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Conservation

Modelling the functional connectivity of the grayish mouse opossum (*Tlacuatzin canescens*) in a highly threatened tropical dry forest of the Mexican Pacific coast

*Modelando la conectividad funcional del ratón tlacuache (*Tlacuatzin canescens*) en un bosque tropical caducifolio altamente amenazado de la costa del Pacífico mexicano*

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Abstract

Landscape connectivity between protected natural areas and their surroundings is essential to maintain wildlife movement and to promote gene flow and genetic diversity. The grayish opossum mouse (*Tlacuatzin canescens*) was used for modeling functional landscape connectivity between the Chamela-Cuixmala Biosphere Reserve, an important biological reserve with large extensions of tropical dry forest in the Mexican Pacific coast, and surrounding vegetation patches. The model was estimated through graph and circuit theory, using a resistance matrix and the calculation of the minimum area of suitable habitat patches. Thirty-eight patches of suitable habitat for *T. canescens* and 60 potential corridors were identified. Three patches adjacent to the CCBR played the most important role in maintaining the connectivity of the tropical dry forest in the region. In contrast, suitable habitat patches with the lowest connectivity were embedded in a landscape matrix composed of areas for cattle raising and agriculture, increasing the loss and isolation of forest patches. Our results highlight not only the importance of maintaining large patches of suitable habitat, but also smaller patches which might play a significant role as stepping stones, promoting habitat connectivity for *T. canescens* and similar species.

Keywords: Deciduous tropical forest; Didelphidae; Protected natural areas; Resistance matrices; Small mammals

Resumen

La conectividad del paisaje entre áreas naturales protegidas y sus alrededores es esencial para mantener el movimiento de la fauna, promover el flujo y la diversidad genética. Usamos al ratón tlacuache (*Tlacuatzin canescens*) para modelar la conectividad funcional entre la Reserva de la Biosfera Chamela-Cuixmala, que mantiene una importante

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extensión de bosque tropical caducifolio (BTC) en la costa del Pacífico mexicano y los parches de vegetación circundante. El modelo de conectividad funcional se realizó a través de la teoría de grafos y circuitos, utilizando una matriz de resistencias y el área mínima de parches de hábitat adecuado. Se identificaron 38 parches de hábitat adecuado para *T. canescens* y 60 corredores potenciales. Tres parches adyacentes a la CCBR jugaron el papel más importante para mantener la conectividad del BTC. En contraste, los parches de hábitat adecuados menos conectados se encuentran inmersos en una matriz compuesta por áreas dedicadas a la ganadería y agricultura, incrementando la pérdida y aislamiento de parches de bosque. Nuestros resultados resaltan no solo la importancia de mantener grandes parches de hábitat adecuado, sino también parches más pequeños que podrían desempeñar un papel importante como peldaños, promoviendo la conectividad del hábitat para *T. canescens* y especies similares.

Palabras clave: Bosque tropical caducifolio; Didelphidae; Áreas naturales protegidas; Matrices de resistencia; Pequeños mamíferos

Introduction

Habitat loss and degradation due to human activities are 2 of the main threats for tropical forests and the main causes of biodiversity loss (Flores-Casas & Ortega-Huerta, 2019; Laurance et al., 2012; Vieira-De Matos et al., 2019; Wilson et al., 2015). It has been estimated that between 1990 and 2015, 10% of the global extent of tropical forests was lost due to deforestation (FAO, 2015; Keenan et al., 2015). This loss of natural habitats affects directly forest-dependent vertebrates by decreasing landscape connectivity, reducing food supply availability and areas for shelter and mating (Merrick & Koprowski, 2017; Morales-Díaz et al., 2019; Theobald et al., 2012). Moreover, habitat loss might increase vertebrate exposure to external threats such as diseases and exotic species (de la Peña et al., 2003; Passamani & Fernández, 2011). The effects of these threats can be exacerbated when an animal's limited dispersal ability and an unsuitable surrounding landscape matrix combine to increase populations isolation (Brooker & Brooker, 2002; Luck & Daily, 2003; Moore et al., 2008). Therefore, the study of animal's habitat connectivity stands out as a topic of major relevance to understand the response of wildlife to anthropic perturbations. Habitat connectivity can be measured based on the continuity of suitable landscape features (i.e., structural connectivity) or by incorporating animal's characteristics such as its ability to disperse through different land use and vegetation covers (Robichaux & Yetman, 2000; Taylor et al., 2006; Tischendorf & Fahrig, 2000; With et al., 1997). Thus, functional connectivity considers the animal's physical cost of moving through portions of the landscape with different degrees of suitability for the species (Adriaensen et al., 2003; Moilanen & Hanski, 2001; Shah & McRae, 2008).

Tropical dry forests (TDFs) are amongst the most biodiverse and endemism-rich ecosystems, but also amongst the natural habitats most heavily impacted by deforestation and fragmentation (Bullock et al., 1995; Janzen, 1988; Miles et al., 2006). Mexico has the largest extent of tropical dry forest in the Americas, covering an area of 181,461 km^2 which accounts for 38% of their total extent in the continent (Portillo-Quintero & Sánchez-Azofeifa, 2010). However, dry forests are being lost at accelerated rates. The area that originally covered dry forests in Mexico has been reduced by ~ 70%, and its annual deforestation rate is 2%, one of the highest among the country's main ecosystems (García, 2006; Trejo & Dirzo, 2000). It is estimated that only 30% of the TDF in the country maintains a good level of conservation and approximately only a 10% is protected (Trejo, 2010; Trejo & Dirzo, 2002). Whereas protected areas help to reduce deforestation in their interior, they are much more limited in terms of reducing the loss of natural habitats in their vicinity (Bennett, 2004; Bruner et al., 2001; Cuenca & Echeverria, 2017; De Clerck et al., 2010; Garmendia et al., 2013). Thus, original habitats within protected areas face an increasing level of isolation which greatly affect the dispersal of individuals and genes of a great variety of taxa (Calabrese & Fagan, 2004; Ricketts, 2001). Among the consequences of connectivity loss are the reduction of genetic diversity within populations and an increase of genetic differentiation among populations due to reduced gene flow and genetic drift (Hutchinson & Templeton, 1999). These consequences in the TDF are particularly serious due to the high biodiversity it harbors. For example, 183 species of mammals have been recorded in TDFs of Mexico, which corresponds to 35% of all mammal species in the country, from which 23% are endemic (Ceballos & García, 1995; Ceballos & Oliva, 2005).

Most mammal species inhabiting TDFs are herbivorous, have small body sizes, short generational times, and small home ranges and some of them bear some level of physiological adaptation to deal with water shortage during the dry season (Ceballos & Miranda, 2000; Stoner & Timm, 2004). For example, some species, including marsupials, are able to reduce their body temperature through diurnal torpor and to store fat in their tails (Lovegrove et al., 1999). However, in spite of these adaptations, mammals can be sensitive to changes brought about by forest fragmentation showing responses at spatial scales of a few meters (Corry, 2005). Many of these small mammal species are involved in fundamental biotic interactions for forest regeneration such as seed dispersal and pollination (Arreola-Gómez & Mendoza, 2020; Ghazoul, 2005; Howe & Smallwood, 1982; Lobova et al., 2009). Therefore, the lack of connectivity throughout the dry forest can have important repercussions not only in terms of the viability of wild mammal populations but also for the regeneration of the forest itself.

Even though numerous ecological and conservation studies have been conducted in the region of Chamela, Jalisco in the Pacific coast of Mexico, to our knowledge, none have made an assessment of habitat connectivity. This study is aimed at analyzing the level of functional habitat connectivity for the endemic grayish mouse opossum (*Tlacuatzin canescens*) in a heterogeneous landscape originally covered by TDF. *T. canescens* is an excellent system to modelling connectivity because is a small species with relatively limited dispersal abilities, highly dependent on trees for its displacement and strongly associated to dry forests. Therefore, deforestation likely represents a main threat for its survival. Specifically, we assessed the level of functional connectivity for *T. cansescens* between the Chamela-Cuixmala Biosphere Reserve (CCBR) and dry forest remnants in its vicinity using graph and circuit theory; identified dry forest patches having the greatest role in maintaining connectivity with the CCBR; and identified potential corridors that can help to maintain habitat connectivity for *T. canescens*. Given the ecological characteristics of the study species, particularly its dependence on arboreal vegetation and its limited dispersal abilities, and given the marked loss of TDF that has affected the study region, we hypothesize that functional connectivity for the species in areas where the original habitat has been transformed to more open vegetation covers, should be limited. Moreover, given the heterogeneity in the features of the landscape we expect the level of habitat connectivity loss to vary across the study area.

Materials and methods

Tlacuatzin canescens (synonym *Marmosa canescens*, J.A. Allen, 1893) is a marsupial species endemic to Mexico that belongs to the family Didelphidae (Ceballos & Arroyo-Cabrales, 2013). *Tlacuatzin* is the only endemic genus of marsupials recognized in Mexico. The distribution of this species spans along the Mexican Pacific coast, from Sonora to Chiapas, including the Balsas river basin, from sea level up to 2,300 m asl (González-Christen & Rodríguez, 2014; Voss & Jansa, 2009; Zarza et al., 2003). *T. canescens* has a great ability to move through the forest canopy but has a more limited ability for displacement on the forest floor (Zarza et al., 2003). There is a lack information on the species demography but a recent study, conducted in the dry forest of the state of Colima, Mexico, found that *T. canescens* accounted for 85.7% of the captures of small mammals, reaching an estimated density of 0.7 - 8.0 individuals/ha (Kennedy et al., 2013). This species is not listed in the Mexican Official Norm 059, which is the national compendium of species of conservation concern, and in the Red List is classified as a species of least concern (Lorenzo & González-Ruiz, 2018; Martin, 2017). However, the strong connection of this species with the dry forest suggests that they are likely under threat due to habitat loss and degradation.

This study was conducted in the Chamela-Cuixmala region, that supports one of the most preserved areas of tropical dry forest in Mexico. In this region 72 mammal species have been recorded, from which 18 are endemic (accounting for 60% of endemic mammal genera in the country), and at least 31% of these species are classified as threatened (Ceballos & García, 1995; Ceballos et al., 2010). The study focused on the Chamela-Cuixmala Biosphere Reserve (CCBR) and a surrounding buffer area of 20 km which totalized 154,836 ha (Supplementary material: Fig. S1). This buffer encompasses at least 10 times the average maximum dispersion distance calculated for similar species (1,904.7 m; Table 1) and duplicates the average buffer suggested to maintain viable populations of a didelphid species similar to *T. cansescens* (Alexandre et al., 2010). Besides, within this buffer most of the historical records for the species have been registered (data not shown). Moreover, it has been suggested that a 10-20 km buffer around a protected area is large enough to identify substantial variation in vegetation cover, but close enough that changes in land cover heterogeneity in the surrounding area likely influence population and ecosystem processes in the protected area (Hansen & Defries, 2007; Seiferling et al., 2012). The surrounding buffer included some villages (Supplementary material: Fig. S1), and the main land uses and cover types in the zone are tropical dry forest, mangrove, crop lands (i.e. sorghum, corn, citrus, bananas, watermelons, and vegetables) and pasture for intensive cattle raising. Beyond the surrounding buffer TDF is interrupted by substantial changes in natural vegetation and by large agricultural fields and pastures for cattle. It has been estimated that 47,200 ha of original vegetation were lost from 1986 to 2017 in this region

(Hernández-Guzmán et al., 2019). Moreover, transition models indicate that the Chamela-Cuixmala Biosphere Reserve (CCBR) is vulnerable to land cover changes occurring in the surrounding environments (Flores-Casas & Ortega-Huerta, 2019).

We developed a resistance model based on the approach used by Beier et al. (2009) and Correa-Ayram et al. (2014). Resistance models involve defining a species' suitable habitat and assigning values that represent the resistance to species movement through the surrounding landscape matrix (Sawyer et al., 2011). Cells with high resistance values represent areas where individuals are unlikely to move under typical conditions due to high energetic, survival, or other ecological costs involved (Adriaensen et al., 2003). We selected landscape variables that have potentially a strong effect on the movement of *T. canescens*. Those variables were: land use and land cover, slope (degrees), road type (width), and river drainage order. In order to rank these variables based on their importance to limit *T. canescens* dispersal, we sent a questionnaire requesting the opinion of mammal´s experts from different Mexican universities and research institutes, however only 4 researches replied to our request (Table 2). These experts were asked to rank each of the variables we included in our analysis in terms of their resistance to displacement from 1 (minimum resistance) to 100 (maximum resistance; Beier et al., 2009; Freeman et al., 2019). We averaged the ranks assigned by the experts to build our resistance model (RM) as follows:

$$RM = LULC + SLP + ORD + Rt$$

where LULC = land use and land cover; SLP = terrain slope; ORD = river drainage order; Rt = road type.

The land use and land cover map was produced through the unsupervised classification of Landsat OLI (Operational Land Imager) images from 2018 using the isocluster algorithm. This algorithm makes use of an iterative process where the user sets the number of clusters to be identified. A set of N clusters are then arbitrarily located in the band space and pixels are assigned to their nearest cluster location. Once all the pixels have been assigned, a new mean location is computed. This algorithm makes use of a full Maximum Likelihood procedure providing a very robust cluster assignment (Eastman, 2016). All the pixels were assigned to 30 spectral classes that were in turn reclassified into the following general informational classes: aquatic surfaces, exposed soils, tropical dry forest, rivers, roads, and other types of vegetation (including mangrove and evergreen forest). Human settlements and river classes were digitized on-screen over high-resolution images available from Google earth Pro, while roads were extracted from the Mexican Institute of Transport and added to the final thematic map.

We derived the slope layer (SLP) from a digital elevation model (DEM) downloaded from the National Institute of Statistics and Geography (INEGI; https://www.inegi.org.mx/app/geo2/elevacionesmex/), with a 30 m of spatial resolution. Slope values were reclassified to have the following intervals: 0° - 5°, 5° - 15°, 15° - 30°, and 30° - 65° (Table 2). We used the same DEM to derive the river drainage order layer (ORD). During a preprocessing procedure all the terrain depressions were identified and removed. We applied the D8 (Deterministic 8) algorithm (Jenson & Domingue, 1988) to assess the flow direction and flow accumulation. To define the river drainage order we used a constant threshold value following Strahler (1957). Order 1 corresponded to links without runoff, order 2 resulted from intercepting 2 links of order 1, order 3 resulted from intercepting 2 links of order 2, and so on (Table 2). Road type layers (Rt) were downloaded from the webpage of the Mexican Institute of Transport (IMT; https://www.gob.mx/imt/acciones-y-programas/red-nacional-de-caminos). These layers were originally vectorial but were rasterized to be classified based on their width into the following categories: 3.5 m; 3.5 - 5 m; 5 - 6 m; 6 - 7 m, and 7 - 8 m (Table 2).

Table 1

Home range values used to estimate the maximum dispersion distance (MDD) of *T. canescens*. We used the home ranges of the species to calculate their maximum dispersal distance. MDD = 40 * linear dimension of home range (Bowman et al., 2002). *T. canescens* has an estimated body weight of 20 - 60 g (Arreola-Gómez & Mendoza, 2020).

Gender	Body weight (g)	Home range (m^2)	MDD (m)	Reference
Marmosa	60	3,800	2,465.6	Melo et al., 2017
Gracilianus	30 - 45	1,800	1,696.8	Olifiers et al., 2004; Pires et al., 2010
Monodelphis	83	1,500	1,551.6	Gordon, 2003; Melo et al., 2017
Average		2,366.7	1,904.7	

Table 2

Resistance values assigned by experts to feed the resistance model. In columns 1 - 4 individual resistance values are shown and the average in the last column.

Variables	Resistance values				
	1	2	3	4	Average
1. Land use and cover					
a) Water	100	100	70	80	87.5
b) Tropical dry forest	1	10	1	1	3.3
c) Exposed soil	85	80	50	70	71.3
d) Other vegetation (mangrove / evergreen forest)	10	10	1	55	19.0
e) Rural zone	95	90	80	90	88.8
2. Roads (width in meters)					
a) 7 - 8	97	80	50	80	76.8
b) 6 - 7	96	80	50	80	76.5
c) 5 - 6	94	80	45	80	74.8
d) 3.5 - 5	92	80	30	60	65.5
e) 3.5	90	60	30	20	50.0
3. Slope (degrees)					
a) 0 - 5	1	10	1	10	5.5
b) 5 - 15	5	10	1	10	6.5
c) 15 - 30	15	10	1	10	9.0
d) 30 - 65	25	20	1	20	16.5
4. Rivers (categories)					
a) Order 1	85	100	70	-	85.0
b) Order 2	90	100	80	-	90.0
c) Order 3	99	100	90	-	96.3
d) Order 4	100	100	90	-	96.7

All the layers used were standardized to have the same grid cell size and projection (30 m pixel size and UTM13N, respectively), maintaining the same number of columns and rows. The average of individual resistance values assigned by the experts was included in the final cumulative resistance model. All the processes were made using ArcMap 10.3.1 (ESRI).

To define suitable habitat patches for *T. canescens* we used as a criterion the size of the area needed to support a population of 500 individuals of this species. This size has been used as a rule of thumb to define the conditions needed for a population to increase its probability of long-term viability (Jamieson & Allendorf, 2012). To estimate the extent of habitat needed to support such population size we used the middle point (2.6 ind/ha) of the abundance estimates reported for the species (Ceballos, 1990; Kennedy et al., 2013). Thus, the estimated area of habitat needed was 192.3 ha. We used this value to define the minimum size of suitable habitat patches of dry forest for *T. canescens*.

We modelled habitat connectivity by using 2 complementary approaches, the circuit theory and the graph theory through the least cost path. We used Circuitscape v4.0 (McRae & Beier, 2007) to estimate connectivity within the study area. For this, 2 input elements were required for the selection of patches to connect and the resistance surface. As a result, we obtained a displacement probability of *T. canescens* between patches. This analysis was complemented by calculating the least cost paths among habitat patches (LCP; Cost Distance tool in ArcMap 10.3) using graph theory, which allows to find the only route that generates less cost for the displacement

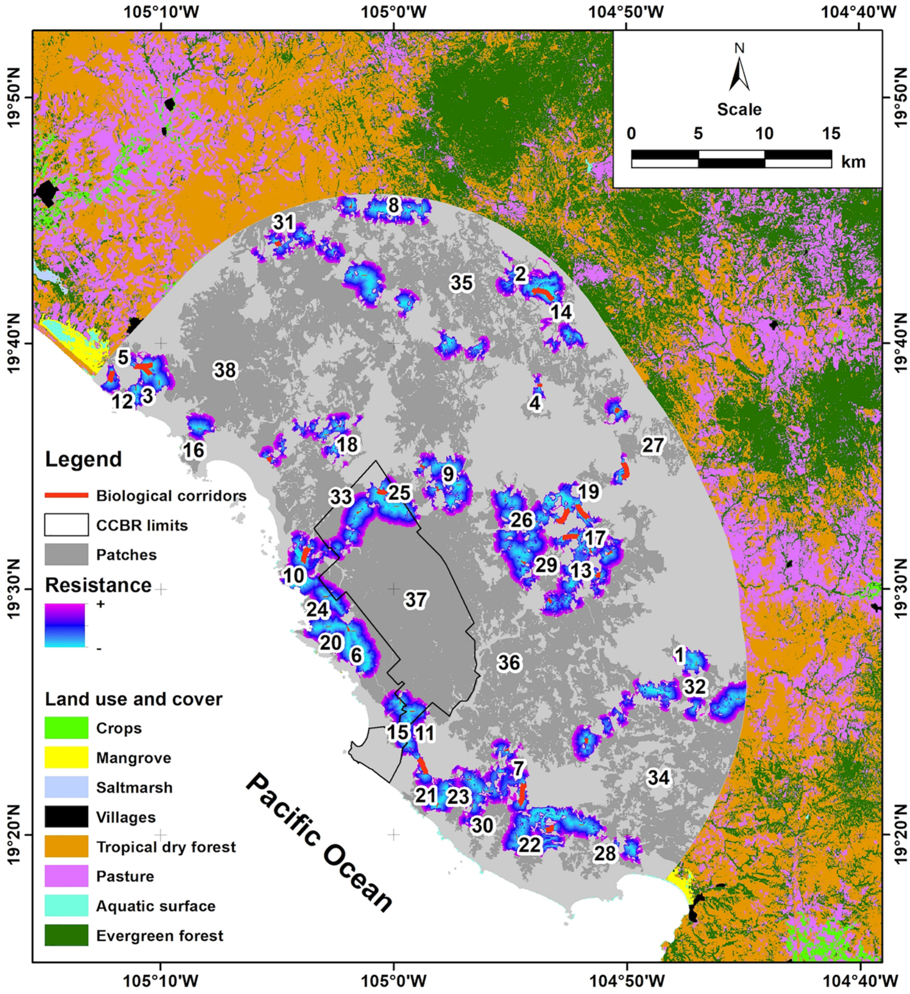

Figure 1. Least cost paths among suitable habitat patches (shown in dark gray) and potential corridors (red lines) for *T. canescens* dispersal. Color gradient shows dispersion resistance. Numbers correspond to suitable patches of tropical dry forest habitat for *T. canescens*. CCBR = Chamela-Cuixmala Biosphere Reserve. Land use and cover beyond the stablished buffer is shown.

of the species. The potential corridors obtained through the LCP were limited by the maximum dispersion distance (MDD) of the focal species. The value of MDD for *T. canescens* was estimated by calculating the average home ranges of closely related species (Bowman et al., 2002; Melo et al., 2017; Table 1). Thus, the maximum length of potential biological corridors was limited to 1,905 m and its width to10 km (corresponding approximately to 4 times the home range of the species).

To assess landscape connectivity, we calculated the Integral Index of Connectivity (IIC) and the Probability of Connectivity (PC) using the software Conefor Sensinode 2.6 (Saura & Torné, 2012). These indices quantify the extent to which landscape connectivity is modified if a particular forest patch is removed (Saura et al., 2011). The application of IIC and PC was evaluated by dIIC and dPC (depending on the selected metric). These node importance indices measure the probability of connectivity loss caused by the removal of a patch from the landscape. dIIC and dPC are composed of the sum of dIICflux + dIICconnector and dpCflux + dPCconnector respectively. dIICflux and dPCflux indicate how well a node is connected to other nodes in the landscape without considering its contribution to intrapopulation connectivity. The dIICconnector and dPCconnector show whether a node contributes to the connectivity between other nodes as a stepping stone. Both, IIC and PC range from 0 to 1, with larger values corresponding to improved connectivity (Saura & Pascual-Hortal, 2007).

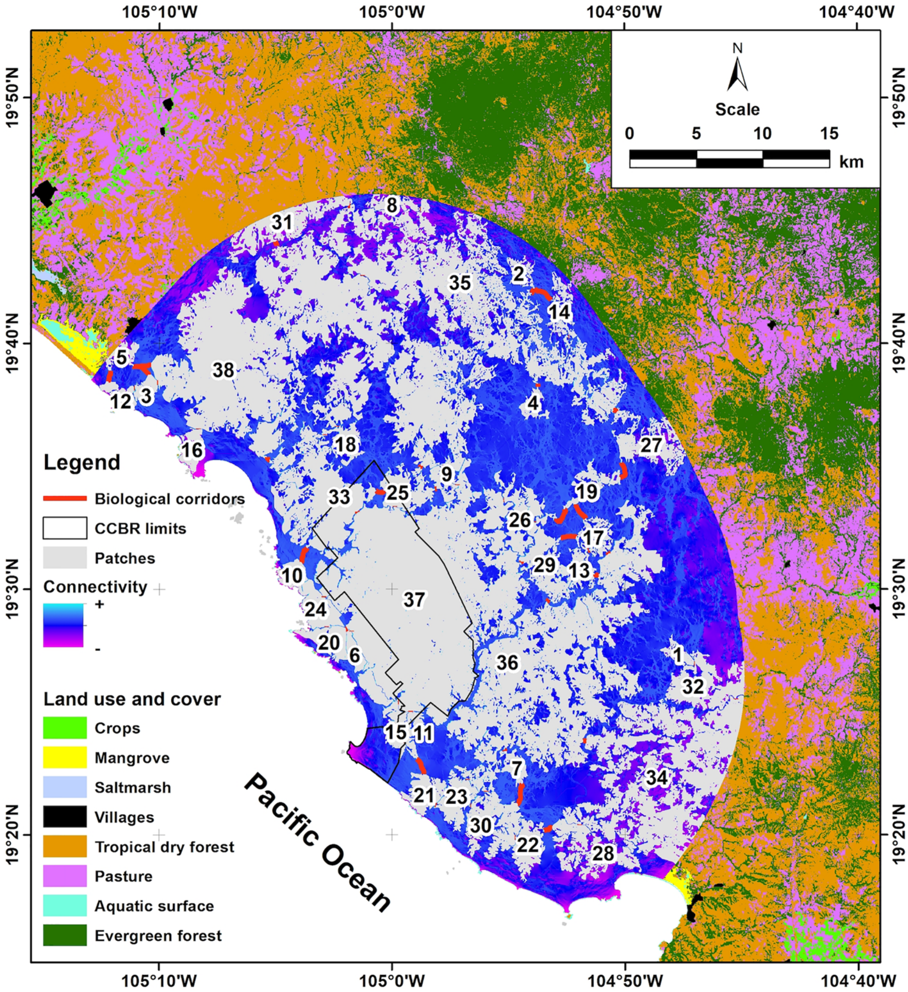

Figure 2. Dispersal probabilities among suitable habitat patches (shown in gray with their corresponding numbers) based on circuit theory for *T. canescens* dispersal and potential corridors (red lines). Color gradient shows the probability of connectivity. CCBR = Chamela-Cuixmala Biosphere Reserve. Land use and cover beyond the stablished buffer is shown.

Results

Tropical dry forest was the dominant vegetation coverage with ~ 95,980 ha (62%) throughout the entire study area. The second largest class was exposed soils with ~ 44,820 ha (28.9%), mainly composed of induced grassland and agricultural lands. Exposed soils were mainly located in the eastern part of the study area, as well as to the north and northeast of the CCBR. Mangrove, riparian vegetation, and evergreen forest were grouped under the category "other types of vegetation" and occupied ~ 9,930 ha (6.4%). Finally, the rest of the categories occupied less than 3% of the study area.

We identified 38 suitable patches of tropical dry forest habitat for *T. canescens* which accounted for a total area of *ca.* 84,100 ha. The smallest patch had 197.5 ha, the largest 18,884 ha and the average size was 2,213.2 ha. The habitat patch 37 had 16,675 ha and contained the largest portion of the CCBR (13,142 ha). Moreover, we identified 60 potential corridors to connect these patches (Fig. 1; Supplementary material: Table S1). The average Euclidean distance among patches was 244.5 m and the average least cost path was 367.5 m. The longest least cost path (1,716 m) connected patches 7 and 30 and required to cross a large expanse of exposed soil. The least connected zone was located at the eastern side of the study area which was characterized by a landscape dominated by forest remnants mixed with agrosystems. In this zone the distance among habitat patches was longer than the MDD of the focal species. We obtained 2 models of current flow connecting suitable habitat patches (Fig. 2). The highest flow probability occurred around the largest patches (36, 37, and 38) and showed a reduction around patches having internal perforations (28, 32, 34, and 35). Overall, the highest flow probability was associated with the presence of the CCBR.

The Integral Index of Connectivity (IIC) and the Probability of Connectivity (PC) are shown in Table S2 (Supplementary material). The highest values of dIIC corresponded to patches 38 (45.5), 37 (44.5), and 36 (29.8) which also had the largest extents of tropical dry forest. Habitat patches 38 and 37 also had the highest values of dIICflux (30.7 and 30.0, respectively) whereas patches 36 and 38 had the largest dIICconnector values. Finally, we found that patches 37, 38 and 36 provided the greatest contribution to patch connectivity (49.0, 49.0, and 33.3) whereas patches 38 and 37 had the largest values of dPCflux (5.3 and 4.1, respectively). The habitat patch 37 had the largest value of dPCconnector (12.4) followed by patches 38 and 36 (8.7 and 8.3, respectively).

Discussion

Despite the fact that the study area is primarily rural and human settlements occupy less than 1% (Flores-Casas & Ortega-Huerta, 2019; Hernández-Guzmán et al., 2019), it is characterized by showing a high level of disturbance due to the conversion of natural areas to agrosystems. The methods used in this study allowed the evaluation of tropical dry forest connectivity among a protected area and their surroundings through the identification of the most important patches and potential corridors for the focal species. The results of our models for *T. cansescens* highlight not only the importance of the maintenance of large patches of suitable habitat but also of some smaller patches that can play a role of stepping stones, favoring connectivity. The region with the best functional connectivity for *T. canescens* was concentrated at the western part of the study area, where the Chamela-Cuixmala Biosphere Reserve (CCBR) is located (patch 37) together with patches 36 and 38. A high connectivity probability was detected among those patches due to their size and their proximity with other patches. However, we did not obtain any potential corridor that directly connected the CCBR with the large patches 36 and 38, partially because the Cuixmala river likely functions as a natural barrier for species displacement. Consequently, intermediate patches, such as 29 and 33, are important for functional connectivity due to their role as stepping stones.

Natural reserves are one of the most important strategies for biodiversity conservation (Bruner et al., 2001; Saura et al., 2019). However, to ensure their effectiveness they require avoid becoming "conservation islands" (Calabrese & Fagan, 2004; Ricketts, 2001). In Mexico, many natural reserves are located in the proximity of growing cities, in regions undergoing intense land cover changes, or near touristic sites. Therefore, fine resolution landscape modelling outside natural reserves, which takes into account the different elements that favor fragmentation and isolation of the natural habitat for different organisms, is essential (Ricketts, 2001; Turchin, 1998; Vandermeer & Carvajal, 2001). This is particularly important for mammals, since 25% of their species are categorized as endangered, and the populations of 52% of known mammals are in decline, including species categorized as "least concern" as a consequence of increased habitat fragmentation and loss (Schipper et al., 2008; Theobald et al., 2012).

Despite the northwestern part of the study area supports larger patches favoring long-distance dispersal of our focal species, there is a potential risk for future connectivity loss. This, due to the fact that primary and several secondary roads are located in that area which can favor the establishment and growth of human settlements (Supplementary material Fig. S1; Decout et al., 2012; Forman & Alexander, 1998). Moreover, an increased traffic in these roads can greatly limit animal dispersal and become an important source of mortality since translocation experiments have shown that small mammals tend to return to their sites of origin, most of the time avoiding crossing roads (Bowne et al., 1999; Delgado-Trejo et al., 2018; Mader, 1984; Merriam et al., 1989).

In contrast to these findings, in the northern part (patches 8, 31, and 35), as well as in the southeastern part of the study area (patches 28, 32 and 34) a higher risk of connectivity loss was shown. This risk exists because there is an ongoing perforation process inside those patches that can lead to fragment size reduction, and thus to landscape fragmentation, increasing the loss and isolation of original habitat. Although this reduction in connectivity may be influenced by the location of the patches in the limits of the established buffer, we think that the effect is minimal due to the fact that the buffer is naturally limited by evergreen forest and large extensions of agricultural fields and pastures for cattle. Likewise, at the eastern part of the study area there is a region with low connectivity and high resistance due to extensive areas for cattle raising and agriculture (e.g., patches 4, 19, and 27). As a result, those isolated patches are under high probabilities of losing connectivity in the short and medium term. Some studies have shown that agrosystems may favor connectivity for some small mammal species, depending on the type of crop, the percentage of coverage they offer and the degree of habitat specialization of the species (Benedek & Sîrbu, 2018; Cruz-Lara et al., 2004; Fahring et al., 2011; Mellink, 1985). However, although some species have been shown to be able to cross areas with unfavorable land use and cover, they may not necessarily inhabit this type of cover, at least not in the long term (Birney et al., 1976; Ruefenacht & Knight, 1995). *Tlacuatzin canescens*, due to its arboreal and low dispersal habits, is likely a species sensitive to habitat modification not able to cross large tracts of unfavorable habitat (Zarza et al., 2003). This could put *T. canescens* and other similar specialists' species inhabiting TDF remnants immersed in agrosystems at risk of local extinction. This effect could be reduced if agrosystems such as corn, coconut, and mango plantations offer enough permeability for the species to disperse. Nevertheless, it is important to take into consideration that providing areas to disperse in the form of corridors or permeable matrices should not be considered as a replacement for the protection of large extensions of primary forest that are needed for the survival of this and other species (Rosenberg et al., 1997). The functional connectivity model we developed could help to guide conservation efforts to benefit not only populations of the study species, but a set of co-distributed populations of small mammals having similar life story attributes and ecological traits as those of *T. canescens* (Supplementary material: Table S3; Ceballos & Miranda, 2000; Wilson & Reeder, 2005).

We acknowledge the lack of empirical evidence to support the construction of surface resistance models for this and many other species of interest, so that the resistance allocation to landscape variables during the functional connectivity modeling was built on the basis of expert knowledge (Foltête, 2018; Wade et al., 2015; Zeller et al., 2011). In addition, the functional connectivity model requires knowledge of the movement patterns of the species of interest. This is challenging since the movement patterns of many small mammal species are unknown, limiting the possibility to have more accurate models (Bowman et al., 2002; Moilanen, 2011; Wikelski et al., 2007). As long as key data on small mammal ecology is missing, we will need to continue relying on indirect methods, as an alternative to deal with the need to support conservation decisions, which are extremely important to maintain wild population of vertebrates and the functioning of ecological systems. We also acknowledge that modifying the size of the buffer the results could change, since connectivity measures based on graph theory require habitat quality thresholds in order to define habitat patches (Moilanen, 2011). However, we consider that the buffer stablished for the analyzes of this study is adequate since it integrates several criteria, such as the dispersal capacity and the historical records of the species, the minimum area to maintain viable populations in similar species, as well as the recommendations on the buffer area that have been suggested to study protected natural areas (Hansen & Defries, 2007; Seiferling et al., 2012). In addition, the buffer used allowed the data to be analyzed with a fine resolution but computationally manageable.

To mitigate the effects of fragmentation, a highly desirable alternative is to maintain the functional connectivity of the landscape by establishing multiple redundant connections between conservation areas (Villers-Ruiz & Trejo-Vázquez, 1998). However, due to conservation constraints an alternative to protect the species is the selection of least cost paths between the protected areas and the patches to be connected. This can provide the basis to plan the purchasing and managing of sites adjacent to conservation areas and to focus efforts of stakeholders (e.g., landowners and the National Commission of Natural Protected Areas, CONANP). Therefore, it is urgent to conduct studies that help to identify priority areas that guarantee maintaining functional connectivity between the protected areas and adjacent patches, as well as promoting alternatives such as live fences and elevated bridges as alternative routes for the dispersal of species.

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