Biodiversity and Conservation
https://doi.org/10.1007/s10531-024-02968-w

ORIGINAL RESEARCH

Connectivity at risk: a critical scenario for the endangered Baird's tapir and the vulnerable white-lipped peccary in the Maya Forest

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Received: 23 October 2023 / Revised: 5 October 2024 / Accepted: 25 October 2024

Abstract

Populations of the threatened Baird's tapir (*Tapirus bairdii*) and the white-lipped peccary (*Tayassu pecari*) face increasing isolation due to rampant deforestation and forest fragmentation across the Greater Maya Forest shared by southeastern Mexico, northern Guatemala, and Belize. We identified (1) the critical areas to ensure the persistence of Baird's tapir and the white-lipped peccary in the Maya Forest; (2) the corridors and sites with the best conditions to maintain connectivity among core habitats, and (3) the nodes with higher risk of habitat loss compromising landscape connectivity. We used a methodological framework combining circuit theory and species distribution modeling to estimate landscape resistance, land use, and the effect of roads and trails on the current distribution of the two focal species in the Maya Forest. We detected that major roads associated with agricultural landscapes are the primary barriers to the movements of tapirs and white-lipped peccaries in the study area. Conserving corridors that link the forests of the Lacandon and the Calakmul regions, along with the protected area network of northern Belize and establishing nodes between remaining forest fragments, are critical measures to mitigate the impact of habitat fragmentation and loss for both species. The critical constriction areas (*pinch points*) and the corridors identified in this study support our prediction of the least-cost paths. Our assessment of threats to landscape connectivity provides useful information to inform effective decision-making for conserving Baird's tapir and white-lipped peccary populations in the Greater Maya Forest.

Keywords Animal movement · Functional connectivity · Least-cost path · Neotropical ungulates · Tapirus bairdii · Tayassu pecari

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Communicated by Emerson Vieira.

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Introduction

The species' long-term persistence depends on their capacity to move to suitable areas for food, shelter, and mates (Taylor et al. 1993; Galantinho et al. 2022). Therefore, land use and cover changes may affect population dynamics, distribution, and movements by limiting access to new resources. This compromises their ability to survive extreme weather, predators, and physical barriers such as roads (Boyers et al. 2019; Passoni et al. 2021; Veldhuis et al. 2019). Land use change, habitat loss, overhunting, and increasing isolation have caused significant declines in population sizes of vulnerable wildlife species in tropical ecosystems (Ripple et al. 2015; Liu et al. 2019). These threats should be addressed by improving our understanding of their interconnectedness and effects on sensitive species to identify critical areas and help reverse their populations' isolation.

Two threatened neotropical mammals currently suffering from land use and cover changes are the endangered Baird's tapir (*Tapirus bairdii*; García et al. 2016) and the vulnerable white-lipped peccary (*Tayassu pecari*; Keuroghlian et al. 2013). Both species are important ecosystem engineers contributing to maintaining forest dynamics through selective herbivory, seed predation and dispersal, trampling, and soil plowing (Keuroghlian and Eaton 2008; Reyna-Hurtado et al. 2017; Naranjo 2019). Their populations have declined drastically in southeastern Mexico and Central America over the last 35 years primarily due to their vulnerability to habitat loss and overhunting (Schank et al. 2020; Thornton et al. 2020; IUCN 2023). Both species require large tracts of tropical forests, montane forests, or wetlands (i.e., $>$ 100 km^2) in relatively good condition to maintain viable populations (Naranjo and Bodmer 2007; Reyna-Hurtado et al. 2012; Moreira et al. 2019; Naranjo 2019; Falconi-Briones et al. 2022).

Other important habitat requirements for these ungulates are water availability, a dense and diverse understory (food sources; Keuroghlian and Eaton 2008), low hunting pressure, and minimal infrastructure (e.g., human settlements and roads) (Reyna-Hurtado et al. 2017; Naranjo 2019; Falconi-Briones et al. 2022; Meyer et al. 2022). In extensive agricultural landscapes, white-lipped peccaries may persist using well-connected networks of native forest patches for movement and feeding (Jorge et al. 2021). The quality and distribution of these forest patches are critical for the survival of this ungulate (Jorge et al. 2019). These requirements have been considered by Aguilera (2020) and Whitworth et al. (2022), who estimated a long-term survival probability of just ~ 50% for Baird's tapir and white-lipped peccary populations in their current distribution ranges. Several authors (e.g., Altrichter et al. 2012; Jorge et al. 2021; Naranjo 2019; Schank et al. 2020) have suggested that conservation efforts for both species should focus on maintaining large tracts of suitable habitat with a good degree of connectivity among them.

Landscape connectivity, the degree to which individual and gene movements between suitable habitat patches are facilitated or impeded by the environment (Taylor et al. 1993; Vasudev et al. 2015; Abrahms et al. 2017), can be increased by creating and maintaining biological corridors (Moilanen and Hanski 2001; Fletcher and Fortin 2018). These corridors enhance the ability of many species to respond to habitat disturbance and climate change, enabling them to persist in changing environments (Vasudev et al. 2015; Costanza and Terando 2019). The assessment of landscape suitability and connectivity are valuable tools for identifying critical areas to facilitate animal movements and inform decision-making when prioritizing both conservation and restoration actions (Oshima et al. 2021).

In this study, we present a framework to assess habitat suitability for the two focal species (Baird's tapir and the white-lipped peccary) in the Greater Maya Forest, which occurs in southeastern Mexico and northern Central America. This framework uses potential distribution models, landscape integrity, and their movement probabilities through limiting barriers (roads and other infrastructure) assessed by experts. We conducted a landscape connectivity assessment through a Least-Cost Path analysis (LCP) for Baird's tapir and the white-lipped peccary in the study area. We expected that agricultural landscapes with higher concentrations of roads and human settlements would present more resistance to the movements of both species compared to heavily forested areas with low human disturbance. The LCP model allowed us to estimate routes with the lowest resistance between suitable habitat fragments, where more frequent animal movements would be expected (Balbi et al. 2019). We identified: (1) critical areas necessary for ensuring the persistence of the two species in the region, (2) corridors and sites with optimal conditions to maintain connectivity among these critical areas, and (3) nodes at a higher risk of habitat loss, which could compromise landscape connectivity.

Methods

Study area

The Greater Maya Forest shared by southeastern Mexico, northern Guatemala, and Belize (Ford and Nigh 2009; Fig. 1) is one of the strongholds of Baird's tapir and the white-lipped peccary (Radachowsky 2002; Toledo et al. 2008; Laako et al. 2022b), which have been severely affected by rampant deforestation (De la Torre et al. 2017; Carrillo et al. 2019; Ellis et al. 2020; Leija and Mendoza 2021). This region ($> 25{,}000\ \mathrm{km}^2$) is covered by different types of tropical ecosystems ranging from rainforests to seasonal forests, montane forests, mangroves, wetlands, and savannas (Olson et al. 2001; Maimone-Celorio et al. 2006; Valero et al. 2022) (Fig. 1). The predominant climate is tropical with latitudinal and altitudinal variations in moisture and temperature (i.e., rainfall increases southward, and higher temperatures prevail at lower elevations; Ford 2019). Agriculture, cattle ranching, timber extraction, apiculture, and tourism are the primary sources of income in the region. In addition, non-timber forest products and wildlife are harvested for subsistence across the area (Piña-Covarrubias et al. 2022).

Focal species records

Baird's tapir and white-lipped peccary records of presence were taken from the following sources: Global Biodiversity Information Facility (GBIF 2022; https://www.gbif.org), Biodiversity Information National System (SNIB from its Spanish name) of Mexico's National Commission for Biodiversity (CONABIO; http://www.conabio.gob.mx/remib), Mexico's National Commission for Protected Areas (CONANP, unpublished monitoring data), Waters and Ulloa (2007), Hidalgo and Contreras (2012), Jordan et al. (2015), Schank et al. (2015), and Falconi (2011; 2017). We also applied questionnaires to key informants (national experts) through e-mail, did face-to-face interviews with researchers working with the focal species in the Maya Forest, and included our field records in the study area. The questionnaires and interviews were conducted in 2021 to gather further information on the records of the two focal species between 1999 and 2021 (i.e., coordinates, vegetation type, and type of record). To avoid autocorrelation, we applied a spatial filter to the data set using the *thin* function in the spThin package (Aiello-Lammens et al. 2015) for R studio

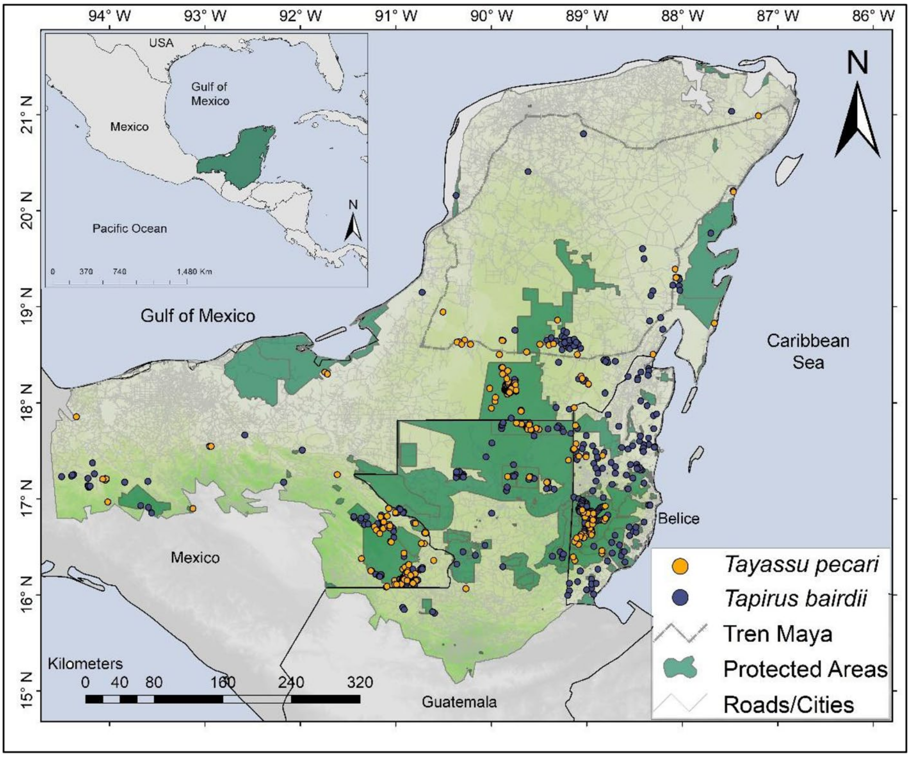

Fig. 1 Records of Baird's tapirs (*Tapirus bairdii*, blue dots) and white-lipped peccaries (*Tayassu pecari*, yellow dots) between 1999 and 2021 in the Greater Maya Forest region. Dark green polygons represent major protected areas. (Color figure online)

software (R Development Core Team 2021). Based on the dispersal distances observed, we discarded the records at distances ≤ 6 km for the tapir and ≤ 3 km for the white-lipped peccary (Reyna-Hurtado et al. 2012; Rivero et al. 2022). After that, our database consisted of 508 records of tapirs and 376 of white-lipped peccaries between 1999 and 2021.

Species distribution models and suitability zones

We ran maximum entropy models to assess environmental suitability for the two focal species in the study area using MaxEnt 3.4.1 software (Phillips et al. 2006; Phillips 2022). For this modeling, we used the bioclimatic layers available in Worldclim Project 2 (Fick and Hijmans 2017) and the climatic layers ENVIREM (Title and Bemmels 2018) as predictors. We discarded some layers based on the variance inflation factor (VIF, Kutner et al. 2004) calculated with USDM 1.1.18 software (Naimi et al. 2014) to avoid over-parametrization and collinearity in the models. This modeling framework is well known for its high predictive precision in habitat studies (Phillips and Dudick 2008) and has been successfully applied in previous tapir studies (Schank et al. 2015, 2020).

Before running the species distribution models, we searched for the optimal parameters through the ENMeval software (Muscarella et al. 2014) with the threshold-independent assessment metrics AUC (area under the curve) to measure the discriminant capacity of the model (Peterson et al. 2011), and Akaike's information criterion with correction for small sample sizes (AICc; Warren and Seifert 2011). For these metrics, we generated 50,000 random locations as background points and partitioned the numbers of records with the "block" method with a cluster factor of 5 (Muscarella et al. 2014).

We assessed the complexity of the models using the regularization multiplier (RM; Muscarella et al. 2014) exploring multiple combinations and different classes (linear, quadratic, product, threshold, and hinge) within a 1–5 RM range with 0.5 increments. Then we built the model through MaxEnt implemented in Dismo 1.1–4 (Hijmans et al. 2017). We applied a receiver operating characteristic curve analysis (ROC) in NicheToolBox (NTBOX) for R (Osorio-Olvera et al. 2020) to measure the performance of the resulting models using the area under the curve (AUC; Peterson et al. 2008; Escamilla-Molgora et al. 2022). The parameters used to select the most parsimonious models are shown in Table 1. We calculated the climatic suitability area for each species by converting potential distribution maps into binary maps with a 10% cut threshold of the training presence (Osorio-Olvera et al. 2020).

The final group of variables used to run the models was composed of temperature seasonality (BIO4), temperature annual range (BIO7), mean temperature of the driest trimester (BIO9), rainfall of the wettest trimester (BIO14), rainfall seasonality (BIO15), rainfall of the warmest trimester (BIO18), potential evapotranspiration (PET) of the driest trimester, PET of the coldest trimester, and PET of the wettest trimester. In addition, based on the life-history traits and habitat requirements of Baird's tapir and the white-lipped peccary (Naranjo 2014; Meyer et al. 2022), we included the topographic moisture and the forest integrity indices (Parrish et al. 2003; Grantham et al. 2020) in the study area as additional layers for our analyses. The resulting models of both species were used to estimate the resistance surface through a re-sampling of the raster layer obtained in ArcMap 10.4 (ESRI 2017). We assigned low resistance values (0–10) to the pixels representing high percentages of suitability and included a layer of roads, infrastructure, and urban areas taken from OpenStreetMap (OSM; http://www.openstreetmap.org/).

Considering the movement ecology and space requirements of both species (Chapman and Reyna-Hurtado 2019), we assigned resistance values based on Theobald et al. (2012) criteria: 10–30 to dirt roads and trails, and 31–100 to human settlements, streets, and paved roads. Finally, the resistance layer was rasterized and rescaled through the

Table 1 Variable contribution to the ecological niche modeling (Maxent ENM), according to the Jackknife test

Variables	*Tapirus bairdii*	*Tayassu pecari*
BIO 7	39.208	1.190
BIO 8	3.568	11.072
FLII	15.802	46.6957
TWI	11.599	20.937
(AICc)	5,487.75	2798.65
Akaike weight (*Wi*)	0.763	0.665
Training AUC	0.8201	0.8152

BIO 7: Temperature annual range, BIO 8: Mean temperature of the wettest trimester, AICc: Akaike's information criterion corrected for small sample sizes. *FLII* Forest landscape integrity index, *TWI* Topographic moisture index, *AUC* Area under the curve

Mosaic to raster tool in ArcMap 10.4 (ESRI 2017). The landscape resistance values ranged from 0 (lowest resistance) to 100 (highest resistance) (McRae et al. 2008).

Connectivity models

We analyzed the functional connectivity among the areas with presence of Baird's tapirs and white-lipped peccaries through the circuit theory (McRae et al. 2008), which allowed us to infer their potential movement patterns in a heterogeneous and complex landscape (Tischendorf and Fahrig 2001; Rudnick et al. 2012). We did this analysis by calculating the effective resistance to movement and examining all potential connecting routes between core areas (focal nodes) with the CIRCUITSCAPE 4.0.5 software (Shah and McRae 2008). In this process, one of the nodes is associated to a current source of 1 A while the other is connected to earth (McRae et al. 2008).

Corridors and least-cost paths

We utilized the current map generated in Circuitscape using Linkage Mapper 3.0.0 software (McRae and Kavanagh 2011) to identify corridors and least-cost paths (LCP). This software employs the Cost Distance algorithm by ArcInfo® (ESRI 2017) to assign cost-weighted movement values to raster cells based on nearby source cells. Subsequently, we calculated the LCP on a vectorial layer of lines representing the optimal routes for establishing corridors that link core habitat areas (Forman and Godron 1986; Adriaensen et al. 2003).

Centrality

We did an analysis of current-flow centrality (Dutta et al. 2016) to estimate the relative importance of the core areas within the Maya Forest. Centrality measures assess the contribution of core habitats facilitating the flow of individuals across the landscape (Mallory and Boyce 2019). Under this approach, we regarded the observed core areas as *nodes* and calculated the current flow throughout the whole network. In this way, we evaluated the importance of each node and corridor linking habitat fragments (Bolom-Huet et al. 2022).

Pinch points

We finally identified the bottlenecks or constriction points (*pinch points*) where the loss of a small area could disproportionately compromise connectivity because alternative movement routes would be unavailable to the focal species across the study area (McRae et al. 2008). Pinch points analysis was used to highlight relevant areas where connectivity could be interrupted if habitat was lost. This analysis applies the current map obtained in Circuitscape based on circuit theory (Fig. S3) and determines the areas in which the species corridors present a high probability of flow between habitat patches. Under the assumptions of the model, high values of this parameter indicate vulnerability to changes in the landscape conditions (McRae et al. 2008, 2012).

Results

Species distribution models and suitability zones

The models built in this study suggest that the potential distribution areas of Baird’s tapir and the white-lipped peccary in the Greater Maya Forest occupy 108,413 km^2 and 141,369 km^2, respectively. The zones of environmental suitability (including proper climate and vegetation) for Baird’s tapir (39.7%) and the white-lipped peccary (51.7%) in the Maya Forest are generally restricted to protected areas with a dense forest cover contrasting with their open or sparsely forested surrounding matrix (51.7%; Fig. 2). This may be conditioning the movements of both species. The zones with the highest climatic suitability for both species are primarily in Belize and northeastern Guatemala (Fig. 2a). In Mexico, these zones are from Calakmul Biosphere Reserve through Sian Ka’an Biosphere Reserve in the Yucatan Peninsula, and in Montes Azules Biosphere Reserve in Chiapas (Fig. 2b).

The variables with the highest weight (AUC: 0.8201; Table 1) for the potential distribution of Baird’s tapir were the temperature annual range (BIO 7 = 39.2%), the forest landscape integrity index (FLII = 15.8%), and the topographic moisture index (TWI = 11.6%). The most relevant variables (AUC: 0.8152; Table 1) for the white-lipped peccary were also FLII (46.7%), TWI (20.9%), and the mean temperature of the wettest trimester (BIO 8 = 11.1%). For both species, the zones with the lowest environmental suitability were detected in the northwestern Yucatan Peninsula, the central and western sectors of Laguna del Tigre National Park, and the southeast of Sierra del Lacandón National Park, Guatemala (Figs. 2a and 2b).

Connectivity models

We identified the zones with the lowest resistance values for the movements of Baird’s tapir and the white-lipped peccary mainly around protected areas (Figs. 3, S1, S2). The connectivity maps showed higher resistance values on major roads and highways, especially those along international borders, which constitute significant barriers to the movements of both species (Fig. 3). The zones of the Maya Forest with the highest potential flow for tapirs were detected in Belize, northern Guatemala, the Lacandon Forest, and the southern part of the Yucatan Peninsula, while those with the highest resistance were in the southwest of the Maya Biosphere Reserve, Guatemala (Figs. 3, S1). For the white-lipped peccary, the zones with the highest connectivity were in northern Guatemala and in the south of the Yucatan Peninsula (Figs. 3, S2).

Corridors and least-cost paths

Our analyses of connectivity showed an important number of corridors between potential habitat areas of the two focal species (Fig. 4 and Fig. S1). The least-cost paths for the movements of tapirs were detected in northern Belize, along the border with the state of Quintana Roo, Mexico, in the surroundings of Calakmul Biosphere Reserve, and in the central-eastern sector of the Maya Biosphere Reserve in Guatemala. The least-cost paths found for the white-lipped peccary were in between the protected areas of central Belize and the Calakmul region in Mexico. In contrast, we observed a lower probability of tapir and white-lipped peccary movements from these areas into northern sites of the Maya Forest (Fig. 3).

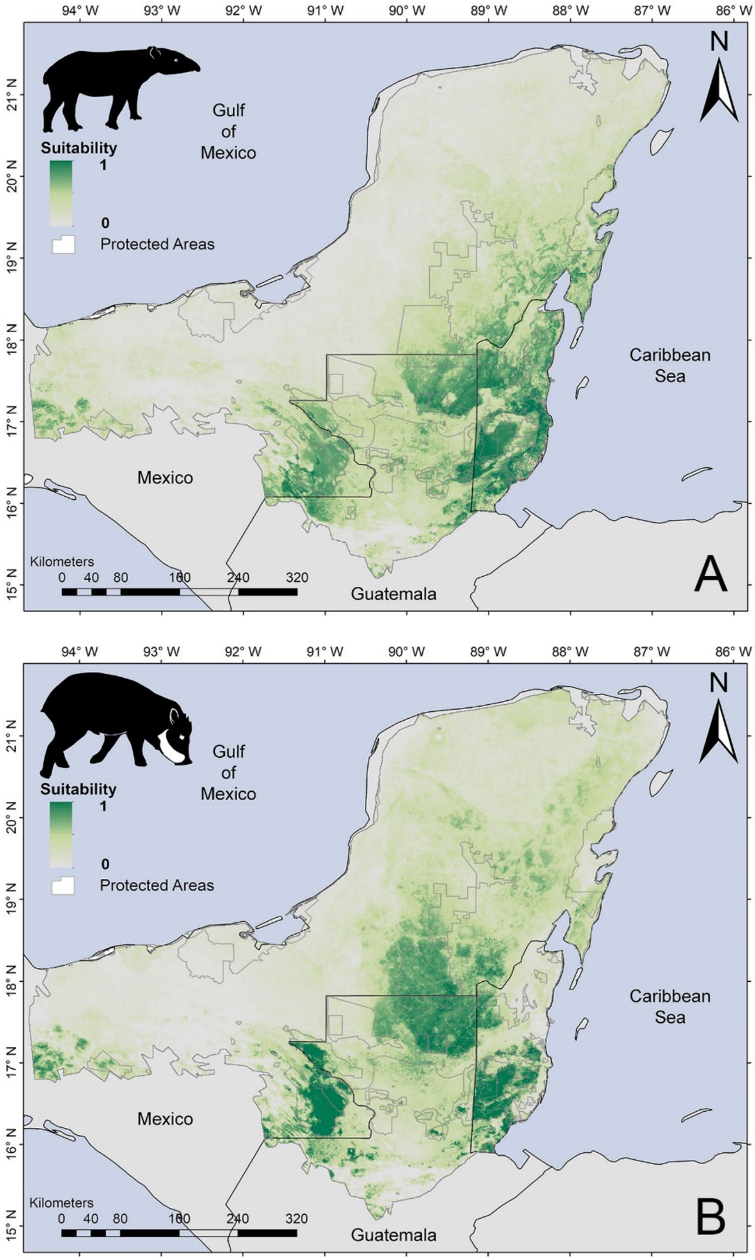

Fig. 2 Areas of suitable habitat for Baird's tapir (*Tapirus bairdii*, a), and the white-lipped peccary (*Tayassu pecari*, b) in the Greater Maya Forest. (Color figure online)

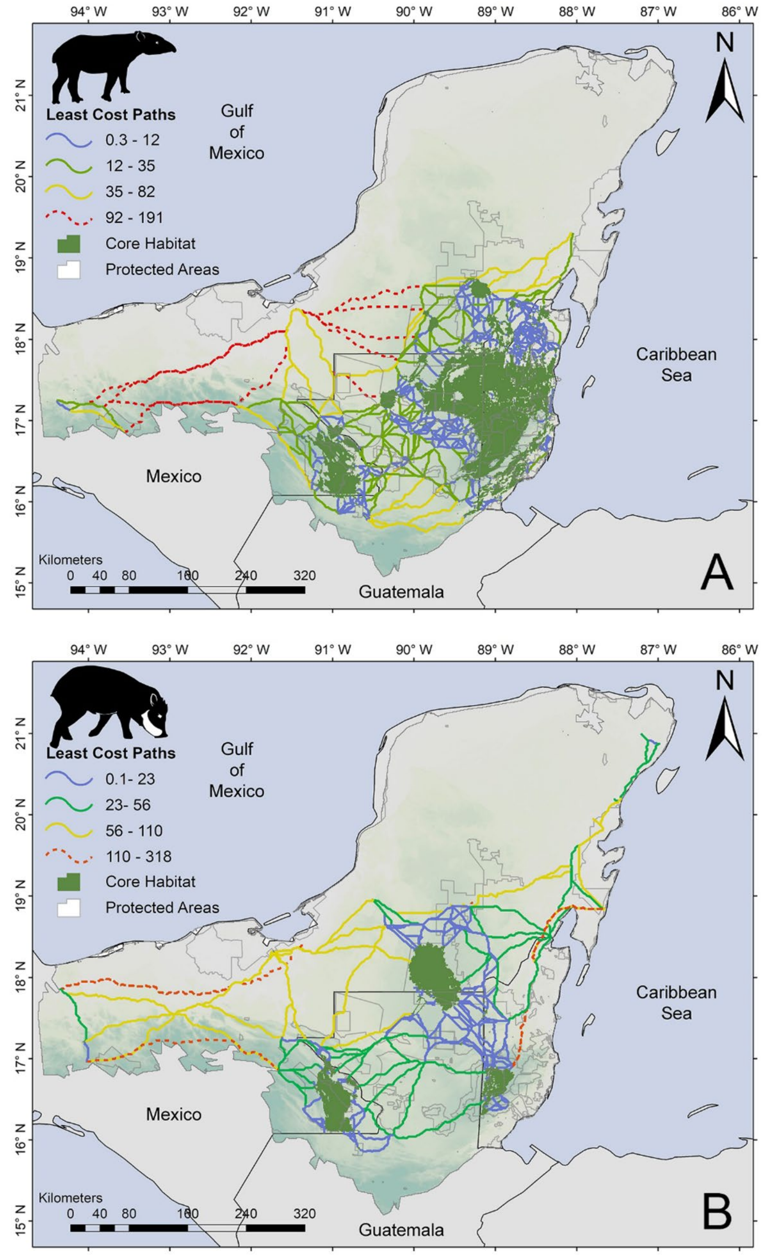

Fig. 3 Core areas of habitat and least-cost paths (LCP) for the movements of Baird's tapirs (*Tapirus bairdii*), and white-lipped peccaries (*Tayassu pecari*) in the Greater Maya Forest. (Color figure online)

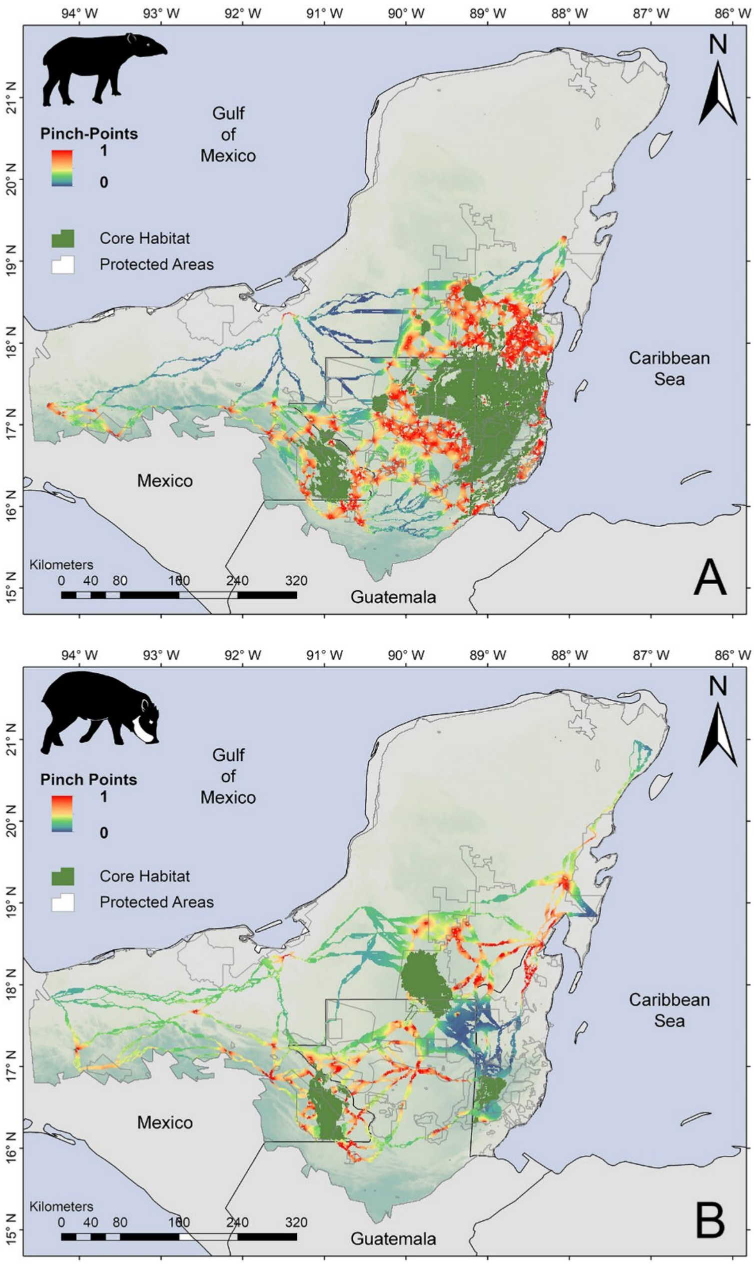

Fig. 4 Potential corridors linking core habitat areas of Baird's tapir (*Tapirus bairdii*) and the white-lipped peccary (*Tayassu pecari*) in the Greater Maya Forest. Colors indicate corridor functionality for the movements of both species considering the p*inch points* identified in this study. (Color figure online)

Centrality

Our centrality analyses for Baird's tapir showed two large core habitat zones where the flow of individuals could be high. The first one (17,908 km^2) is between the tropical forests of northern Belize, the eastern part of the Maya Biosphere Reserve in Guatemala, and the southern Calakmul area (Fig. 4). The second one (3296 km^2) is within Montes Azules Biosphere Reserve in Chiapas, Mexico. We also identified two smaller centrality zones in the Maya Biosphere Reserve and around Calakmul Biosphere Reserve (a total of 502.2 km^2). For the white-lipped peccary, we identified three zones with the highest centrality: 1) Calakmul-NE of the Maya Biosphere Reserve (3812.7 km^2); 2) Montes Azules Biosphere Reserve-Sierra del Lacandón National Park, Guatemala (2907.9 km^2); and 3) Chiquibul Reserve- Mountain Pine Ridge, Belize (1,315.8 km^2; Fig. 4).

Pinch points

Our pinch point detection analysis suggested that the flows of tapirs and white-lipped peccaries occur more frequently in the tropical forest fragments surrounding the protected areas of Belize, northern Guatemala, and southeastern Mexico (Fig. 4). The zone with the highest potential flow of Baird's tapirs was between the southern Yucatan Peninsula and northern Belize. In Guatemala, the pinch points for tapirs are mainly south of the cluster of protected areas within the Maya Biosphere Reserve, and between the Laguna Lachuá National Park and the Lacandon Forest in southeastern Mexico (Fig. 4). We found a lower density of pinch points for the white-lipped peccary in the study area. However, these points suggest more extended flows primarily between the Calakmul region and the Maya Mountains of Belize (Fig. 4).

Discussion

Our results highlight that efforts to restore or improve linkage among core areas of suitable habitat should be focused on the *pinch points* identified in our modeling, where the exposure of Baird's tapirs and white-lipped peccaries to mortality through overhunting, road collisions, and other anthropic disturbances is probably the highest in the Greater Maya Forest. At the regional level, the distribution of both ungulates is related to the landscape integrity and topographic moisture, which together mirror the conservation status of the landscape and water availability. Both of them are important limiting factors for the persistence of their populations (Schank et al. 2020; Thornton et al. 2020). Our analysis of functional connectivity revealed that core areas of suitable habitat, corridors, and potential routes are limited by the presence of protected areas and non-protected forests in good condition surrounded by secondary forest fragments in our study area. As previously observed by Jorge et al. (2019, 2021) and Thornton et al. (2020) for white-lipped peccaries, and by Schank et al. (2020) for Baird's tapirs, these well-connected forest fragments probably facilitate the movement of both species between core areas and contribute to their gene flow (Frankham et al. 2017). The Lacandon Forest region (~ 12,000 km^2), one of the largest and best-preserved rainforests in Mexico (Meave et al. 2008; Santos-Hernández et al. 2021), together with some reserves in northern Guatemala and southern Belize are the only areas with similar proportions of suitable habitat for the sympatric presence of both focal species in the Maya Forest. Likewise, the complex Calakmul (Mexico)-Maya Biosphere Reserve (Guatemala)-Maya Mountains (Belize) constitutes the largest core area for the two species in the region (Fig. 3). In Belize, the network of protected areas (with montane forests and savannas) provides suitable habitat for tapirs, but not necessarily for white-lipped peccaries, whose distribution is restricted to the southwest of the country (Hofman et al. 2018).

The distribution models built in this study showed that suitable landscape conditions for Baird's tapir occur in three large areas: 1) the Lacandon Forest (the most isolated), 2) the Calakmul-Maya Biosphere Reserve; and 3) the network of protected areas of Belize and the Maya Mountains and Maya Forest regions (excepting for the farther north and the central-western regions of the country). Belize still maintains ~ 60% of its original forest cover (Hofman et al. 2018) and supports relatively large populations of Baird's tapirs (e.g., ~ 60 individuals in the Río Bravo conservation area; Monette et al. 2020), and white-lipped peccaries (e. g., ~ 6000 in the Maya Mountains; Hofman et al. 2018).

The fact that the most significant predictive variables in our distribution models for both species were linked to the landscape integrity index, temperature, and moisture correspond to the environmental conditions prevalent in the Maya Forest. In the Maya Biosphere Reserve, there is a bioclimatic gradient where the north is drier than the south, and the east is warmer than the west (CONAP 2015). This could be positive for the presence of Baird's tapirs, which appear to benefit from cooler temperatures (< 26 °C) and high humidity (≥ 1400 mm) (Carrillo-Reyna et al. 2015; García et al. 2019). This concurs with the findings of Schank et al. (2015), who predicted that low seasonality and mild temperatures favored habitat selection by Baird's tapirs (Schank et al. 2017, 2020).

The probability of Baird's tapir presence also increases where food and water are abundant, and where human activity is minimal (Cortéz et al. 2012; Carrillo-Reyna et al. 2015). We assume that climatic conditions currently do not constitute a drastic limiting factor for both tapirs and white-lipped peccaries in the study area. However, ongoing changes in landscape integrity and connectivity (i.e., deforestation and forest fragmentation) aggravated by the effects of climate change (e.g., drought and heat stress) may produce negative impacts on food and water resources for these mammals in the long term (Aguilera 2020; Thornton et al. 2020; Peterson et al. 2024).

The projection of suitability areas resulting from our analysis resembles those suggested by Schank et al. (2020). However, our predictions look more conservative for areas such as the Yucatan Peninsula (Fig. 2). We propose that variables related to the ecological integrity of the study area (i.e., the topographic moisture and the landscape integrity indices; Krosby et al. 2015; Walston and Hartmann 2018) should be considered in future habitat suitability analyses for Baird's tapir and the white-lipped peccary. The occupancy and abundance of the two species in areas that were not classified as suitable in our models could be partially explained using a metapopulation approach (Hanski and Gilpin 1997). Under this assumption, our connectivity models suggest that secondary forest fragments may be relevant as stepping stones (Yang et al. 2016) linking large, protected areas (core habitat) and surrounding smaller areas (sink habitat; Naranjo and Bodmer 2007). Population and habitat viability analyses (PHVA; Lacy 1994) applied to Baird's tapir (Medici et al. 2006) and the lowland tapir (*Tapirus terrestris;* Medici and Desbiez 2012) suggested that the presence of corridors linking and facilitating gene flow among habitat patches increases population persistence in the long term (Frankham et al. 2017).

As mentioned earlier, we detected two large core areas for Baird's tapir covering 21,203 km^2, and three core areas for the white-lipped peccary comprising 8,036.4 km^2, with some surrounding fragments probably favoring the dispersal of both species (Gilpin and Soulé

1986; Brook et al. 2006). Even though these ungulates may show resilience to adapt to moderately adverse conditions (Naranjo 2019; Falconi et al. 2022; Magioli et al. 2022), our results coincide with those of Schank et al. (2017; 2020) and Thornton et al. (2020) in suggesting a negative scenario threatening landscape connectivity for the populations of the two species in the Maya Forest. This scenario supports the possibility that current trends in the expansion of infrastructure over the region (i.e., urban development, new major roads and railways, high tension lines, and aqueducts, among others) will restrict movements and increase mortality of both species in the near future (Naranjo 2018; Benítez et al. 2021).

Corridors and least-cost paths

The isolation of tropical forest fragments out of the Maya Forest is evident (see Fig. 3). This isolation makes us assume that tapirs and peccaries have a very low probability of dispersing and succeeding within a large buffer around this region. For instance, it seems very unlikely that a young tapir or a small peccary herd could be capable of moving west from the Lacandon Forest to a new territory in the Selva El Ocote Biosphere Reserve or Los Chimalapas region in southeast Mexico (Fig. 3). Such a movement would imply traversing through a matrix of severely deforested areas, multiple villages, and many roads for over 200 km.

Gallo et al. (2019) proposed two ways of maintaining landscape connectivity: (1) management of as many core areas as possible to facilitate animal movements among them; and 2) reducing landscape elements limiting movements such as roads, train tracks, and urban development. Connectivity assessments and mapping have become more frequent through modeling allowing the incorporation of numerous variables on the life-history traits of species, habitat attributes, and others (Rudnick et al. 2012). Our models helped examine the linkage among protected areas and other core habitat fragments in the Greater Maya Forest. This analysis contributes to improving our understanding of gene flow, migration, recolonization, local extinction, and climate change adjustments of tapirs and white-lipped peccaries in the study area (Rudnick et al. 2012; Correa-Ayram et al. 2016). This knowledge will also aid in anticipating risks to small populations and propose actions to avoid further isolation and inbreeding depression of the two focal species (Frankham et al. 2017; Díez del Molino et al. 2018; Sullivan et al. 2019).

Haines-Young and Chopping (1996) advised analyzing the landscape with the highest resolution possible given the rapid global decline of native large herbivore populations. This task demands large-scale geographic data to support effective planning and management for wildlife conservation (Thornton et al. 2020). The eco-regional/biogeographical scale (*Eco-front;* Laako et al. 2022a; 2022b), used in this study was appropriate for our goal of generating information useful to support explicit conservation public policy and management actions for Baird's tapirs, white-lipped peccaries, and their habitats in the Maya Forest.

The results of our analysis suggest that urgent conservation actions at local and regional scales are needed to maintain and improve landscape connectivity for Baird's tapir and white-lipped peccary populations in the Greater Maya Forest. The extant network of protected areas could not be sufficient to ensure the long-term viability of these populations. Further widespread local initiatives for habitat restoration coupled with international collaboration between the governments of Belize, Guatemala, and Mexico to expand that network and improve linkage among core areas and their surrounding forest fragments would be key to conserving both species in the region.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-024-02968-w.

Acknowledgements We thank the Comisión Nacional de Áreas Naturales Protegidas (CONANP), Sian Waters, Carlos Muench, Bart Harmsen's team, and Boris Arevalo for facilitating data on the presence and distribution of the focal species in the Maya Forest. To the Global Baird´s Tapir Conservation Program (2015-2019) of the IUCN Tapir Specialist Group (TSG/SSC) and Fondation Segré, Guatemalan Baird´s Tapir Conservation Program of the Centro de Estudios Conservacionistas and Fundación Defensores de la Naturaleza, Dirección General de Investigación de la Universidad de San Carlos (projects implemented in 2016, 2017 and 18: 4. 8.63.4.04, 4.8.63.2.03 and 4.8.63.2.35), Tikal National Park and Yaxhá Nakum Naranjo National Park. Emerson M Vieira and two anonymous reviewers provided insightful comments to improve the manuscript.

Author contributions FAF and RBH conceived the ideas, designed the methodology, and analyzed the data. RRH, JMR, and MJG provided field data. FAF, EJN, and RBH wrote the original manuscript and the subsequent versions. EJN, PLE, RRH, MJG, JMR, and RAM revised the manuscript. All authors contributed to the drafts and gave final approval for publication.

Funding The Consejo Nacional de Humanidades, Ciencias y Tecnologías (CONAHCYT) provided a grant (#734379) to the first author for doctoral studies. The Rufford Foundation and Idea Wild partially funded this project.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interests The authors declare no competing interests.

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