



Modelling jaguar gene flow in fragmented landscapes offers insights into functional population connectivity

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Abstract

Context Preserving functional connectivity is a conservation priority to secure the long-term viability of geographically dispersed subpopulations, such as the jaguar (*Panthera onca*) populations in Central America. However, managing connectivity in this region is limited due to the scarcity of local assessments of the connectivity between existing populations, some

of which exhibit low levels of gene flow and genetic admixture.

Objectives We selected the jaguar as a model species to understand how gene flow of large carnivores is shaped in a heavily human-impacted landscape in the Neotropics. We assessed the impact of landscape features and spatial scale on jaguar gene flow across northern Central America, predicted synoptic, landscape-wide functional connectivity across the region; and compared connectivity predictions based

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on models of gene flow, habitat suitability, and expert knowledge.

Methods We employed genetic data based on 335 faecal samples collected from 72 individual jaguars. We parameterized gene flow resistance surfaces using linear mixed effects models and the maximum likelihood population-effects method. We evaluated nine landscape variables at six spatial scales, selecting the optimal scale and transformation for each variable according to univariate models and AIC. To predict jaguar gene flow, we developed multivariate models and implemented resistant kernels to forecast functional connectivity between jaguar populations across the study region under three dispersal distance scenarios. Furthermore, we compared the connectivity estimates based on gene flow against those based on habitat suitability and the corridors delineated by expert knowledge in the region.

Results Low resistance to jaguar gene flow was associated with greater tree cover and vegetation, lower areas of built-up, and intermediate distances from water bodies. Notably, tree cover affected jaguar gene flow on a smaller scale compared to the rest of variables. Higher connectivity, indicated by lower resistance, was found within and around the largest jaguar conservation units (JCU) such as the Reserva-de-Biosfera-Transfronteriza, Selva-Maya and Maya-Mountains. This contrasted with the smallest JCUs, like Sierra-Santa-Cruz and Sierra-de-las-Minas in eastern Guatemala, and Cordillera-Nombre-de-Dios in Honduras. Across the region, lower connectivity was observed in the Caribbean connection between eastern Guatemala and midwestern Honduras, as well as in the Honduran and Nicaraguan Miskito area. Models based on gene flow and habitat suitability were similar in their predictions of areas of high connectivity; however, the habitat suitability models predicted larger areas of low connectivity than did the gene flow models. Moreover, the expert knowledge corridors were consistent with areas of high and medium connectivity as predicted by the gene flow model.

Conclusions Gene flow of jaguars is positively driven by the presence of forest and water sources, while human impact (built-up and non-vegetation areas) has a negative effect. Areas of lowest resistance largely correspond to the location of JCUs, which serve as crucial reservoirs of high-quality jaguar habitat within the region. While the largest JCU in the

region displayed high connectivity, the low connectivity between the smallest JCUs (i.e. Sierra-Santa-Cruz, Sierra-de-las-Minas and Cordillera-Nombre-de-Dios) underscores the need for conservation attention in these areas. Conservation and management actions such as habitat loss-prevention/restoration and anthropogenic impact mitigation should be prioritized in the binational region of Guatemala-Honduras, a key connectivity bottleneck between the species' northern and southern ranges. Similarly, attention is warranted in the Honduran-Nicaraguan Miskito area.

Keywords Landscape resistance · Resistant kernel · Central America · Large carnivores · Carnivore conservation · Movement corridors

Introduction

Dispersal and gene flow between wildlife populations are the cornerstones for maintaining genetic diversity and ensuring the long-term viability of these populations (Bonte et al. 2012). Preserving the exchange of individuals and genes becomes more important than ever in the Anthropocene, as habitat loss and fragmentation threaten most of the world's vertebrates (Haddad et al. 2015; Tilman et al. 2017; Díaz et al. 2019). In fragmented and degraded landscapes, animals often exhibit altered movement behaviours in response to land cover change and human development (Doherty and Driscoll 2018; Tucker et al. 2018), with consequences that can have cascading effects on populations and increase their extinction risk (Kramer-Schadt et al. 2005; Thatte et al. 2018). Decreased population persistence can occur via direct mortality resulting from unsuitable areas (e.g., anthropogenic barriers; Kramer-Schadt et al. 2004; Schwab and Zandbergen 2011), persecution associated with human-wildlife conflict exacerbation (Vickers et al. 2015), reduced gene flow due to dispersal barriers (Dixon et al. 2007), and ultimately, inbreeding depression and demographic decline (Roelke et al. 1993).

The permeability of landscapes to the movement of animals is defined as connectivity (Taylor et al. 1993). Landscape connectivity is the result of the individuals' response to the landscape structure in terms of movement and survival ability (Tischendorf and Fahrig 2000). The functional aspect of

connectivity can be better understood as successful gene flow occurring across the landscape (Baguette and Van Dyck 2007; Pe'er et al. 2011). Functional connectivity enables populations to adapt to changing conditions, thus its accurate assessment can help inform effective wildlife management strategies (Aufret et al. 2015; Schmidt et al. 2020).

Several models have been developed and adapted to provide insights into the connectivity of populations across various species. These models have been derived either directly from movement data (Richard and Armstrong 2010; Elliot et al. 2014), or indirectly from occurrence data (Mohammadi et al. 2022) or genetic data and associated patterns (Kimmig et al. 2020; Lecis et al. 2022; Portanier et al. 2022). While movement-based models provide detailed information about individuals' real-time movement decisions, they require measuring animal dispersal at relevant spatial and temporal scales (Tesson and Edelaar 2013). Measuring animal dispersal is challenging, particularly for wide-ranging species of conservation concern, such as large carnivores, where studies require extensive spatial scales that can be difficult to implement due to economic and logistical limitations. Alternatively, occurrence data has been used to create habitat suitability models to link landscape structure to animal movement (Mohammadi et al. 2022), whereas genetic data has been utilized to associate landscape structure to gene flow patterns (Holderegger and Wagner 2008). Nonetheless, habitat selection and movement may be impacted by different factors, leading habitat models to potentially underestimate species' movement capabilities through low suitability areas, as well as overlook infrequent dispersal events which can have strong implications for populations' genetic structure and long-term persistence (Mateo-Sánchez et al. 2015). In comparison to occurrence and habitat suitability, genetic data and associated patterns provide further insights, as they reveal more information on how landscapes affect individual movement, dispersal, and breeding over multiple generations (Lowe and Allendorf 2010). Therefore, genetic data and associated analyses present valuable and cost-effective approaches to modelling gene flow and functional connectivity (Zeller et al. 2012; Tesson and Edelaar 2013), shedding light on population processes that cannot be exclusively assessed using movement data alone (e.g., effective population sizes [Ne], bottlenecks, inbreeding [FIS], population

structure, contemporary versus historic genetic isolation; Willi et al. 2022).

Gene flow of several large carnivore populations is negatively impacted by human development, including that of pumas (*Puma concolor*; Ernest et al. 2014) and American black bears (*Ursus americanus*; Cushman and Lewis 2010) in North America, tigers and leopards in India (*Panthera tigris* and *Panthera pardus*; Thatte et al. 2020), Eurasian lynx in Europe (*Lynx*; Bull et al. 2016), and jaguars in Mexico and Brazil (*Panthera onca*; Roques et al. 2016). In this study, we used the jaguar as a model species to investigate how gene flow is shaped in a heavily human-impacted landscape in the Neotropics. We aim to map the anticipated functional connectivity of jaguar populations in northern Central America. The jaguar is an ideal model species for studying functional connectivity due to its large area requirements (Thompson et al. 2021), high level of conservation concern (91% of subpopulations show medium to high threat; de la Torre et al. 2017), and reduced genetic exchange in landscapes heavily influenced by human activities (Roques et al. 2016; Wulsch et al. 2016a). Source jaguar populations (Fig. 1, jaguar conservation units—JCU) and corridors to facilitate their connectivity have been delineated across the species' range with expert input (Rabinowitz and Zeller 2010; Petracca et al. 2018), aiming to improve jaguar population connectivity on a continental scale, however, these corridors are not based on impartial quantitative analyses.

Jaguar populations have shown moderate to high levels of genetic diversity and a lack of strong population structure across most of their range (Eizirik et al. 2001; Ruiz-Garcia et al. 2006; Roques et al. 2014). However, there are small, isolated jaguar populations existing in fragmented areas within the South American range, which currently face bottlenecks, loss of genetic diversity, and heightened genetic differentiation due to pronounced signals of anthropogenic-driven drift (Haag et al. 2010; Lorenzana et al. 2020). Likewise, indications of restricted gene flow and anthropogenic impact, particularly between Guatemala and Honduras, were identified in a previous study (Wulsch et al. 2016a).

We focus this study in northern Central America for three primary reasons. Firstly, this region holds the largest stronghold of jaguars after the Amazon (Rabinowitz and Zeller 2010). Secondly, prime jaguar

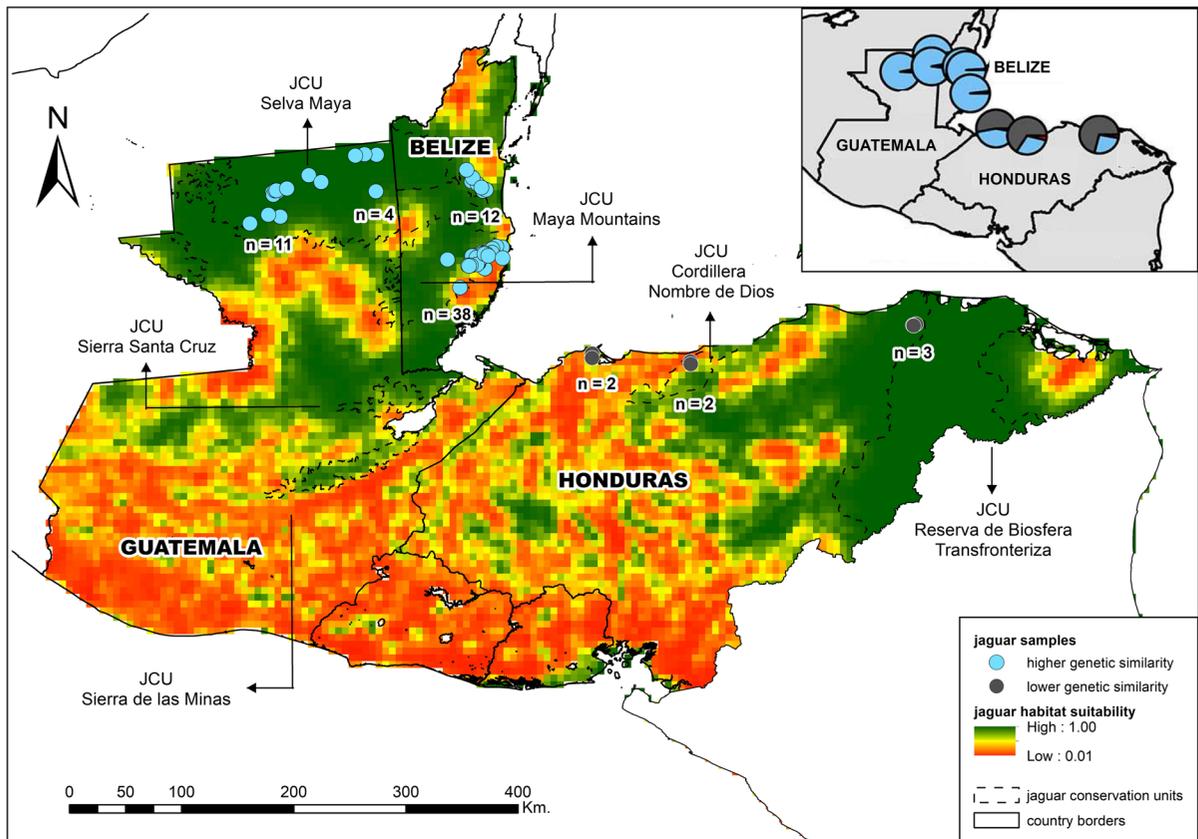


Fig. 1 Study region encompassed by Belize, Guatemala, and Honduras in Central America, showing sampling locations and habitat suitability for jaguars. Main map: location of the collected scat samples (light blue and grey circles), sampling size n (number of individuals) of each sampling group, Jaguar Conservation Units (black dashed borders), and jaguar habitat suitability (areas of high habitat suitability in green, and low suitability in red; Calderón et al. 2022). Insert in right upper corner:

Genetic structure of jaguar populations, as reported by Wultsch et al. (2016a, b), within the study region, illustrating genetic differentiation existing among jaguars from Belize, Guatemala, and Honduras, despite their close geographical proximity. The pie charts represent the genetic clusters corresponding to groups of jaguar individuals studied across sampling sites. The colours within these pie charts represent the proportions of membership for each of these sampled groups

habitat in this region faces serious threats from land use change (Powers and Jetz 2019) and deforestation (Olsoy et al. 2016). And lastly, jaguar populations in this region already exhibit low levels of gene flow and heightened genetic differentiation (Wultsch et al. 2016a). Previous research indicates that while gene flow is high among jaguars in the Selva-Maya (northern Guatemala and central Belize), geographically close jaguar populations in the Selva Maya and Honduras display differences in genetic structure (Wultsch et al. 2016a). Therefore, it is likely that jaguar gene flow may be impacted not only by geographic distance but also by the dynamic landscape changes experienced across the region.

To our knowledge, this is the first study to assess jaguar functional connectivity using empirical data at a regional extent. Previous research in the region has been based solely on literature or local/expert input, either to assess structural connectivity at a large regional scale (Rabinowitz and Zeller 2010; Petracca et al. 2018), or functional (de la Torre et al. 2017) and habitat connectivity (Menchaca et al. 2019) at small, local scales. Furthermore, the present research has the overarching goal to respond to regional jaguar conservation priorities, by “genetic ground-truthing” (assess functional connectivity) of dispersal corridors for jaguars, to improve and maintain population interconnectedness, particularly in northern Central

America (Wultsch et al. 2016a; de la Torre et al. 2017). Here, we determine jaguar gene flow using microsatellite data and address four main objectives: (i) identify landscape variables that facilitate or hinder gene flow between jaguar populations in northern Central America, (ii) assess functional connectivity of jaguar populations in the study landscape, (iii) compare spatial predictions of functional connectivity based on gene flow versus expert input (Rabinowitz and Zeller 2010; Petracca et al. 2018) and jaguar habitat suitability data (Calderón et al. 2022); and (iv) identify priority areas for corridor planning that promote genetic exchange among Central American jaguar populations.

We hypothesized that jaguar gene flow would be positively influenced by the availability of shelter habitat (i.e. sites for resting, nursing, protection from humans, and cover for ambush hunting), such as forest cover and water sources (de la Torre and Rivero 2019; Nuñez-Perez and Miller 2019), as well as areas with high net primary productivity (as a proxy for prey biomass). Conversely, we anticipated that gene flow would be negatively impacted by high elevation, extensive human development, areas devoid of vegetation (non-vegetation zones) and the presence of roads (Haag et al. 2010; Valdez et al. 2015; Kantek et al. 2021; Thompson et al. 2021).

Methods

Study area

Central America is a biodiversity hotspot (Myers et al. 2000), serves as the primary stronghold for jaguar populations following the Amazon (trinational ‘Selva-Maya’), and connects the two largest jaguar populations in the region (‘Selva-Maya’ and ‘Reserva-Biosfera-Transfronteriza’; Fig. 1). This region is characterized by a highly diverse pattern of land uses and a notably higher mean human density of 94 ind./km² compared to other Latin American countries, (World Bank 2020). The landscape predominantly consists of broadleaved evergreen and deciduous trees (61%) along with a mosaic of natural vegetation with croplands (21%). The remaining land uses encompass a diverse mix, including croplands (6%), secondary growth forests (4%), grasslands (3%), wetlands (1%) and urban areas (0.5%, ESA 2015). Due to land use

change, Central America holds the highest predicted loss of suitable vertebrate’s habitat in the continent (Powers and Jetz 2019), and the highest deforestation rates and the forest degradation worldwide proportionally (Redo et al. 2012). We focus our study on northern Central America, specifically Belize, Guatemala, and Honduras (Fig. 1).

Genetic data and measures

We worked with a dataset of 335 jaguar faecal samples that had been previously collected across northern Central America during the period of 2003–2012 (Wultsch et al. 2016a), timespan within a generation length in our region (Harmsen et al. 2017). Sampling sites were predominantly located in lowland regions characterized by subtropical and tropical climates and a diverse range of land cover types within Belize, Guatemala, and Honduras. The samples were opportunistically collected in the field (Fig. 1) and genotyped using 12 microsatellite loci (Wultsch et al. 2016a, b; Menchaca et al. 2019; Appendix S1). Seventy-two jaguar individuals were identified, comprising 59 males, 3 females, and 10 individuals with unknown sex. Population genetic summary statistics (Appendix S2), gene flow and genetic structure assessments for these sites were published by Wultsch et al. (2016a, b). To assess genetic differentiation between jaguar populations across northern Central America, we calculated pairwise genetic distances based on Factorial Correspondence Analysis (FCA; She et al. 1987) in two steps. First, we performed FCA on a multi-contingency table of the microsatellite genotypes with the software GENETIX v. 4.05.2 (Belkhir et al. 2001). Second, we generated a distance matrix by computing Euclidean distances between the first two FCA axes (the only significant) using the R package ‘ecodist’ v.2.0.9 (Goslee and Urban 2007).

Landscape covariates, resistance surface generation

We selected nine environmental and anthropogenic covariates that influence jaguar habitat use, density, movement, and potentially gene flow (Jędrzejewski et al. 2018; Thompson et al. 2021; Calderón et al. 2022). These covariates include distance from water bodies, distance from rivers, distance from roads, elevation, ruggedness, net primary productivity, percentage of built-up, percentage of non-vegetation, and

percentage of tree cover (Table S3). We projected all datasets to the Universal Transverse Mercator coordinate system (EPSG: 32,616) and resampled to a 1000 m resolution.

We modelled genetic distances between individuals as a function of resistance and Euclidean distance by following the method provided by Zeller et al. 2023 (Fig. 2, Appendix S4): We first assessed the scale of effect of each of our variables (Jackson and Fahrig 2015; Mcgarigal et al. 2016) on jaguar gene flow, given that gene flow processes and functional connectivity are dependent on spatial scale (Cushman and Landguth 2010; Cushman et al. 2016). To identify the optimal scale for each variable, we smoothed

each variable raster using a Gaussian kernel and varied its bandwidth across six scales: 1000 m; 3000 m; 6000 m; 8000 m; 16,000 m; 32,000 m. At each scale, landscape variables were transformed into a gene flow resistance surface hypothesis, converting the values of the raw variables into resistance values using seven transformational forms using fixed values (Fig. 2a; Appendix S5), namely linear, monomolecular convex and monomolecular concave functions, in both their positive and negative forms, as well as the inverse Ricker transformation (Peterman 2018). Lastly, resistance surfaces were re-scaled from 1 to 100 using the raster calculator in ArcGIS 10.8. (ESRI 2022).

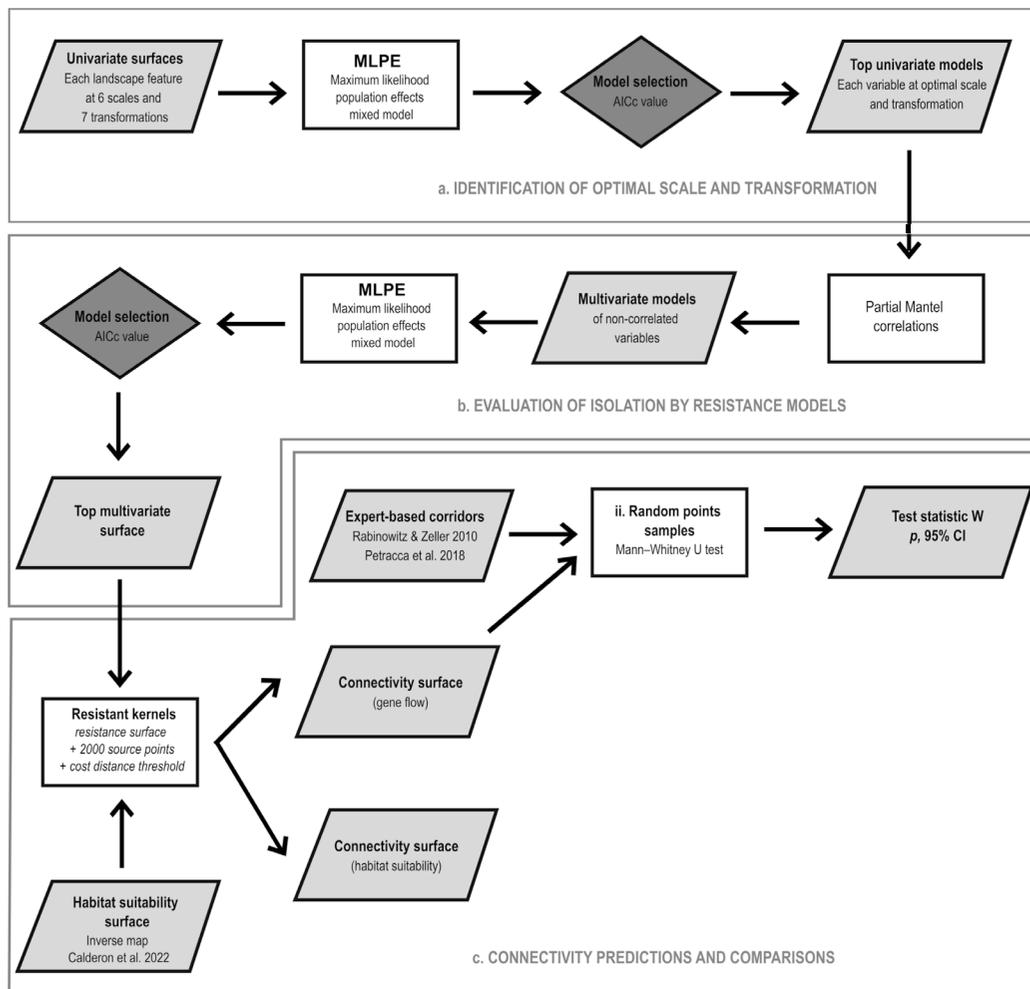


Fig. 2 Conceptual flow diagram for analysis of jaguar gene flow and functional connectivity in northern Central America. For details on the methods, refer to Appendix S4

To optimize landscape resistance values and evaluate how landscape features affect jaguar gene flow in our study region, we evaluated scenarios of isolation by distance (IBD; Wright 1942) and isolation by resistance (IBR; McRae 2006; Peterman et al. 2014). To this end, we identified the optimal scale and transformation for each covariate by running univariate models across all scales and transformational forms. We evaluated these models using Akaike's Information Criterion corrected for small sample sizes AIC_c (Burnham and Anderson 2002) and retained the model with the lowest AIC_c value for each covariate (Fig. 2a). We then combined all non-correlated covariates at their optimal scale and transformation to create all plausible multi-variable, multi-scale models of resistance. Correlations among predictors were assessed by running partial Mantel correlations between the covariates' resistance distance matrices using the 'vegan' R-package v.2.6-2 (Oksanen et al. 2022). Non-correlated covariates (Pearson's moment correlation; $|r| < 0.6$) at their optimal scale and transformation were combined to create multi-variable, multi-scale models of resistance (Fig. 2b, Table S8). For these multivariate models, we summed all variables in each model to create a single composite resistance surface across which resistance distances were calculated (i.e. for each multivariate model there is one composite resistance surface). We did so because animals do not experience elements separately while moving through a landscape, thus composite surfaces better reflect animal's responses to aggregated landscapes (Peterman and Pope 2021). All composite surfaces were rescaled from 1 to 100. Functional connectivity of jaguar populations was assessed using cumulative resistant kernels (Compton et al. 2007), a synoptic modelling approach that predicts and maps expected functional connectivity as a continuous surface, accounting for species' dispersal abilities (Fig. 2c). Resistant kernels were calculated using source locations obtained by sampling the top resistance surface with the 'spatially balanced point tool' in ArcGIS v.10.8.0 (ESRI 2022). We applied this last step to the connectivity surfaces based on gene flow, and for comparison, to a recently developed habitat suitability model (Calderon et al. 2022). Given the lack of information on dispersal distances of jaguars in Central America, we developed three connectivity scenarios based on estimates of dispersal distances of females (75 km; Bernal-Escobar et al. 2015), males

(250 km; Bernal-Escobar et al. 2015; Wultsch et al. 2016b), as well as the maximum average dispersal distance based on Sutherland et al. (2000) and the average body size reported for male jaguars in Central America (90 km. for an average weight of 56 kg; Aranda 1992; de la Torre and Rivero 2017; Nuñez-Perez and Miller 2019). For further details on the methods, refer to Appendix S4.

Lastly, we compared the connectivity predictions obtained using our genetic model (this study) with two other models: (i) the habitat suitability model described earlier (raster data; Calderón et al. 2022), and (ii) the model derived from expert input (vector data; Rabinowitz and Zeller 2010; Petracca et al. 2018). For the first comparison, we calculated the difference between the inverse habitat suitability-based (i.e. 1—Habitat Suitability) and gene flow-based connectivity surfaces with the 'raster calculator' in ArcGIS v.10.8.0 (ESRI 2022). For the second comparison, we used our gene flow connectivity surface (this study) and compared the values of 200 randomly selected points located within the expert-based corridors (Rabinowitz and Zeller 2010; Petracca et al. 2018) with 1,701 randomly selected points spanning the jaguar extent of occurrence within our study region (see Fig S7). We compared these two random samples of gene flow connectivity points using a two-sided Mann–Whitney U test with R package 'stats' v.4.0.4. We expected that the sample from the expert-based corridors would exhibit a higher median connectivity compared to the random sample from across the full extent of our study region.

Results

Landscape resistance and connectivity modelling

Resistance to jaguar gene flow decreased with higher levels of tree cover and primary productivity, while it increased with higher values of built-up areas, non-vegetation, elevation, ruggedness, and proximity to roads and rivers (Fig. S6). Notably, gene flow resistance was lowest at intermediate distances from water bodies, progressively increasing with greater distances from these water sources, and being highest in close proximity to them. Tree cover and ruggedness had the smallest scale of effect for jaguars (16,000 m; Table 1), while the other variables had

Table 1 Best performing univariate resistance models of gene flow for jaguar populations in northern Central America

Variable	Scale (m)	Transformation	AIC	BIC	mR ²	cR ²
Tree cover	16,000	Negative linear	- 1013.09	-983.89	0.68	0.82
Primary productivity	32,000	Negative monomolecular convex	- 1000.48	- 971.27	0.68	0.83
Distance from rivers	32,000	Negative linear	- 856.34	- 827.14	0.64	0.82
Non-vegetation	32,000	Positive monomolecular concave	- 832.08	- 802.88	0.66	0.83
Distance from roads	32,000	Negative monomolecular concave	- 750.48	- 721.27	0.62	0.81
Terrain ruggedness	16,000	Positive monomolecular convex	- 736.98	- 707.78	0.62	0.80
Elevation	32,000	Positive monomolecular convex	- 734.00	- 704.80	0.62	0.81
Distance from water bodies	32,000	Inverse Ricker	- 593.97	- 564.76	0.59	0.79
Built-up area	32,000	Positive linear	- 558.88	- 529.67	0.53	0.80
Euclidean distance (IBD)	NA	NA	- 146.13	- 122.76	0.26	0.63

Values for the variables' scale of effect, AIC_c, BIC, and marginal and conditional R² values are reported for each model. Variables highlighted bold were included in the best performing composite resistance surfaces

a scale of effect of 32,000 m. All univariate models outperformed the model of isolation by distance (IBD; Euclidean distance).

All competitive resistance surfaces (i.e. within $\Delta 4$ AIC) included tree cover and built-up area. The top composite resistance surface additionally included distance from water bodies and non-vegetation (AIC_c = - 1084.168, BIC = - 1054.961) and explained 83% of the variance observed in the genetic differences between individuals (mR² = 0.69, cR² = 0.83; Table 2; complete model list in Appendix S6; results of Partial Mantel tests in Table S7). Therefore, we proceed to describe and discuss the results derived from this top model.

Lower resistance was found within and around the largest JCU in the region (i.e. Reserva-de-Biosfera-Transfronteriza), in comparison to the smallest JCUs (i.e. eastern-Guatemala: Sierra-Santa-Cruz and Sierra-de-las-Minas; and Honduras:

Cordillera-Nombre-de-Dios; Fig. 1a, 3). Across all dispersal distance scenarios (Fig. 1b–d, 3), connectivity was highest around the JCU Reserva-de-Biosfera-Transfronteriza, lower along the Caribbean edge of the Honduran-Nicaraguan Miskito region (northeastern border of Honduras and Nicaragua); and lowest across all the Pacific area in the south of the study region. Only in the 250 km scenario, high connectivity expanded from the Reserva-de-Biosfera-Transfronteriza towards the Caribbean coast between eastern Guatemala and midwestern Honduras (Fig. 1d, 3).

The resistance and kernel connectivity surfaces obtained from the inverse of the jaguar habitat suitability map showed lowest resistance (Fig. 2a, 3) and higher connectivity in the east of the study region across all dispersal distance scenarios (Fig. 2a–d, 3). Predictors indicated very limited connectivity for most areas in western Honduras as well as eastern and central Guatemala. The highest

Table 2 Top-ten multivariate resistance models of gene flow for jaguar populations in northern Central America, including the isolation by distance model for reference (IBD)

No	Model	AICc	BIC	mR ²	cR ²
1	Distance from water bodies + tree cover + built-up area + non-vegetation	- 1084.17	- 1054.96	0.69	0.83
2	Distance from water bodies + tree cover + built-up area	- 1083.40	- 1054.19	0.69	0.83
3	Tree cover + built-up area + non-vegetation	- 1080.16	- 1050.95	0.70	0.84
4	Tree cover + built-up area	- 1080.04	- 1050.83	0.70	0.84
5	Distance from rivers + tree cover	- 1065.78	- 1036.57	0.69	0.83
53	IBD (Euclidean distance)	- 146.13	- 122.76	0.26	0.63

Values for AICc, BIC, and marginal and conditional R² are reported for each model. The top model is highlighted in bold

connectivity was primarily predicted in eastern Honduras and northeastern Nicaragua, and to a lesser degree between Guatemala and Belize; these areas encompass the three largest JCUs in the region (i.e. Reserva-de-Biosfera-Transfronteriza, Selva-Maya and Maya-Mountains).

Comparison of spatial predictions of functional connectivity: gene flow vs habitat suitability vs expert input

Overall, the gene flow model displayed more distinct movement pathways throughout the region and across all dispersal scenarios, even in areas of lower predicted connectivity, such as eastern Guatemala and western Honduras. Across various dispersal scenarios, there was consistency between the gene flow and habitat suitability-based connectivity predictions around the largest JCU in the region (i.e. Reserva-de-Biosfera-Transfronteriza), as well as some areas in Guatemala and Belize (i.e. Selva-Maya and Maya-Mountains; Fig. 4a–c: turquoise areas). However, the habitat suitability-based model predicted much lower levels of connectivity in comparison to gene flow (Fig. 4a–c: blue areas) across dispersal scenarios and across the study region, particularly outside JCUs and within the region between Guatemala and Honduras. In the latter case, the habitat suitability data alone did not reveal clear connectivity pathways. Lastly, the habitat suitability model predicted higher connectivity than gene flow along the Caribbean edge of the Honduran-Nicaraguan Miskito, in Guatemala's Lacandon region, the northern tip of Belize, and central Honduras (Fig. 4a–c: green areas).

Connectivity values within the corridors for jaguar movement delineated based on expert knowledge (Rabinowitz and Zeller 2010; Petracca et al. 2018) were significantly higher than those calculated across the jaguar range in the study region across all dispersal scenarios ($W_{75\text{km}}=170,538$, $P_{75\text{km}}=0.039$; $W_{90\text{km}}=173,216$, $P_{90\text{km}}=0.014$; $W_{250\text{km}}=191,685$, $P_{250\text{km}}<0.0001$), evidencing that expert-based corridors are located within the areas with higher predicted gene flow and connectivity (Fig. 3). However, our genetic model revealed alternative areas of connectivity, which are not included in the expert-based corridor delineation. Specifically, in the region between Honduras and Guatemala, our genetic model identified higher gene flow-based connectivity

extending south of the expert-based corridor along the Caribbean Coast between these two countries.

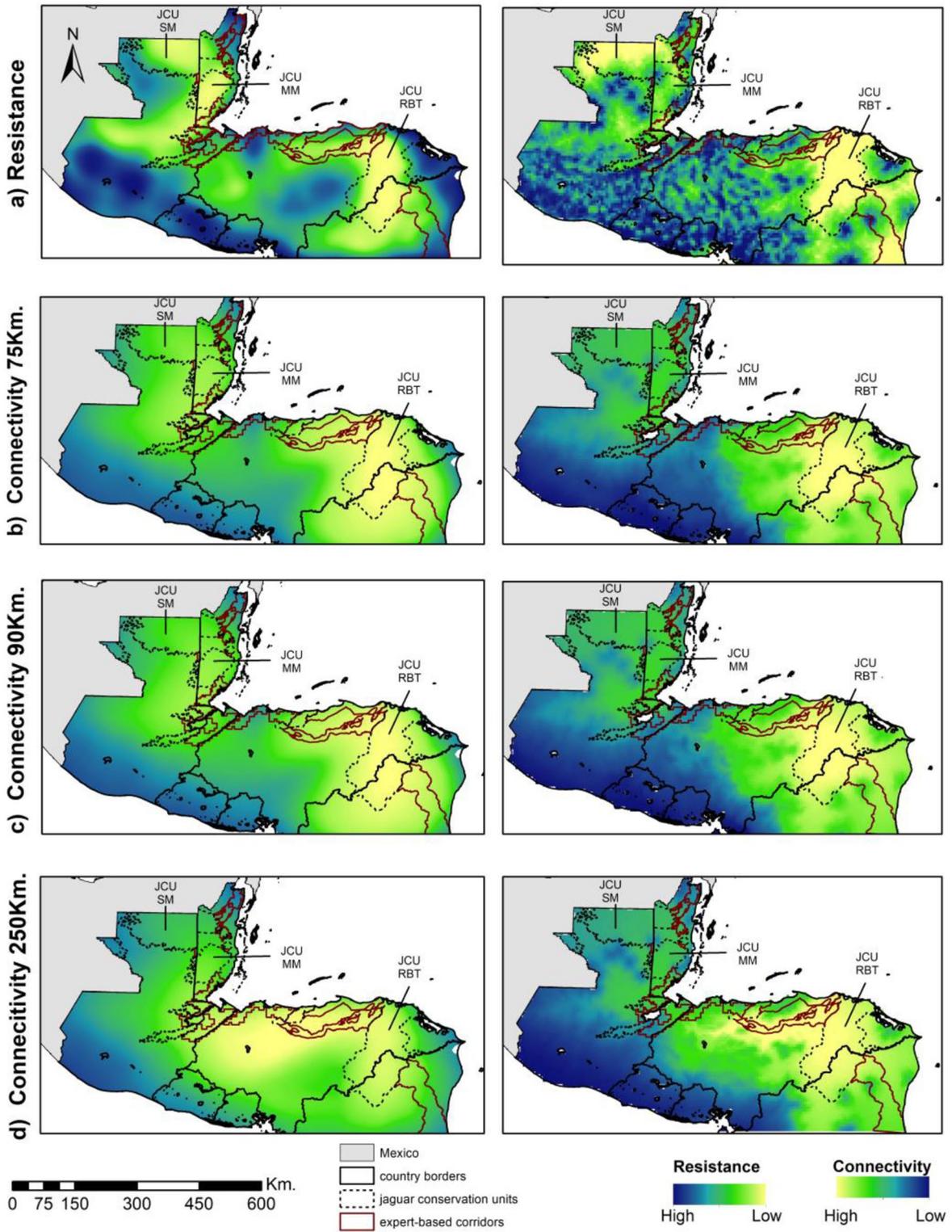
Discussion

Utilizing recent advancements in resistance surface estimation and conducting genetic sampling across international boundaries, our study stands as the first to model jaguar gene flow and connectivity across a large, heterogeneous, regional extent of conservation concern in Central America. Our top gene flow resistance model predicted lowest resistance in areas with higher tree cover and vegetation, lower built-up areas, and intermediate distances from water sources. These areas of lowest resistance closely align with the locations of the JCUs, which constitute the main reservoirs of high-quality jaguar habitat in the region (Calderón et al. 2022). Tree cover exhibited a smaller scale effect on jaguar gene flow in comparison to the other variables. This might imply that tree cover may be mediating gene flow most strongly through local breeding or short-distance dispersal (as exhibited by philopatric female jaguars; Kantek et al. 2021), while built-up areas, non-vegetation, and water sources may play a role in long-distance dispersal. Similar findings have been reported for cougars in North America (Zeller et al. 2023).

Jaguar gene flow appears to be primarily driven by availability of shelter habitat. However, the high resistance posed by built-up and non-vegetation areas to gene flow may also encompass the effects of direct human-jaguar interactions that are prevalent in anthropogenic landscapes. In such landscapes, jaguar populations exhibit lower levels of gene flow (Roques et al. 2016) and increased human-caused mortality due to human-related causes, including hunting (Jędrzejewski et al. 2017a, b; Arias et al. 2021), vehicle collisions (Srbek-Araujo et al. 2015), and retaliatory killing (Garcia-Alaniz et al. 2010; Moreno et al. 2015; Jędrzejewski et al. 2017a, b); the latter being a significant driver of jaguar extirpation (Jędrzejewski et al. 2017a, b; Villalva and Palomares 2022). The impact of human-caused mortality on population viability can be significantly large, especially when it disproportionately affects important demographic groups (i.e. juveniles), and when limited connectivity restricts demographic rescue (Lamb et al. 2020). Therefore, securing connectivity between jaguar

1. GENE FLOW

2. HABITAT SUITABILITY



◀**Fig. 3** Resistance (a) and functional population connectivity surfaces based on dispersal distance scenarios (b–d) for jaguars in northern Central America obtained using genetic data (1. Gene flow) and habitat use data based on the inverse of the habitat suitability map of Calderón et al. 2022 (2. Habitat suitability). Red polygons depict expert-based delineated corridors proposed by Petracca et al. (2018) and Rabinowitz and Zeller (2010). Text labels represent the following JCU: Selva Maya (SM), Maya Mountains (MM), Reserva de Biosfera Transfronteriza (RBT)

populations in anthropogenic landscapes is currently a pivotal conservation priority for the populations' long-term viability (de la Torre et al. 2016).

Our model-based predictions across all dispersal scenarios showed similar general patterns and produced plausible scenarios of jaguar population connectivity. Nevertheless, we believe that those based on 75 km and 90 km dispersal distances are the most plausible for our study region, as they were most consistent with the current extent of jaguar occurrence (Quigley et al. 2017) and with previous studies focused on landscape connectivity and gene flow within our study area (Wultsch et al. 2016a; Petracca et al. 2018). Accordingly, we believe the results from the 75 km and 90 km dispersal distance scenarios are robust enough to inform current conservation efforts, and we refer specifically to these scenarios from here on unless otherwise stated.

Functional connectivity for jaguar populations was found to be concentrated within and around the JCUs in the region, decreasing further from these areas, which is likely caused by the high concentration of source points selected in those regions of high habitat quality. The highest connectivity was observed along and around the biggest JCU (i.e. Reserva-Transfronteriza in Nicaragua; Fig. 1), followed by the next largest JCUs in Belize and northern Guatemala (i.e. Selva-Maya and Maya-Mountains). These findings support previous research on jaguar genetic diversity and population structure in the region (Wultsch et al. 2016a). Areas of lower population connectivity were predicted along the Caribbean coast between Guatemala and Honduras, as well as in the Honduran-Nicaraguan Miskito region. The former area is consistent with high human development and forest loss (Aide et al. 2013; Olsoy et al. 2016), high loss of suitable jaguar habitat (Calderón et al. 2022), extremely low jaguar occurrence (Hoskins et al. 2018), and jaguar populations exhibiting low levels of genetic diversity

(Wultsch et al. 2016a). Similarly, the Honduran-Nicaraguan Miskito region has also undergone habitat degradation (Mora et al. 2016), resulting in low densities of jaguars (Gonthier and Castañeda 2013) and high levels of retaliatory killing of jaguars due to cattle predation (Chinchilla et al. 2022). Our findings in the Miskito area are further supported by previous studies of landscape connectivity based on camera trap records in the region (Hernández Potosme 2019).

Our study builds upon previous connectivity assessments in the region in two significant ways. First, it employs a rigorous statistical modelling approach that explicitly takes into account the spatial scale dependence in jaguar-landscape interactions. This approach enables us to identify the appropriate functional scale for each landscape predictor studied. This step often overlooked, is critical as it ensures robust inference and improves the effectiveness of management inputs that support habitat and population connectivity efforts on the ground (Jackson and Fahrig 2015; Krishnamurthy et al. 2016). Second, we provide spatially explicit, synoptic connectivity maps for jaguar populations in the region, accounting for the species' dispersal ability.

We believe that our model-based predictions are robust enough to support current and future conservation and management efforts for this species of conservation concern, living in a hotspot of range loss for vertebrate species (Powers and Jetz 2019). However, there are three potential sources of uncertainty that need consideration. First, despite our extensive sampling efforts and research collaborations across Central America, we were unable to obtain samples from the entire extent of jaguar occurrence in our study region. We collected data on 72 individual jaguars primarily from lowland subtropical and tropical areas. Nonetheless, our individual-based approach for analysis (i.e. analysing all individuals within sampling sites instead of a selection of individuals, see: Seaborn et al. 2019) remains a robust method for studying connectivity in mobile species, even when dealing with samples as small as <5 individuals per sampling site (Prunier et al. 2013). Additionally, the microsatellites used in this study exhibited moderate to high polymorphism between populations (Wultsch et al. 2016a), enhancing their ability to detect population differentiation and structure (Pritchard and Rosenberg 1999). Therefore, while our sample

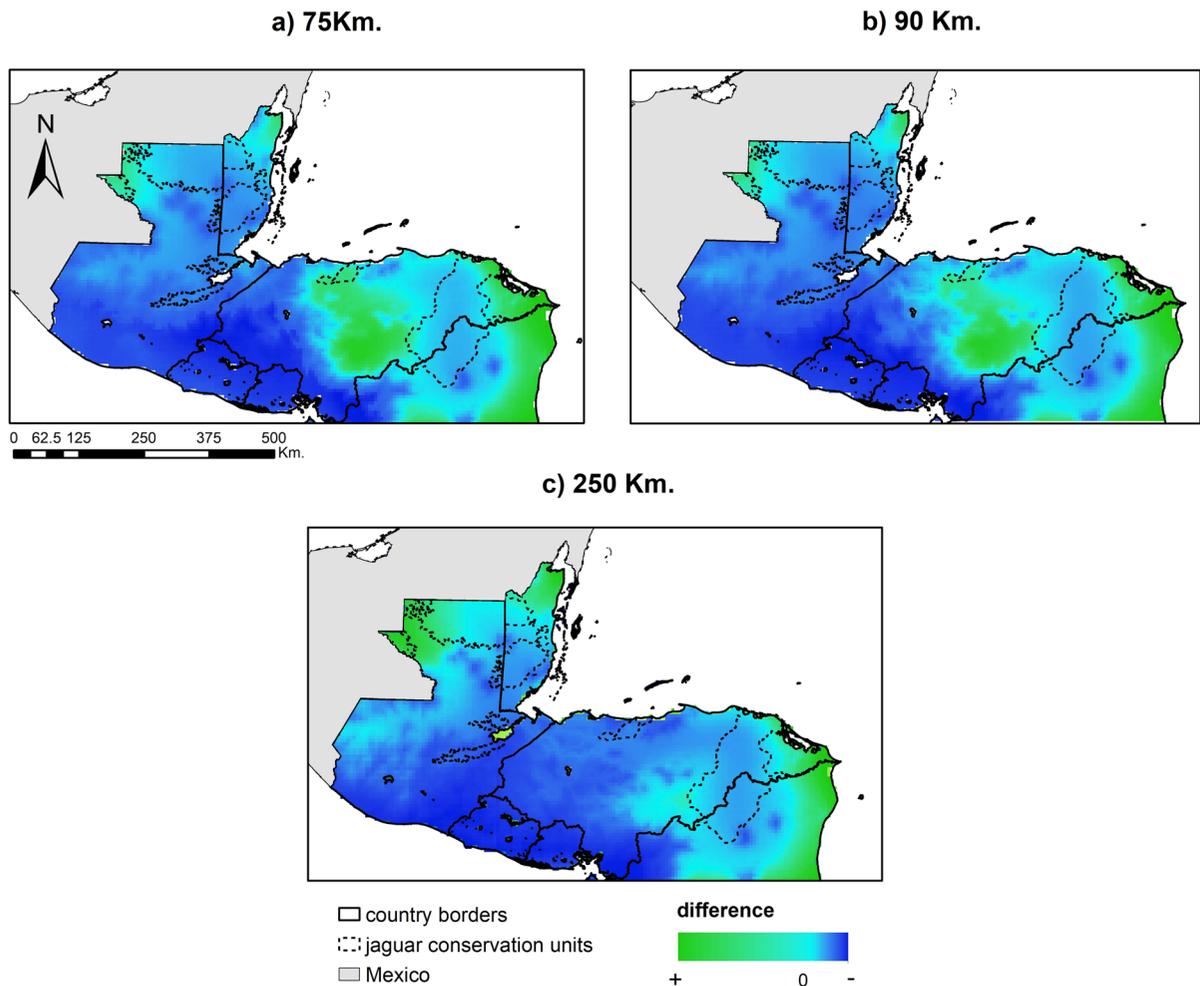


Fig. 4 Difference between jaguar population connectivity estimates based on habitat use versus gene flow across **a** 75 km, **b** 90 km, and **c** 250 km dispersal distance scenarios. Values range from positive, for areas where habitat suitability estimated higher connectivity than gene flow (green), zero

for areas where habitat suitability and gene flow predicted similar connectivity (turquoise), and negative for areas where gene flow predicted higher connectivity than habitat suitability (blue)

size might seem small, it allowed us to effectively examine genetic patterns in jaguar populations within this region. Nevertheless, the genetic differentiation patterns reported here may be influenced by our clustered sampling design and the data gaps in central Guatemala and southern Honduras. Hence, we emphasize the importance of conducting continuous genetic sampling in these areas in the future to provide a more comprehensive understanding of functional connectivity patterns across this region. Second, due to our limited sample size, we were unable to validate our model using

internal cross-validation folds (Row et al. 2017) or using an external dataset. While this prevented us from quantitatively assessing the uncertainty of our model predictions, we are confident that we have addressed most potential sources of uncertainty by: (i) using resistance surfaces that correspond to ecological processes (Peterman et al. 2014) and are parameterized with empirical data (Clevenger et al. 2002; Shirk et al. 2010; Cushman et al. 2013), (ii) using genetic data that focuses solely on movements relevant for populations' viability (i.e. successful breeding), representing the long-term average of

effective dispersal without being limited to observational periods (Spear et al. 2010); (iii) accounting for spatial-scale dependence and species' dispersal ability in the assessment of connectivity; and (iv) considering different scenarios of dispersal distance based on allometric scaling and field data (Sutherland et al. 2000; Bernal-Escobar et al. 2015; Wulsch et al. 2016b). Third, we were also unable to explicitly account for human-caused mortality, a decisive factor impacting gene flow resistance with important implications for functional connectivity. There is scarce data on anthropogenic jaguar mortality across the species range (Altrichter et al. 2006; Jędrzejewski et al. 2017a, b; Romero-Muñoz et al. 2019), especially in Central America (Moreno et al. 2015). We rely on built-up area and tree cover maps to encompass the effects of this anthropogenic-driven mortality in the absence of appropriate data, supported by the fact that jaguar extirpation is mostly driven by anthropogenic activities, such as deforestation, cattle breeding, and retaliatory killing (Jędrzejewski et al. 2017a, b).

We emphasize two key findings arising from the connectivity patterns derived from gene flow, habitat suitability, and expert-input data, which have important implications for guiding future work. First, we highlight that gene flow connectivity differs from habitat connectivity and one may not be used as a proxy for the other (Sartor et al. 2022), since habitats suitable for permanent establishment do not necessarily correspond to those facilitating dispersal (Reding et al. 2013; Mateo-Sánchez et al. 2015; Keeley et al. 2017). Regarding expert input, we found a general alignment between the proposed expert knowledge-based corridors and our gene flow-predicted high and medium connectivity areas. We highlight that empirical data tend to offer more optimal parameterization of environmental variables in comparison to expert input (Clevenger et al. 2002; Shirk et al. 2010; Cushman et al. 2013). However, the expert-input corridors for jaguar movement evaluated in this study have been systematically updated using field data and robust inference methods (Zeller et al. 2011; Petracca et al. 2018) subsequent to their first delineation (Rabinowitz and Zeller 2010). Accordingly, we agree that expert-input, supported by field data and robust statistical methods proves valuable for synthesizing knowledge about complex animal-habitat relationships,

particularly in situations with limited empirical data available.

Our second recommendation for future research is that the effect of landscape covariates on gene flow may be assessed across a wide range of multiple spatial scales (Jackson and Fahrig 2015; Moraga et al. 2019). We found the strongest support for broader scale effects, which varied depending on the type of landscape feature. This is not surprising, as the spatial scales of gene flow are typically much larger than those for abundance or occurrence (Jackson and Fahrig 2014), with the latter two being the usual inputs for habitat suitability models. Future research incorporating spatial-scale dependence across the species' range will yield important management implications for regional jaguar conservation and management. Such studies will provide insights on whether jaguar-landscape interactions are dependent on the environmental context (see Jackson and Fahrig 2015) or whether they can be generally applied to management actions across the entire geographical range of the species.

Conservation implications

Our jaguar model highlights key areas for population connectivity, while informing concrete conservation actions for securing the long-term persistence of the species in the region. Among the highlighted areas, the binational area between Guatemala-Honduras as well as the Miskito region may be considered a priority for management actions. The former region, identified as having low connectivity by both the habitat suitability and expert-based models, not only holds the smallest JCU in the region but also serves as a critical connection point between jaguar populations from North America and the rest of the continent. In the short and medium terms, maintaining jaguar genetic connectivity in this region could involve preventing habitat loss and degradation and implementing restoration efforts, along with mitigating anthropogenic impacts. One approach to achieving these goals is the adoption of sustainable land management practices compatible with jaguar conservation, such as community managed reserves (Mena et al. 2020) or forestry concessions (Tobler et al. 2018) in the buffer zones of the JCUs. This would be especially useful for the smallest JCUs in eastern

Guatemala and Honduras, preventing the loss of the last jaguar source populations in this area. Similarly, this strategy would apply to the Miskito Caribbean slope, avoiding the expansion of habitat degradation towards the region's largest JCU, the Reserva-de-Biosfera-Transfronteriza. Additionally, to reduce habitat loss between Honduras and Guatemala, there is a significant opportunity for governments, projects, and organizations to support community-based initiatives that seek to officially declare watersheds and corridors in this binational area. Furthermore, mitigation of anthropogenic pressure could be achieved by two key actions: (a) the implementation of integral wildlife-human coexistence approaches (e.g. König et al. 2020) that promote jaguar-human coexistence and minimize jaguar anthropogenic mortality; and (b) fostering deeper engagement of local communities in conservation goals through community-based projects (e.g. community monitoring; Valsecchi et al. 2022) that promote the social acceptance of conservation efforts (e.g. inclusive participation and decision-making in conservation solutions; Volski et al. 2021). In the long term, however, achieving effective carnivore conservation in this region of increasing human development will require the implementation of holistic conservation approaches, grounded not only in wildlife-human coexistence principles and participatory bottom-up approaches but also in socio-environmental justice for the local communities inhabiting these landscapes (Büscher and Fletcher 2020; Toncheva et al. 2022).

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Data availability In the Supplementary information we provide the microsatellite data (Table S1) as well as a sample code of our core analysis for running the Maximum likelihood population effects mixed model (Appendix S9).

Declarations

Competing interests The authors declare no competing interests.

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