conservation of large mammals in Honduras. Among the main threats to tapirs are habitat loss due to the conversion of lowland tropical forest to oil palm plantations in northern and eastern Honduras, and the conversion of cloud forest to coffee farms along the Atlantic mountain ranges. Poaching is also an important threat in the cloud forest of middle Honduras, where these isolated forest remnants are surrounded by high density human settlements (McCann et al., 2012). However, for tapir that occur on indigenous lands, hunting levels are usually relatively sustainable (Dunn et al., 2012; Estrada 2004).

Nicaragua

ur results suggest that there are two areas of suitable habitat that likely serve as strongholds for tapirs in the Caribbean Region of Nicaragua: the Bosawás Biosphere Reserve and the Indio-Maíz Biosphere Reserve. Results also indicate that the remainder of the Caribbean Coast may function as an important corridor of suitable habitat between the Baird's tapir populations in these two strongholds. However, in the past ten years, increasing rates of deforestation both inside and outside of protected areas, the expansion of oil palm plantations and large development projects, widespread unsustainable poaching, and poor to no environmental law enforcement in the Caribbean Coast have probably eliminated connectivity between tapir populations in the far north of the country and those in the far south (Jordan et al., 2014).

Uncontrolled hunting and deforestation along a cattle ranching frontier that is quickly advancing from west to east across the Caribbean Coast threaten the survival of Nicaragua's tapirs over the long-term (Jordan et al., 2014). Due to these same phenomena, much of the suitable habitat west of our detection data in the Caribbean region, perhaps with the exception of the regions to the far north, are unlikely to harbor tapirs. Indeed, most remaining forests far from the Caribbean Coast are typically hunted unsustainably and isolated within cattle ranches (C. Jordan, unpublished). Other regions, such as volcanic islands in Lake Nicaragua, appear as suitable habitat in our maps but do not harbor tapirs. Despite the overprediction of tapir distribution and the increasing threats to Nicaraguan tapirs, the country remains a significant link in the Baird's tapir's global range, especially given the apparent corridor of suitable habitat connecting Honduras and Costa Rica and the large portion of the remaining suitable habitat that enjoys nationally protected status (55.16%). Our modeling results corroborate the conclusion of Jordan and Urquhart (2013) concerning the greater importance of the Caribbean Region of Nicaragua compared with the Pacific Region, which differs from some prior Baird's tapir range maps (i.e., Figure 1).

Costa Rica

Nosta Rica is well known for its reliance on ecotourism as a primary driver in the national economy (Fennel and Eagles, 1990). With nearly 25% of the country protected as national parks, forest reserves, and wildlife refuges, Costa Rica has among some of the highest proportions of the total land mass in protected habitat. However, of the 66% of the country classified as suitable, our models suggest that only 35% of that potential tapir habitat is located in protected areas. Costa Rica's government incentives for landowners to reforest fallow lands has led to an increase in forest cover in some areas with secondary forest and tree plantations (Morse et al., 2009). These private lands can function as suitable corridors between protected areas and many of these areas are represented in our models of suitable habitat. Cove et al. (2014) observed tapirs utilizing secondary forest and even exotic tree plantations in the northern zone of Costa Rica, further suggesting tapirs might be resilient to colonize new forest patches if there is enough forage and cover available in the biological corridors between them.

Although the model accurately predicts most of the tapir habitat in Costa Rica, there are several areas that are likely overpredicted and some that are underpredicted which require further examination. For example, Santa Rosa National Park in northwestern Costa Rica is an area that was not identified as suitable habitat, yet the adjacent Guanacaste National Park was identified as suitable tapir habitat within our predicted distribution map. Tapirs occur in both of these national parks (Janzen, 1982; Wainwright, 2007). This exemplifies a case of underprediction due to climatic data because Santa Rosa is largely dry forest. Similarly, Wainwright (2007) suggested that tapirs occur in Palo Verde National Park which was also identified as non-habitat in our models due to the dry climate of that park. Underprediction of tropical dry forests as suitable habitat is most likely an artifact of sampling biases with a lack of data points from these regions. This issue might extend beyond the dry forests of Costa Rica and warrants further study of tapir occurrence and ecology in drier climates to further update the model. Areas of suitable habitat on the Nicoya peninsula are likely not occupied by tapir, since they have been extirpated from protected areas such as Cabo Blanco (Timm et al., 2009) and Wainwright (2007) suggested no tapir occurrence on the entire peninsula. Additionally, there are some areas extending along the Caribbean coast between Limon and Cahuita National Park that have undergone recent development and expansion of plantations that likely represent areas where tapir are no longer present. These areas might, however, warrant further survey to validate our model predictions.

The agricultural expansion of pineapple production has increased dramatically over the past decade, particularly in northeastern Costa Rica, and this land clearing practice is likely the largest threat to available tapir habitat in the country (Cove et al., 2013). Whereas, exotic tree plantations provide cover, pineapple fields prevent movement by tapirs as they function as effective barriers to tapir dispersal in the absence of biological corridors (Gonçalves da Silva 2007; Medici 2010). The increasing economic growth of pineapple production might further increase the infrastructure of these areas, and could potentially lead to more paved roads and multi-lane highways, which have been identified as threats to tapir conservation in other countries (Castellanos et al., 2008). Although there is significant habitat in Costa Rica and hunting pressure is relatively limited, the potential expansion of pineapple plantations, urbanization, and roads could play a role in reducing suitable habitat and increasing the likelihood of human-tapir conflict.

Panama

Panama is particularly important for Baird's tapirs because it constitutes the only link between tapirs in Colombia and those in Central America. Most of the suitable habitat predicted in Panama is along the Atlantic coast, especially farther east where large protected areas are connected by the primary forests of the indigenous territories Embera and Guna. The model overpredicts tapir distribution nationally, especially in the pacific side of the country, which has experienced widespread deforestation. With the exception of the Darién National Park, the few large

patches of forest remaining in the Pacific region host endangered species such as the jaguar (Moreno et al. in press) and could potentially harbor tapirs, but no evidence of tapir occurrence has been reported for decades (Meyer et al. 2013). Even though some of these forests are protected, they are too far from contiguous forests that do support tapir populations to allow their recolonization by the species. Another overprediction of tapir distribution occurs in Central Panama. Outside of Barro Colorado Island, there is probably no resident population of tapirs in the area (Meyer et al. in press). Central Panama is heavily fragmented, and although illegal, hunting pressure is high throughout the area including in the numerous protected areas of the Canal watershed that are easily accessible (Wright et al. 2000). The rapid economic development that Panama is currently experiencing leads to habitat loss and fragmentation (Heckadon-Moreno 1993) and combined with hunting (killing events are regularly reported), these factors threaten the long term viability of tapir populations in Central Panama. Only 38% of predicted suitable habitat for tapirs is protected, thus conservation strategies should focus on maintaining forests with no protected status between the large protected areas along the Atlantic Coast in order to enable connectivity and ensure the long term persistence of tapirs along the Isthmus of Panama.

Colombia/Ecuador

The model predicts suitable tapir habitat in Colombia across a wide range of climates, including the extremely wet Chocó region, where Baird's tapir was recorded recently by several researchers in Los Katios National Park (Mejia-Correa et al. 2014), and also the dry forests and savannas of the upper Sinu River (Caribbean region), where Philip Hershkovitz registered the species in the first half of the 20th century, sympatric to Tapirus terrestris colombianus (Hershkovitz 1954). Despite the model predicting suitable habitat there, Baird's tapirs have not been recently recorded in the upper Sinu river (Solari et al. 2013), while explorations have recorded Tapirus terrestris colombianus in the municipalities of Segovia and Remedios in Antioquia (Arias Alzate et al. 2009). It is interesting that no suitable tapir habitat was predicted by the model in the Bahia Solano region, were Baird's tapir was reported as locally extinct in the second half of 20th century due to overhunting (Ulloa et al. 2004), even though substantial forest cover still remains.

The southernmost record of Baird's tapir in Colombia is from Departamento de Nariño on the Pacific slopes of the Andes in southern Colombia, where Baird's tapirs were reported as declining in the 1980s due to overhunting (Orejuela 1992). However no records have been recently obtained in southern Colombia. Interestingly, habitat predicted as suitable by our model in Ecuador coincides with the region north of Guayaquil where Hershkovitz (1954) reported an individual of Baird's tapir (though the exact locality is unknown). Baird's tapirs are depicted in the red book of mammals of Ecuador, however it is included as almost extinct (Tirira 2001). There have been no records of Baird's tapirs in Ecuador in the last 50 years despite survey efforts (Urgilés-Verdugo *et al.* 2013).

Conclusion

This study represents a clear improvement of our knowledge on the global distribution of Baird's tapir habitat, particularly when it is compared with previous maps (such as that used in the IUCN Red List - Figure 1). Use of climatic and forest layers produced a more sensitive description of potential tapir distribution, which is particularly clear in its northernmost limit in Mexico. Thus, this study provides a more realistic and updated description of current Baird's tapir habitat distribution that can be used as a baseline for more comprehensive and refined analyses in the future.

The present study resulted from a collaborative effort involving researchers from several countries (including all of the countries in which Baird's tapir is present) and with many different fields of expertise. Our collaboration yielded not just a unified database of tapir presence data and tapir distribution maps, but also allowed us to compile detailed information on current threats in each of the participating range countries. The main threat is habitat loss due to land use change for agriculture, pastures, and infrastructure, causing habitat connectivity loss and isolation of tapir populations. Additionally, poaching and collisions with vehicles are another relevant threat in most range countries. The formal continuation of this partnership between global tapir researchers will ensure that we can efficiently produce the maps and supporting documents needed to design and implement the actions that will be necessary in coming years to ensure the survival of Baird's tapir populations and the conservation of their habitat.

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