





Landscape genetics outperforms habitat suitability in predicting landscape resistance for congeneric cat species

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Funding information

Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 454551/2014-2 and 424361/2016-7; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: 001; Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul

Handling Editor: Thais Guedes

Abstract

Aim: The use of landscape resistance maps to model connectivity has become an indispensable tool for species conservation. However, different methods can be used to estimate landscape resistance, but there is no consensus on which is the most reliable one. Therefore, comparing the performance of those methods in predicting resistance can be quite useful to understand their limitations and conservation implications. Our goal was to evaluate the accuracy of two commonly used approaches, habitat suitability modelling and landscape genetics, in estimating landscape resistance to genetic connectivity of two species of Neotropical cats (*Leopardus guttulus* and *L. geoffroyi*) across their ranges.

Location: South America.

Taxon: Felidae—*L. guttulus* and *L. geoffroyi*.

Methods: For both species, we optimized a landscape genetics resistance surface using a restricted multivariate optimization approach and transformed a habitat suitability map into a resistance layer. We compared landscape resistance models created by these two approaches based on the models' Akaike information criterion scores and evaluated the similarities and differences in their predictions by calculating the correlation between the resistance layers and generating difference maps.

Results: The genetic approach greatly outperformed the habitat suitability approach in explaining movement driving gene flow for both species. For the studied species, habitat preference and genetic connectivity are influenced by different landscape features. Habitat alteration imposes great resistance for genetic connectivity, and the presence of natural vegetation remnants within altered environments is essential for their conservation.

Main conclusions: For the studied species, the transformation of habitat suitability models into resistance surfaces is a poor proxy for permeability to dispersal, and the use of genetic data is more reliable in modelling connectivity for species conservation. Habitat suitability and landscape resistance are not equivalent or even proportional for these species.

KEYWORDS

carnivores, connectivity, *Leopardus geoffroyi*, *Leopardus guttulus*, microsatellite, multispecies



1 | INTRODUCTION

The long-term survival of many species depends on the protection of natural areas that support viable populations, and also on the maintenance of ecological corridors that provide connectivity among local subpopulations (Cushman et al., 2013; Haddad et al., 2015). Population size and connectivity are both essential elements for providing sufficient gene flow to prevent loss of genetic diversity. Without gene flow, populations become isolated and more susceptible to inbreeding and genetic drift, which can increase population extinction probability (Frankham et al., 2010). Therefore, techniques that predict population dynamics and connectivity are critical tools for both ecological research and conservation applications.

Connectivity modelling studies are usually based on landscape resistance maps, which represent the cost of movement experienced by an organism when going from one point in the landscape to another (Cushman et al., 2013; Zeller et al., 2012). Despite its common usage, there is no consensus on which methods are most reliable in assigning resistance values to a landscape (Spear et al., 2010; Zeller et al., 2012). The incorrect identification of landscape resistance can mask the true influence of landscape features on species movement, leading to ineffective conservation actions (e.g. Cushman et al., 2014). In this context, comparing different approaches to derive the most accurate landscape resistance surface is important yet rarely performed (Peterman et al., 2019). As gene flow represents not only dispersal movement patterns but also whether there is successful dispersal that has resulted in reproduction over time (Zeller et al., 2018), it can be a good measure of landscape connectivity to be used to compare the performance of these approaches.

One of the most common methods to estimate landscape resistance uses habitat suitability to derive resistance values, typically based on some form of inverse relationship. Since detection data are often the only empirical data available for many species and can be used for developing habitat suitability models, this approach has been broadly used to develop resistance surfaces (e.g. Macdonald et al., 2018; Mateo-Sánchez et al., 2014; Wan et al., 2019). This approach is based on the notion that animals select dispersal movement paths based on the same features that they use to select habitat. If this assumption is correct, habitat suitability would be the inverse of landscape resistance (i.e. areas with high habitat suitability would have low resistance to dispersal movement and gene flow; Beier et al., 2008; Chetkiewicz et al., 2006). However, some studies have shown that habitat suitability is often not a good proxy for resistance to movement driving gene flow. For example, for American martens, brown bears and Bengal tigers, it was demonstrated that factors that determine occurrence are different from those that affect gene flow (Mateo-Sánchez et al., 2015a; Reddy et al., 2017; Wasserman et al., 2010, 2012). Zeller et al. (2018), however, compared habitat-based approaches for estimating landscape resistance with landscape genetics and movement models based on GPS telemetry data for pumas and found that all three approaches selected the same variables and produced similar resistance surfaces, but different predictions of landscape connectivity.

This inconsistency of results between habitat-based and genetics-based resistance surfaces is less surprising when one considers that they represent different processes and are not necessarily influenced by the same landscape features (Wasserman et al., 2012). Habitat suitability reflects a combination of conditions that allow/induce individuals to settle, establish their home ranges and reproduce. Resistance to movement, which can be measured by gene flow and GPS telemetry data, reflects how the landscape affects dispersal. Dispersing individuals are usually juveniles, which may tolerate sub-optimal conditions while looking for territories, and therefore may select different features relative to residents (Elliot et al., 2014; Gastón et al., 2016; Wasserman et al., 2012).

Although habitat suitability may not be the best surrogate for landscape resistance, given the large availability of presence data for many species, and the fact that they may be the only empirical data available for rare taxa, in many cases, using habitat suitability as a proxy for landscape resistance likely will remain the best available approach. Furthermore, for some species, habitat preference of dispersing individuals might be similar to the habitat preference of residents (Newby, 2011; Zeller et al., 2018). For these species, using habitat suitability as a proxy for landscape resistance to movement is likely to produce satisfactory results. However, for most species, it is unknown whether they select similar habitat features for dispersal and home range residency. When such information is lacking and more sophisticated data such as movement or genetics data are available, comparing the performance of the habitat suitability method with other approaches in estimating landscape resistance is prudent to help us better identify the advantages and limitations of the different approaches (Mateo-Sánchez et al., 2015a, 2015b; Zeller et al., 2018).

The functional form employed to transform habitat suitability maps into resistance surfaces might also affect predictions (Beier et al., 2008). Recent studies have demonstrated that a negative exponential transformation of habitat suitability may be the most appropriate one (Keeley et al., 2016, 2017; Mateo-Sánchez et al., 2015a, 2015b; Trainor et al., 2013; Zeller et al., 2018). Limitations in occurrence related to habitat suitability are usually more stringent than limits to dispersal movement, because dispersers are often willing to take more risks in their movement and habitat selection than residents (Elliot et al., 2014). For this reason, the exponential transformation of habitat suitability is thought to better reflect the resistance to dispersal movement, since it assumes that areas of moderate to high habitat quality have low resistance to dispersal movement, and only the areas of the lowest habitat quality have very high resistance (e.g. Mateo-Sánchez et al., 2015a; Wan et al., 2019).

Landscape genetics is another commonly used approach to estimate landscape resistance (Balkenhol et al., 2016; Cushman et al., 2006). Landscape genetic approaches are becoming increasingly popular due to technological advancements and cost reduction in genetic techniques (Balkenhol et al., 2016; Zeller et al., 2012), along with its superiority, demonstrated in some systems, relative to expert opinions (Shirk et al., 2010) or habitat suitability (Mateo-Sánchez et al., 2015a; Wasserman et al., 2010).

In landscape genetic analyses, genetic data are used to compute the genetic distance (GD) between individuals, which is then correlated with measures of cost distance (CD) from different resistance models (Balkenhol et al., 2016). Genetic data provide robust information about gene flow between locations, which makes landscape genetics a powerful tool to parameterize landscape resistance values, especially when applied in a multivariate optimization framework (Cushman et al., 2006; Mateo-Sánchez et al., 2015a; Shirk et al., 2010; Wasserman et al., 2010; Zeller et al., 2018).

In this study, we compared landscape resistance predictions produced from a habitat suitability approach and a landscape genetics optimization approach for two congeneric species of Neotropical cats, *Leopardus guttulus* and *L. geoffroyi*. Little is known about the relationship between habitat selection and resistance to movement for South American carnivores. To our knowledge, no study has empirically tested such relationships for any Neotropical carnivore. For small Neotropical felids, information about their ecological requirements is scarce, which poses challenges for effective conservation planning. The two species we studied have largely allopatric distributions and different ecological requirements: *L. guttulus* is considered a closed-forest habitat specialist (Cruz et al., 2019; de Oliveira et al., 2016), while *L. geoffroyi* is considered a habitat generalist (Cuyckens et al., 2016; Pereira et al., 2015). Given the large ecological differences between the species, comparing the performance of habitat proxy and landscape genetic methods for predicting resistance for both species would be particularly informative.

We addressed four hypotheses: (1) In model comparison, genetic-based resistance surfaces will outperform the habitat-based surfaces in explaining movement driving gene flow for both species; (2) the exponential conversion of habitat suitability into resistance surfaces will improve the performance of the habitat-based model and will reflect relatively less restrictive dispersal than the linear conversion, since only very low quality areas will present high resistance to movement; (3) predicted landscape connectivity based on the habitat suitability model will be more restrictive than connectivity predicted based on genetic data, as resident individuals are usually less tolerant to low quality habitat than dispersing individuals; (4) *L. guttulus* will be more affected by habitat conversion than *L. geoffroyi*, since *L. guttulus* is considered a forest specialist while *L. geoffroyi* is considered a more generalist species.

2 | MATERIALS AND METHODS

2.1 | Study species and study area

The southern tigrina, *L. guttulus*, has been recently recognized as an independent species (Trigo, Schneider, et al., 2013). Its current distribution is documented in southern-southeastern Brazil, Argentina and Paraguay, but the full extent of its occurrence and

its ecological requirements are not completely clear. Its distribution seems to be coextensive with the Atlantic Forest, although some individuals have been recorded in the Cerrado biome, a savanna habitat (de Oliveira et al., 2016; Nascimento & Feijó, 2017; Trigo, Schneider, et al., 2013). However, the Cerrado biome is highly heterogeneous, ranging from closed woodlands to grasslands (Ratter et al., 1997), and it is largely unknown how the species utilizes the different features in this biome. Its occurrence seems to be mainly determined by abiotic features (precipitation, temperature, elevation and solar radiation) related to the presence of the Atlantic Forest, making it a forested habitat specialist (Sartor et al., 2021). Some studies have suggested that the southern tigrina can inhabit disturbed areas, but its occurrence is limited by the presence of tree cover (Cruz et al., 2019; de Oliveira et al., 2010; Sartor et al., 2021).

Geoffroy's cat, *L. geoffroyi*, in contrast, is the most abundant wild felid in South America and has a broad distribution, occurring from the Andes of southern Bolivia to the southernmost parts of Argentina and Chile (Cuyckens et al., 2016; de Oliveira & Cassaro, 2005). Within this distribution, *L. geoffroyi* occupies several habitat types, such as dry forests, savannas, shrublands and grasslands (Cuyckens et al., 2016; Pereira et al., 2015), but most of its range is composed of arid or semi-arid habitat with low tree cover (Pereira et al., 2006). It is traditionally considered an open-habitat species (Sunquist & Sunquist, 2002). However, some studies have demonstrated that in human-dominated landscapes, it selects closed vegetation within open habitats (Caruso et al., 2016; Manfredi et al., 2012; Tirelli et al., 2019). It also seems to be tolerant to some degree of habitat alteration (Pereira et al., 2011, 2012; Sartor et al., 2021) and may sometimes benefit from it, expanding its occurrence and taking advantage of the higher prey density found in the border of agricultural areas (Caruso et al., 2016; Cuyckens et al., 2016).

The study area comprised the entire range of both species, covering an area of approximately 9,000,000 km² (Figure 1). There is a restricted zone of overlap, contact and hybridization between the two species along the southern edge of Brazil; however, their known ranges are mostly non-overlapping (Sartor et al., 2021; Trigo, Tirelli, et al., 2013; Trigo et al., 2014).

2.2 | Sample collection

In this study, we used genetic information from 13 microsatellite loci of 135 individuals of *L. guttulus* and 140 of *L. geoffroyi* generated previously (Sartor et al., 2020, 2021). These samples were distributed across almost the entire range of both species. As *L. geoffroyi* and *L. guttulus* hybridize at the edge of their distributions (Trigo, Schneider, et al., 2013; Trigo et al., 2014), to prevent any potential bias that the ecological preferences of hybrids might cause (Culumber et al., 2012; Sartor et al., 2021; Walsh et al., 2016), individuals identified as possible hybrids by Sartor et al. (2021) were not included in the analyses. In addition, samples with more than 20% of missing data were also excluded.

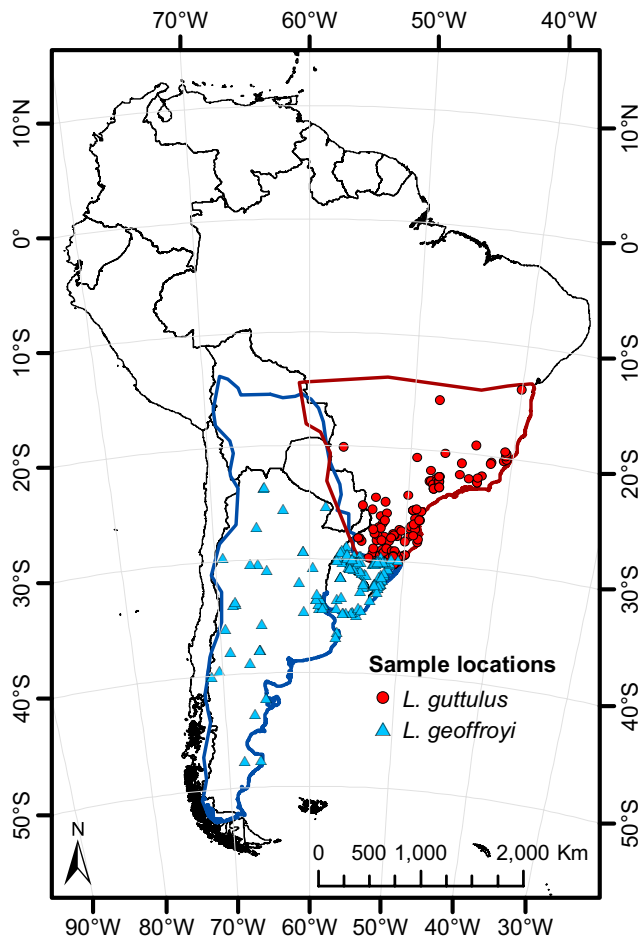


FIGURE 1 Study area and genetic sample points for *Leopardus guttulus* and *L. geoffroyi* in South America. Area delimited by a continuous red line is the geographic distribution of *L. guttulus*, while the area delimited by a blue dotted line is the geographic distribution of *L. geoffroyi* according to de Oliveira et al. (2016) and Pereira et al. (2015), respectively. Map projection: South America equidistant conic.

2.3 | Genetic distance

We calculated pairwise GDs among individuals using a principal components analysis (PCA; Shirk et al., 2010, 2017). This method is more sensitive to detect genetic dissimilarities because alleles that capture the greatest proportions of genetic variation within a population have a more significant contribution to the GDs than common alleles (Castillo et al., 2014; Shirk et al., 2010, 2017). We constructed a matrix in which the columns represented the alleles at each locus and the rows represented the sampled individuals. Each cell was given a value of 0, 1 or 2, based on the number of occurrences of that allele in each individual. We used the Euclidean distance function in the 'Ecodist' package in R (Goslee & Urban, 2007) to generate a GD matrix based on the distances between individuals along the first 64 axes of the PCA, which was shown by Shirk et al. (2018) to provide optimal capture of genetic signal. For alleles with missing data, we assigned the modal value for each allele among all individuals.

2.4 | Landscape variables

To optimize the genetic-based resistance surface, we used the same set of variables used by Sartor et al. (2021), including temperature, precipitation, solar radiation, elevation, tree canopy cover, land cover, river width, cropland areas and livestock per km². For the genetic-based analysis, we also included roads (Meijer et al., 2018) and human footprint (Venter et al., 2016, 2018; see Table S1, for more details on landscape variables). These two variables were not used by Sartor et al. (2021), because a large number of location points were from road-killed animals located close to urban areas, and the high correlation of the presence data with these variables could lead to the erroneous prediction of high habitat suitability near urban areas and roads. However, since this is unlikely to affect landscape genetic analysis, as it is based on cumulative differentiation across space rather than conditions at a sampled location (Cushman & Landguth, 2010), they were added to the present study.

2.5 | Genetics-based resistance surface

For the genetic approach for estimating landscape resistance, we used a restricted multivariate optimization method to evaluate which landscape variables drive genetic connectivity in these two felids (Castillo et al., 2014; Shirk et al., 2010). This optimization is based on the idea that the relationship between a landscape variable and gene flow might change with its thematic resolution (functional shape and maximum resistance) and the value of other landscape variables. Individual-based landscape genetics modelling to predict resistance to dispersal movement is based on associating GD (described above) with alternative cost-distance hypotheses, reflecting different ways in which the landscape can influence gene flow (Cushman et al., 2006). To compute CDs for each alternative hypothesis (landscape variables), we used the 'sGD' package (Shirk & Cushman, 2011) in R to generate a pairwise CD matrix between the sampling points.

To optimize the relationship between landscape variables and resistance to dispersal movement in these Neotropical cats, we evaluated the relationship between GD and each of the CD matrices with linear mixed effects models. This statistical test has higher accuracy than other regression methods in predicting the influence of the landscape on gene flow (Shirk et al., 2018). We used the *MLPE.lmm()* function from the package 'ResistanceGA' (Peterman, 2018) in R to fit maximum-likelihood population effects (MLPE; Clarke et al., 2002) models relating GD to CD for each candidate model. We compared the models generated based on the lowest Akaike information criterion (AIC) score, using the parameter `REML = FALSE` in the *MLPE.lmm()* function, which results in a valid AIC score fit with maximum likelihood (Shirk et al., 2018).

The optimization analysis was conducted in several steps. First, for the land cover variable, each land cover class was given a value of resistance from 1 (lowest resistance) to 10 (highest resistance) in increments of 1. We optimized resistance values by changing the value of one class

while holding the others constant until the AIC was minimized. After having optimized the values for land cover, we added roads and rivers to the layer and optimized them with the same method. The resistance value of roads varied between 1 and 100 and rivers between 1 and 10,000 because these features usually have a greater impact on species movement. Finally, we tested different power functions (0.5, 0.75, 1, 1.5, 1.75, 2, 2.5) to produce a range of functional shapes, and optimized the maximum relative resistance (R_{max}; Shirk et al., 2010) by stepping R_{max} from 50 to 300 in steps of 10. For the optimization of the gradient variables, we rescaled them linearly to values between 1 and 10, and the same process was applied (Vergara et al., 2016). We calculated Pearson's correlation coefficient between each pair of CD matrices to check for multicollinearity. When two CD matrices were correlated (i.e. $r > 0.8$; Figure S2), we kept the variable with the lowest AIC value. Cushman et al. (2014) showed that individual-based landscape genetics model selection has high ability to correctly identify the driving factor when the correlation among hypotheses is 0.8 or lower, which was subsequently confirmed by Shirk et al. (2018). Cushman and Landguth (2010) demonstrated that finer resolutions increase the power of landscape genetics analysis. Therefore, for the genetic-based analysis, all layers were projected at 1 km² resolution.

In addition, we tested the influence of geographic distance on genetic differentiation (isolation by distance hypothesis). We calculated a geographic distance matrix, based on the Euclidean distance between the localities of all individuals, using the package 'Ecodist' in R.

2.6 | Habitat-based resistance surface

To estimate landscape resistance based on the habitat approach, we used habitat suitability models developed by Sartor et al. (2021). Briefly, Sartor et al. (2021) used presence records and pseudo-absence data to generate habitat suitability models for both species, for their entire ranges, with the Random Forest algorithm. In addition to the genetic samples described above, presence records from museum collections, databases and literature were used in the analysis (Figure S1). As presence records were unbalanced, the data were subsampled in order to maintain a similar density of points across the range of each species. Only noncorrelated variables were used in the analysis. An 8 km² resolution was used, as it encompasses the average home range of both species (de Oliveira et al., 2016; Pereira et al., 2015) and it has been shown that carnivores usually select habitat on broad spatial scales (e.g. Hearn et al., 2018; Mateo-Sánchez et al., 2014; Vergara et al., 2016). This resolution was different than the one used for the genetic-based approach because, although this may influence the results, we believe that the comparison will be fairer and more instructive if the models of each method were generated with the most suitable methodology available. Models were selected based on the lowest total out-of-bag error and lowest maximum within-class error.

We converted the predicted probability maps generated by Sartor et al. (2021) into resistance surfaces using an exponential decay function as in Wan et al. (2019) and a linear function. We rescaled the values, so the areas with highest habitat suitability prediction had the

lowest resistance, with the R_{max} proportional to the R_{max} optimized for the genetic data for each species. We calculated CD matrices for the linear and exponential decay function for both species.

2.7 | Model comparisons

For each species, we initially compared the habitat-based models with the geographic distance and all genetic-based models based on their AIC scores using MLPE. Then, to evaluate how effective habitat suitability models are in predicting landscape effects on movement driving gene flow, similar to Mateo-Sánchez et al. (2015a), we compared the best resistance surface created by the genetic approach with the best resistance surface created by the habitat approach. To do this, we calculated the correlation between the best habitat-based landscape resistance and the landscape resistance from the optimized genetics-based model. We compared the direction and nature of the relationship with landscape variables between the genetics-based and habitat-based models to identify differences in how landscape features affect the probability of occurrence and resistance to dispersal movement in each species. We also created difference maps for this comparison by subtracting the habitat-based resistance surface from the genetics-based resistance surface. To compare the landscape connectivity restrictiveness of the resistance layers generated by the approaches, we determined two arbitrary resistance values thresholds of 10 and 50 and compared the total amount of area of the resistance layers with resistance value below the thresholds.

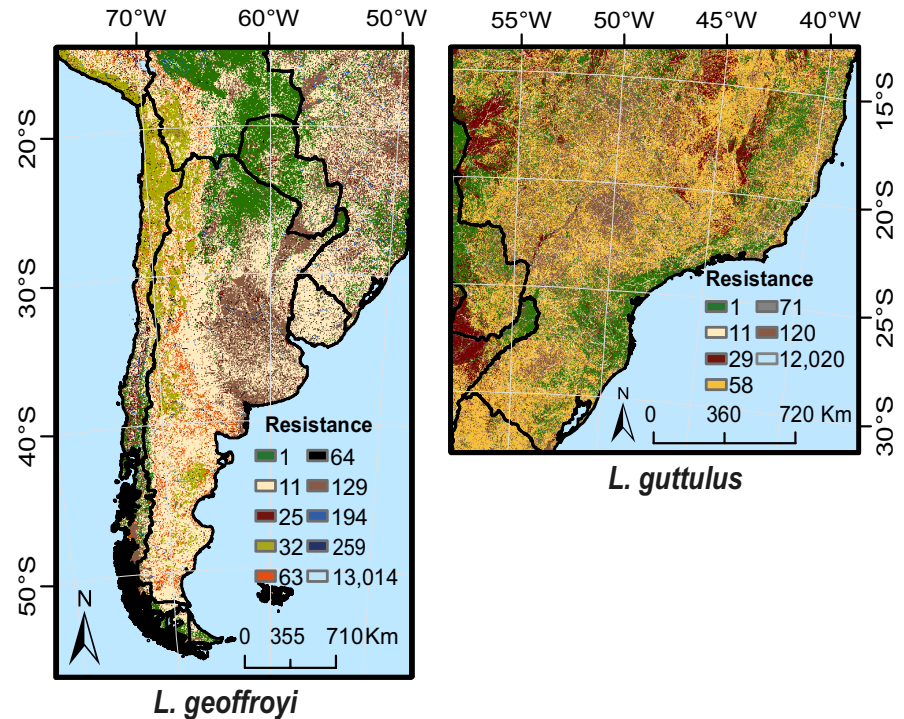
The influence of landscape features on dispersal and genetic differentiation cannot be detected until they become limiting to movement (Cushman et al., 2011, 2013). Thus, as both species inhabit altered environments, we decided to test if their dispersal movements were influenced by similar limiting factors, despite presenting different habitat preferences (Sartor et al., 2021). To do that, we compared the optimized genetics-based landscape resistance models for the two species. Specifically, we calculated landscape resistance across the full study area (including the range of both species) for each species' model and then calculated a pixelwise correlation between the surfaces. We generated difference maps by subtracting the resistance map of one species from the resistance map of the other species in both areas. We also compared the habitat suitability maps generated by Sartor et al. (2021) in the same way to further analyse how habitat preference and dispersal might be affected by different landscape features in each species.

3 | RESULTS

3.1 | Genetic-based optimized resistance models

For the genetic-based approach, the land cover variables had the strongest correlation with GD for both species (Figure 2). For *L. guttulus*, we tested 112 models. The optimized thematic resolution was exponential = 2 and R_{max} = 120. For *L. geoffroyi*, we tested 174 models. The

FIGURE 2 Genetics-based optimized landscape resistance model for *Leopardus geoffroyi* and *L. guttulus* generated with a restricted multivariate optimization approach. The resistance values in the legends correspond to the optimized landscape resistance values (see Table 1). For a better resolution of the map, the reader should refer to the online version. Location: South America. Map projection: South America equidistant conic.



optimized thematic resolution was exponential = 2 and $R_{max} = 260$. For both species, forest was the class with the lowest resistance (resistance = 1), and they presented similar resistance values for cropland, primary and secondary roads. Nevertheless, for the remaining landscape classes, *L. geoffroyi* presented lower resistance values when compared to *L. guttulus*, with the exception of flooded areas and rivers (Table 1).

3.2 | Habitat-based optimized resistance models

For the habitat-based approach, the linear transformation had a significantly better performance than the exponential transformation for both species (Figure S3a–d). For *L. guttulus*, the linear transformation had a $\Delta AIC = 26.77$, and the exponential transformation had a $\Delta AIC = 75.71$ (Table S2). For *L. geoffroyi*, the ΔAIC values of these models were $\Delta AIC = 138.28$ and $\Delta AIC = 204.89$, respectively (Tables S3).

3.3 | Model comparisons

Across all the models that we generated, genetic-based models had the best performance and the habitat-based models consistently exhibited the worst performance in predicting observed genetic differences between individuals of both species. The isolation by distance model (IBD) also did not perform well, being the eighth worst model ($\Delta AIC = 47.52$) for *L. guttulus* and the fifth worst model ($\Delta AIC = 102.27$) for *L. geoffroyi* (Figure 3; Tables S2 and S3).

The resistance surfaces generated by the genetic-based approach were very different from those obtained by transforming habitat suitability (Figure S3). For both species, the comparison between the two methods resulted in a very low correlation ($r = 0.04$; $p < 0.01$ for *L.*

TABLE 1 Optimized landscape resistance values for *Leopardus guttulus* and *L. geoffroyi* for the different landscape classes considered in the genetics-based resistance surfaces analyses

Landscape class	<i>L. geoffroyi</i>	<i>L. guttulus</i>
Forest	1	1
Shrubland	11.41	29.85
Grasslands	63.47	120
Sparse vegetation	11.41	120
Bare areas	32.24	120
Flooded areas	129.85	29.85
Cropland with natural remnants	11.41	58.70
Cropland	129.85	120
Primary roads	64.77	71.92
Secondary roads	25.73	11.82
Small rivers	194.92	11.82
Medium rivers	260	120
Large rivers	13,014.77	12,020

geoffroyi; $r = -0.029$; $p < 0.01$ for *L. guttulus*; Figure 4). The two approaches also selected different variables. The genetic approach selected land cover variables, while the habitat suitability models generated by Sartor et al. (2021) selected mainly climatic variables and elevation. Cropland was the only variable selected by both approaches, for both species, and showed the opposite direction of influence for *L. guttulus*. According to the genetic approach, cropland areas have high resistance to *L. guttulus* movement. However, the habitat suitability approach suggested a positive correlation between the cropland areas and this species occurrence (Sartor et al., 2021).

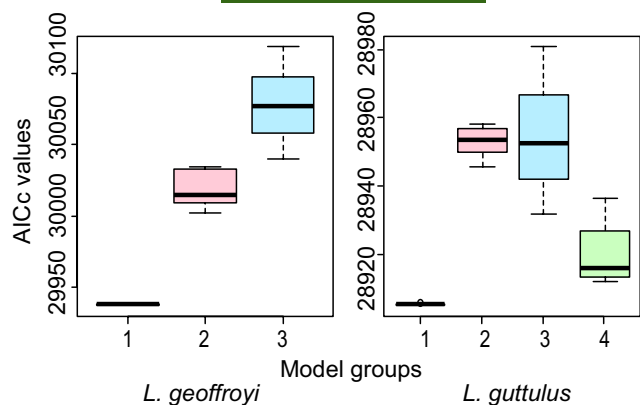


FIGURE 3 Boxplot comparing model groups based on their corrected AIC (AICc) values. Model group 1 represents the 20 best optimized genetic-based models, model group 2 represents the extra environmental and anthropogenic variables considered during models' optimization individually without the optimized model, model group 3 represents the IBD and habitat-based models for *Leopardus geoffroyi* and *L. guttulus*. Model group 4, for *L. guttulus*, represents the best optimized genetic-based model with the additional extra parameters. The AICc values of these models can be seen in tables S2 and S3.

Regarding the restrictiveness of the predicted resistance layers, for both species the habitat-based models generated with the linear transformation had the most restrictive patterns of predicted landscape connectivity, regardless of the threshold considered, while the less restrictive models varied between species. For *L. guttulus*, for both thresholds, the habitat-based model generated with the exponential transformation presented the less restrictive layer, and for *L. geoffroyi*, it was the genetic-based model (Table S4).

The genetic-based resistance model comparisons between the two species demonstrated a high and positive correlation value for both areas ($r = 0.98$; $p > 0.01$; Figure S4a,b). The same variables were selected in the optimized model for both species, and they had consistent relative influence, with *L. geoffroyi* exhibiting lower values for almost all variables than *L. guttulus* (Table 1). The comparison of habitat suitability maps between the two species demonstrated a low negative correlation. The projection of the *L. guttulus* model onto the *L. geoffroyi* range resulted in a correlation of $r = -0.3982$ ($p < 0.01$; Figure S4c), while the projection of *L. geoffroyi* onto the *L. guttulus* range yielded a correlation of $r = -0.289$ ($p < 0.01$; Figure S4d). In addition, the models generated by Sartor et al. (2021) selected mainly the same variables for both species, with the opposite direction of influence between them.

4 | DISCUSSION

4.1 | Habitat-based versus genetics-based resistance surfaces

The optimized genetic resistance models greatly outperformed the resistance models created from the habitat suitability approach in predicting resistance to movement for both studied species, as

measured by the association with observed genetic differentiation among individuals. Our results confirm and strengthen the conclusion that habitat suitability does not accurately reflect how the landscape influences genetic connectivity (Mateo-Sánchez et al., 2015a; Reddy et al., 2017; Wasserman et al., 2010; Zeller et al., 2018). In contrast to the results of Zeller et al. (2018), who found relatively high utility in habitat quality as a surrogate for landscape resistance, in our study, the habitat suitability approach produced poorly validated models that were considerably different in resistance and the variables selected in comparison with the genetics-based models. For example, the only variable selected by both models, cropland, presented a high negative correlation with genetic resistance for both species, but a positive correlation with habitat suitability for *L. guttulus*. The correlation between the resistance surfaces produced by the two approaches for both species was virtually null, which emphasizes how different their surfaces were.

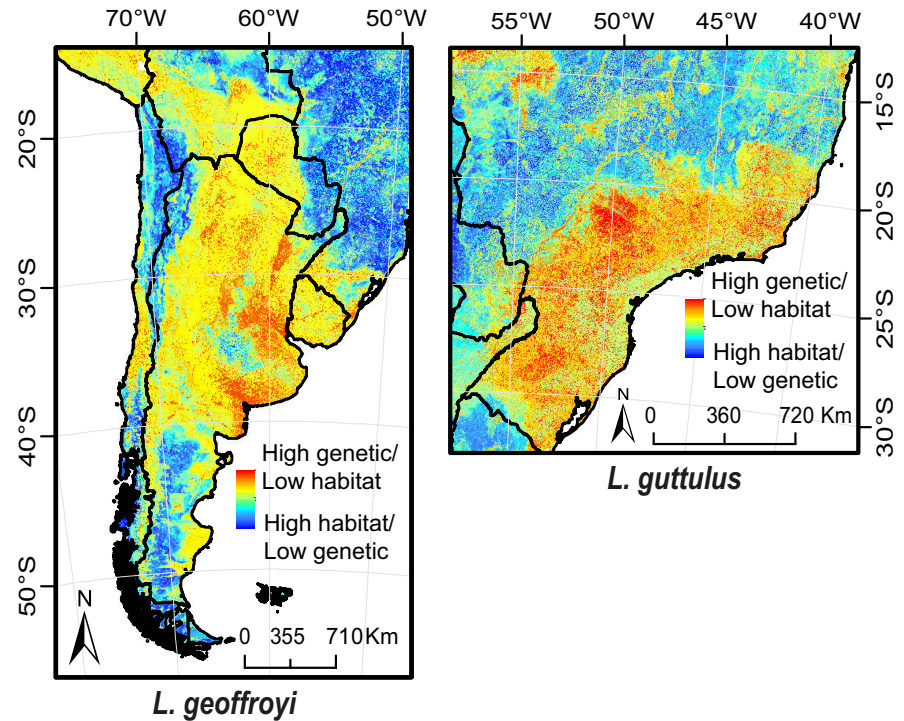
The low negative correlation observed in the comparison of the habitat suitability models between the two species demonstrates how different their ecological niches are (Sartor et al., 2021). However, the high positive correlation observed in the comparison of the optimized landscape genetic resistance model suggests that they select similar landscape features when dispersing. These results indicate that gene flow and habitat selection are related to different landscape aspects, as also seen by Wasserman et al. (2010), Cushman and Lewis (2010), Elliot et al. (2014) and Mateo-Sánchez et al. (2015a). This is extremely important as it shows how the method chosen for analysis affects the conclusions regarding what landscape features influence connectivity and in what way they affect it.

Contrary to our expectation, the negative exponential conversion of habitat suitability into resistance surface did not improve the performance of the habitat-based resistance surface, although it presented a less restrictive dispersal than the linear conversion, as we predicted. In our model comparisons, the habitat-based resistance models were ranked as the worst models for both species even using this transformation, and a linear transformation, although much weaker than the genetics-based models, outperformed the exponential transformation based on the ΔAIC value. This result is the opposite to what has been previously reported (e.g. Keeley et al., 2017; Mateo-Sánchez et al., 2015a; Trainor et al., 2013; Zeller et al., 2018), demonstrating that the performance of the functional form employed to transform habitat suitability maps into resistance surfaces may differ between species.

Also, contrary to our expectation, for *L. guttulus*, not all resistance surfaces created by the habitat suitability models were more restrictive than the ones created by the genetics-based models. It is possible that the extensive habitat alteration in this region has overcome the species tolerance to move through less suitable habitats, as most of its habitat has been transformed into agricultural areas or urban spaces. This would reflect the increasing emergence of limiting factors that hamper movement as habitat is lost and becomes more fragmented (e.g. Cushman et al., 2013; Short Bull et al., 2011; Vergara et al., 2017).



FIGURE 4 Landscape resistance comparison between the genetic approach and the habitat approach in the range of *Leopardus guttulus* and *L. geoffroyi*. Difference maps were generated by the subtraction of the habitat-based resistance surface from the genetics-based resistance surface. Hotter colours indicate areas with high genetics-based resistance values and low habitat-based resistance values, while cooler colours indicate the opposite relationship. Intermediate colours indicate areas where resistance values of both approaches are similar. Location: South America. Map projection: South America equidistant conic.



It is important to highlight that, in our study, the genetic approach selected land cover variables that measure habitat fragmentation and alteration, while the habitat suitability models from Sartor et al. (2021) selected mainly climatic variables that do not carry this information, and this difference in variables may explain this result. The inverse of these results was seen by Wasserman et al. (2012), in which habitat selection of American marten was highly affected by landscape heterogeneity and fragmentation of forest cover, while gene flow, as measured by landscape genetics, was primarily affected by climate (elevation as a surrogate). Such observation demonstrates how each species' biology may affect its response to habitat features for suitability and/or dispersal in unique ways, highlighting the need to explore these relationships in multiple systems.

4.2 | Landscape resistance to felid movement based on the genetic-based approach

Despite occurring in very different environments, our analysis showed that gene flow of both species was constrained by similar limiting factors. As we expected, the *L. guttulus* model suggested low resistance values for forested areas, while the *L. geoffroyi* model showed a more plastic and general response to landscape features, with different landscape classes (shrubland, sparse vegetation and cropland with natural remnants) presenting relatively low resistance values. Interestingly, forest was the class optimized with the lowest resistance for both species. Although some studies have demonstrated that *L. geoffroyi* selects forested habitats in areas with human disturbance (Caruso et al., 2016; Manfredi et al., 2012; Tirelli et al., 2019), this result was still unexpected, since it is considered an open-habitat species. In addition, forested areas are mainly found

in the northern part of *L. geoffroyi*'s distribution, covering a small portion of the species' range. It is possible that our sampling effort, more concentrated in this area, is not fully sampling the resistance values in the central and southern parts of its distribution, which in turn could reduce the resistance value of forests. Another possibility is that the species is influenced by different features in different portions of its distribution (e.g. Vergara et al., 2017) and our results better reflect the resistance to dispersal movement within the northern area. Therefore, more studies in this area are necessary to fully understand how forest cover affects the movement of this species.

The resistance value for the river classes differed considerably between the two species. While rivers less than 200m-wide do not seem to impose large dispersal barriers for *L. guttulus* movement, they seem to be substantial natural barriers to *L. geoffroyi*. We also found a similar relationship between species regarding resistance to flooded areas, with *L. geoffroyi* showing higher resistance values. These high resistance values optimized for *L. geoffroyi* were surprising since its occurrence is considered common in flooded areas such as the Esteros del Iberá or the Delta of Paraná (Pereira JA personal observation). However, recent studies suggest the existence of genetic structure within *L. geoffroyi*'s range (Bou et al., 2021; Gómez-Fernández et al., 2020), coinciding with the region of the Uruguay, Paraná and Paraguay rivers. These rivers are recognized as important barriers to the dispersal of other small Neotropical felids (da Silva Santos et al., 2018; Johnson et al., 1999), and it is possible that they also affect the dispersal of *L. geoffroyi*, as indicated by our analysis.

Consistent with other studies (de Oliveira et al., 2016; Sartor et al., 2021; Trigo, Tirelli, et al., 2013), our results demonstrated that *L. guttulus* is a greater habitat specialist and therefore is likely

to be more susceptible to habitat conversion than *L. geoffroyi*. Our resistance optimization for *L. geoffroyi* showed that agricultural areas do not impose high resistance to movement, as long as these areas maintain some percentage of natural vegetation, highlighting the ecological plasticity of the species. However, we demonstrate that intensive agriculture, which does not have a natural vegetation component, imposes high resistance to movement for this species.

Leopardus guttulus seems to be highly dependent on forested environments for both habitat and dispersal movement, and the conversion of its natural habitat into agricultural lands imposes great resistance to dispersal and loss of habitat for residency. The resistance value optimized for cropland was very high, and it seems that even with the maintenance of natural vegetation within agricultural lands, this species will avoid crossing these areas. Nonetheless, for both species, the resistance values for cropland without natural vegetation are much higher than the values for cropland that retains some percentage of natural vegetation. This result demonstrates the importance of maintaining natural vegetation remnants within disturbed areas. These areas with natural vegetation probably favour dispersal between patches in highly disturbed landscapes and may even sustain small populations, depending on the size of the natural fragments.

The presence of roads was predicted to impose substantial resistance for dispersal movement of both species, but with higher values for *L. guttulus*. This was the case for the class of primary roads, but not for the class of secondary roads. The values, however, were not greatly different between species, and it seems that they affect the dispersal of both species in a similar way. For both species, our results suggest that large roads act as major barriers to movement driving gene flow, which is similar to results found in a number of other species, such as black (Short Bull et al., 2011) and brown (Mateo-Sánchez et al., 2015a) bears, African lions (Elliot et al., 2014) and pumas (Zeller et al., 2018). The great importance of roads in the landscape genetics models suggests that removing roads and human footprint from the habitat suitability models may have impacted the performance of the models. However, as said above, the high correlation of these variables with our presence data would probably bias the results. This situation demonstrates another benefit of landscape genetics analysis, because, as it uses the cumulative differentiation across space, it is less likely to be biased by uneven sampling.

5 | CONCLUSIONS AND IMPLICATIONS

Earth is facing a biodiversity crisis in which anthropogenic landscape change synergizing with rapid climatic warming is driving a mass extinction episode. To effectively design conservation actions in the face of rapid habitat loss and fragmentation, it is critical to understand how landscape features affect both patterns of occurrence and connectivity (Cushman, 2006). In this context, the lack of knowledge on Neotropical cats' ecological requirements prevents the design and implementation of adequate management and conservation measures.

In this study, we identified the landscape features that drive gene flow in two species of Neotropical cats across their entire ranges. To our knowledge, this is the first landscape genetic study ever conducted across the full range of different species using comparable methods. It is also one of the few studies that used the same methodology to compare the patterns that drive habitat preference and gene flow in two congeneric species. We demonstrated that for both species, habitat preference and gene flow are driven by different landscape features, and that, for these species, resistance surfaces created based on genetic data are more suitable for connectivity analysis, and habitat suitability models are a poor proxy for landscape resistance to dispersal movement.

These results have important implications for connectivity modelling. Habitat-based models may produce very different connectivity maps than landscape genetic optimization, which may lead to incorrect management decisions. Therefore, when possible, landscape genetics analysis should be prioritized over habitat suitability models. However, genetic data are not always available, and sometimes, the conversion of habitat suitability models into resistance surfaces is the only option and should be used. In these cases, however, it is important to make assumptions carefully. Given the complexity of this problem, and the distinct patterns observed in different species, it is important that more studies comparing the performance of methods to estimate landscape resistance be urgently performed, and we thus recommend increased research focusing on this topic.

ACKNOWLEDGEMENTS

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. This work was also supported by CNPq/Brazil (grants no. 454551/2014-2 and 424361/2016-7) and FAPERGS/Brazil. No collection permit was required to conduct this study. Samples in Brazil were transported under permit 42491 (Brazilian Federal Government – Instituto Chico Mendes de Conservação da Biodiversidade).

CONFLICT OF INTEREST

The authors declare no conflicts of interest (no copyright, financial or ethical issues).

DATA AVAILABILITY STATEMENT

The genotype file is available from the FigShare Repository, accessible at <https://doi.org/10.6084/m9.figshare.13235537.v1> (Sartor et al., 2020). Sample locations are provided in the supporting information of Sartor et al. (2021).

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REFERENCES

- Balkenhol, N., Cushman, S. A., Storfer, A. T., & Waits, L. P. (2016). *Landscape genetics: Concepts, methods, applications*. John Wiley & Sons Ltd.



- Beier, P., Majka, D. R., & Spencer, W. D. (2008). Forks in the road: Choices in procedures for designing wildland linkages. *Conservation Biology*, 22(4), 836–851. <https://doi.org/10.1111/j.1523-1739.2008.00942.x>
- Bou, N., Soutullo, Á., Hernández, D., Mannise, N., González, S., Bartesaghi, L., Pereira, A., Merino, M., Espinosa, C., Trigo, T. C., & Cosse, M. (2021). Population structure and gene flow of Geoffroy's cat (*Leopardus geoffroyi*) in the Uruguayan Savanna ecoregion. *Journal of Mammalogy*, 102(3), 879–890. <https://doi.org/10.1093/jmammal/gyab043>
- Caruso, N., Lucherini, M., Fortin, D., & Casanave, E. B. (2016). Species-specific responses of carnivores to human-induced landscape changes in Central Argentina. *PLoS One*, 11(3), e0150488. <https://doi.org/10.1371/journal.pone.0150488>
- Castillo, J. A., Epps, C. W., Davis, A. R., & Cushman, S. A. (2014). Landscape effects on gene flow for a climate-sensitive montane species, the American pika. *Molecular Ecology*, 23(4), 843–856. <https://doi.org/10.1111/mec.12650>
- Chetkiewicz, C. L. B., St. Clair, C. C., & Boyce, M. S. (2006). Corridors for conservation: Integrating pattern and process. *Annual Review of Ecology, Evolution, and Systematics*, 37, 317–342. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110050>
- Clarke, R. T., Rothery, P., & Raybould, A. F. (2002). Confidence limits for regression relationships between distance matrices: Estimating gene flow with distance. *Journal of Agricultural, Biological, and Environmental Statistics*, 7(3), 361–372. <https://doi.org/10.1198/108571102320>
- Cruz, P., De Angelo, C., Martínez Pardo, J., Iezzi, M. E., Varela, D., Di Bitetti, M. S., & Paviolo, A. (2019). Cats under cover: Habitat models indicate a high dependency on woodlands by Atlantic Forest felids. *Biotropica*, 51(2), 266–278. <https://doi.org/10.1111/btp.12635>
- Culumber, Z. W., Shepard, D. B., Coleman, S. W., Rosenthal, G. G., & Tobler, M. (2012). Physiological adaptation along environmental gradients and replicated hybrid zone structure in swordtails (Teleostei: Xiphophorus). *Journal of Evolutionary Biology*, 25(9), 1800–1814. <https://doi.org/10.1111/j.1420-9101.2012.02562.x>
- Cushman, S. A. (2006). Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation*, 128(2), 231–240. <https://doi.org/10.1016/j.biocon.2005.09.031>
- Cushman, S. A., & Landguth, E. L. (2010). Scale dependent inference in landscape genetics. *Landscape Ecology*, 25(6), 967–979. <https://doi.org/10.1007/s10980-010-9467-0>
- Cushman, S. A., & Lewis, J. S. (2010). Movement behavior explains genetic differentiation in American black bears. *Landscape Ecology*, 25(10), 1613–1625. <https://doi.org/10.1007/s10980-010-9534-6>
- Cushman, S. A., Lewis, J. S., & Landguth, E. L. (2014). Why did the bear cross the road? Comparing the performance of multiple resistance surfaces and connectivity modeling methods. *Diversity*, 6(4), 844–854. <https://doi.org/10.3390/d6040844>
- Cushman, S. A., McKelvey, K. S., Hayden, J., & Schwartz, M. K. (2006). Gene flow in complex landscapes: Testing multiple hypotheses with causal modeling. *The American Naturalist*, 168(4), 486–499. <https://doi.org/10.1086/506976>
- Cushman, S. A., Raphael, M. G., Ruggiero, L. F., Shirk, A. S., Wasserman, T. N., & O'Doherty, E. C. (2011). Limiting factors and landscape connectivity: The American marten in the Rocky Mountains. *Landscape Ecology*, 26(8), 1137–1149. <https://doi.org/10.1007/s10980-011-9645-8>
- Cushman, S. A., Shirk, A. J., & Landguth, E. L. (2013). Landscape genetics and limiting factors. *Conservation Genetics*, 14(2), 263–274. <https://doi.org/10.1007/s10592-012-0396-0>
- Cuyckens, G. A. E., Pereira, J. A., Trigo, T. C., Da Silva, M., Gonçalves, L., Huaranca, J. C., ... Eizirik, E. (2016). Refined assessment of the geographic distribution of Geoffroy's cat (*Leopardus geoffroyi*) (Mammalia: Felidae) in the neotropics. *Journal of Zoology*, 298(4), 285–292. <https://doi.org/10.1111/jzo.12312>
- da Silva Santos, A., Trigo, T. C., de Oliveira, T. G., Silveira, L., & Eizirik, E. (2018). Phylogeographic analyses of the pampas cat (*Leopardus colocola*; carnivora, Felidae) reveal a complex demographic history. *Genetics and Molecular Biology*, 41(1), 273–287. <https://doi.org/10.1590/1678-4685-GMB-2017-0079>
- de Oliveira, T., Trigo, T., Tortato, M., Paviolo, A., Bianchi, R., & Leite-Pitman, M. R. P. (2016). *Leopardus guttulus*. *The IUCN Red List of Threatened Species*: eT54010476A54010576. <https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T54010476A54010576.en>
- de Oliveira, T. G., & Cassaro, K. (2005). *Guia de campo dos felinos do Brasil* (2nd ed.). Sociedade de Zoológicos do Brasil.
- de Oliveira, T. G., Tortato, M. A., Silveira, L., Kasper, C. B., Mazim, F. D., Lucherini, M., ... Sunquist, M. (2010). Ocelot ecology and its effect on the small-felid guild in the lowland neotropics. In D. W. Macdonald & A. J. Loveridge (Eds.), *Biology and conservation of wild felids* (pp. 559–580). Oxford University Press.
- Elliot, N. B., Cushman, S. A., Macdonald, D. W., & Loveridge, A. J. (2014). The devil is in the dispersers: Predictions of landscape connectivity change with demography. *Journal of Applied Ecology*, 51(5), 1169–1178. <https://doi.org/10.1111/1365-2664.12282>
- Frankham, R., Jonathan, D. B., & Briscoe, D. A. (2010). *Introduction to conservation genetics* (2nd ed.). Cambridge University Press.
- Gastón, A., Blázquez-Cabrera, S., Garrote, G., Mateo-Sánchez, M. C., Beier, P., Simón, M. A., & Saura, S. (2016). Response to agriculture by a woodland species depends on cover type and behavioural state: Insights from resident and dispersing Iberian lynx. *Journal of Applied Ecology*, 53(3), 814–824. <https://doi.org/10.1111/1365-2664.12629>
- Gómez-Fernández, M. J., Fameli, A., Rojo Gómez, J., Pereira, J. A., & Mirol, P. (2020). Phylogeographical spatial diffusion analysis reveals the journey of Geoffroy's cat through the quaternary glaciations of South America. *Biological Journal of the Linnean Society*, 129(3), 603–617. <https://doi.org/10.1093/biolinnean/blz207>
- Goslee, S. C., & Urban, D. L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, 22(7), 1–19. <https://doi.org/10.18637/jss.v022.i07>
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1(2), e1500052. <https://doi.org/10.1126/sciadv.1500052>
- Hearn, A. J., Cushman, S. A., Goossens, B., Macdonald, E., Ross, J., Hunter, L. T., ... Macdonald, D. W. (2018). Evaluating scenarios of landscape change for Sunda clouded leopard connectivity in a human dominated landscape. *Biological Conservation*, 222, 232–240. <https://doi.org/10.1016/j.biocon.2018.04.016>
- Johnson, W. E., Slattery, J. P., Eizirik, E., Kim, J. H., Raymond, M. M., Bonacic, C., Cambre, R., Crawshaw, P., Nunes, A., Seuánez, H. N., Moreira, M. A., Seymour, K. L., Simon, F., Swanson, W., & O'Brien, S. J. (1999). Disparate phylogeographic patterns of molecular genetic variation in four closely related South American small cat species. *Molecular Ecology*, 8, S79–S94. <https://doi.org/10.1046/j.1365-294X.1999.00796.x>
- Keeley, A. T., Beier, P., & Gagnon, J. W. (2016). Estimating landscape resistance from habitat suitability: Effects of data source and nonlinearities. *Landscape Ecology*, 31(9), 2151–2162. <https://doi.org/10.1007/s10980-016-0387-5>
- Keeley, A. T., Beier, P., Keeley, B. W., & Fagan, M. E. (2017). Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. *Landscape and Urban Planning*, 161, 90–102. <https://doi.org/10.1016/j.landurbplan.2017.01.007>
- Macdonald, E. A., Cushman, S. A., Landguth, E. L., Hearn, A. J., Malhi, Y., & Macdonald, D. W. (2018). Simulating impacts of rapid forest loss on population size, connectivity and genetic diversity of Sunda clouded leopards (*Neofelis diardi*) in Borneo. *PLoS One*, 13(9), e0196974. <https://doi.org/10.1371/journal.pone.0196974>
- Manfredi, C., Vidal, E. L., Castillo, D. F., Lucherini, M., & Casanave, E. B. (2012). Home range size and habitat selection of Geoffroy's

- cat (*Leopardus geoffroyi*, Felidae, carnivora) in the pampas grassland. *Mammalia*, 76(1), 105–108. <https://doi.org/10.1515/mammalia-2011-0039>
- Mateo-Sánchez, M. C., Balkenhol, N., Cushman, S., Pérez, T., Domínguez, A., & Saura, S. (2015a). A comparative framework to infer landscape effects on population genetic structure: Are habitat suitability models effective in explaining gene flow? *Landscape Ecology*, 30(8), 1405–1420. <https://doi.org/10.1007/s10980-015-0194-4>
- Mateo-Sánchez, M. C., Balkenhol, N., Cushman, S., Pérez, T., Domínguez, A., & Saura, S. (2015b). Estimating effective landscape distances and movement corridors: Comparison of habitat and genetic data. *Ecosphere*, 6(4), 1–16. <https://doi.org/10.1890/ES14-00387.1>
- Mateo-Sánchez, M. C., Cushman, S. A., & Saura, S. (2014). Connecting endangered brown bear subpopulations in the Cantabrian range (north-western Spain). *Animal Conservation*, 17(5), 430–440. <https://doi.org/10.1111/acv.12109>
- Meijer, J. R., Huijbregts, M. A., Schotten, K. C., & Schipper, A. M. (2018). Global patterns of current and future road infrastructure. *Environmental Research Letters*, 13(6), 064006. <https://doi.org/10.1088/1748-9326/aabd42>
- Nascimento, F. O., & Feijó, A. (2017). Taxonomic revision of the tigrina *Leopardus tigrinus* (Schreber, 1775) species group (carnivora, Felidae). *Papeis Avulsos de Zoologia*, 57, 231–264. <https://doi.org/10.11606/0031-1049.2017.57.19>
- Newby, J. R. (2011). *Puma dispersal ecology in the central Rocky Mountains* [Master dissertation]. University of Montana.
- Pereira, J., Lucherini, M., & Trigo, T. (2015). *Leopardus geoffroyi*. *The IUCN Red List of Threatened Species*: e.T15310A50657011. <https://doi.org/10.2305/IUCN.UK.2015-2.RLTS.T15310A50657011.en>
- Pereira, J. A., Di Bitetti, M. S., Fracassi, N. G., Paviolo, A., De Angelo, C. D., Di Blanco, Y. E., & Novaro, A. J. (2011). Population density of Geoffroy's cat in scrublands of Central Argentina. *Journal of Zoology*, 283(1), 37–44. <https://doi.org/10.1111/j.1469-7998.2010.00746.x>
- Pereira, J. A., Fracassi, N. G., & Uhart, M. M. (2006). Numerical and spatial responses of Geoffroy's cat (*Oncifelis geoffroyi*) to prey decline in Argentina. *Journal of Mammalogy*, 87(6), 1132–1139. <https://doi.org/10.1644/05-MAMM-A-333R2.1>
- Pereira, J. A., Walker, R. S., & Novaro, A. J. (2012). Effects of livestock on the feeding and spatial ecology of Geoffroy's cat. *Journal of Arid Environments*, 76, 36–42. <https://doi.org/10.1016/j.jaridenv.2011.08.006>
- Peterman, W. E. (2018). ResistanceGA: An R package for the optimization of resistance surfaces using genetic algorithms. *Methods in Ecology and Evolution*, 9(6), 1638–1647. <https://doi.org/10.1111/2041-210X.12984>
- Peterman, W. E., Winiarski, K. J., Moore, C. E., da Silva Carvalho, C., Gilbert, A. L., & Spear, S. F. (2019). A comparison of popular approaches to optimize landscape resistance surfaces. *Landscape Ecology*, 34(9), 2197–2208. <https://doi.org/10.1007/s10980-019-00870-3>
- Ratter, J. A., Ribeiro, J. F., & Bridgewater, S. (1997). The Brazilian cerrado vegetation and threats to its biodiversity. *Annals of Botany*, 80(3), 223–230. <https://doi.org/10.1006/anbo.1997.0469>
- Reddy, P. A., Cushman, S. A., Srivastava, A., Sarkar, M. S., & Shivaji, S. (2017). Tiger abundance and gene flow in Central India are driven by disparate combinations of topography and land cover. *Diversity and Distributions*, 23(8), 863–874. <https://doi.org/10.1111/ddi.12580>
- Sartor, C. C., Cushman, S. A., Wan, H. Y., Kretschmer, R., Pereira, J. A., Bou, N., Cosse, M., González, S., Eizirik, E., de Freitas, T. R. O., & Trigo, T. C. (2021). The role of the environment in the spatial dynamics of an extensive hybrid zone between two neotropical cats. *Journal of Evolutionary Biology*, 34(4), 614–627. <https://doi.org/10.1111/jeb.13761>
- Sartor, C. C., Eizirik, E., Trigo, T. C., & Freitas, T. R. O. (2020). Data from: The role of the environment in the spatial dynamics of an extensive hybrid zone between two neotropical cats. *FigShare*. <https://doi.org/10.6084/m9.figshare.13235537.v1>
- Shirk, A. J., & Cushman, S. A. (2011). sGD: Software for estimating spatially explicit indices of genetic diversity. *Molecular Ecology Resources*, 11(5), 922–934. <https://doi.org/10.1111/j.1755-0998.2011.03035.x>
- Shirk, A. J., Landguth, E. L., & Cushman, S. A. (2017). A comparison of individual-based genetic distance metrics for landscape genetics. *Molecular Ecology Resources*, 17(6), 1308–1317. <https://doi.org/10.1111/1755-0998.12684>
- Shirk, A. J., Landguth, E. L., & Cushman, S. A. (2018). A comparison of regression methods for model selection in individual-based landscape genetic analysis. *Molecular Ecology Resources*, 18(1), 55–67. <https://doi.org/10.1111/1755-0998.12709>
- Shirk, A. J., Wallin, D. O., Cushman, S. A., Rice, C. G., & Warheit, K. I. (2010). Inferring landscape effects on gene flow: A new model selection framework. *Molecular Ecology*, 19(17), 3603–3619. <https://doi.org/10.1111/j.1365-294X.2010.04745.x>
- Short Bull, R. A., Cushman, S. A., Mace, R., Chilton, T., Kendall, K. C., Landguth, E. L., ... Luikart, G. (2011). Why replication is important in landscape genetics: American black bear in the Rocky Mountains. *Molecular Ecology*, 20(6), 1092–1107. <https://doi.org/10.1111/j.1365-294X.2010.04944.x>
- Spear, S. F., Balkenhol, N., Fortin, M. J., McRae, B. H., & Scribner, K. I. M. (2010). Use of resistance surfaces for landscape genetic studies: Considerations for parameterization and analysis. *Molecular Ecology*, 19(17), 3576–3591. <https://doi.org/10.1111/j.1365-294X.2010.04657.x>
- Sunquist, M., & Sunquist, F. (2002). *Wild cats of the world*. The University of Chicago Press.
- Tirelli, F. P., Mazim, F. D., Crawshaw, P. G., Albano, A. P., Espinosa, C., Queirolo, D., ... Eizirik, E. (2019). Density and spatio-temporal behaviour of Geoffroy's cats in a human-dominated landscape of southern Brazil. *Mammalian Biology*, 99(1), 128–135. <https://doi.org/10.1016/j.mambio.2019.11.003>
- Trainor, A. M., Walters, J. R., Morris, W. F., Sexton, J., & Moody, A. (2013). Empirical estimation of dispersal resistance surfaces: A case study with red-cockaded woodpeckers. *Landscape Ecology*, 28(4), 755–767. <https://doi.org/10.1007/s10980-013-9861-5>
- Trigo, T., Schneider, A., Lehugeur, L., Silveira, L., Freitas, T. R. O., & Eizirik, E. (2013). Molecular data reveal complex hybridization and a cryptic species of neotropical wild cat. *Current Biology*, 23(24), 2528–2533. <https://doi.org/10.1016/j.cub.2013.10.046>
- Trigo, T. C., Tirelli, F. P., Freitas, T. R., & Eizirik, E. (2014). Comparative assessment of genetic and morphological variation at an extensive hybrid zone between two wild cats in southern Brazil. *PLoS One*, 9(9), e108469. <https://doi.org/10.1371/journal.pone.0108469>
- Trigo, T. C., Tirelli, F. P., Machado, L. F., Peters, F. B., Indrusiak, C. B., Mazim, F. D., ... Freitas, T. R. O. (2013). Geographic distribution and food habits of *Leopardus tigrinus* and *L. geoffroyi* (carnivora, Felidae) at their geographic contact zone in southern Brazil. *Studies on Neotropical Fauna and Environment*, 48(1), 56–67. <https://doi.org/10.1080/01650521.2013.774789>
- Venter, O., Sanderson, E. W., Magrath, A., Allan, J. R., Beher, J., Jones, K. R., ... Watson, J. E. (2018). *Last of the wild project, version 3 (LWP-3): 2009 human footprint, 2018 release*. NASA socioeconomic data and applications center (SEDAC). <https://doi.org/10.7927/H46T0JQ4>
- Venter, O., Sanderson, E. W., Magrath, A., Allan, J. R., Beher, J., Jones, K. R., ... Watson, J. E. (2016). Global terrestrial human footprint maps for 1993 and 2009. *Scientific Data*, 3, 160067. <https://doi.org/10.1038/sdata.2016.67>
- Vergara, M., Cushman, S. A., & Ruiz-González, A. (2017). Ecological differences and limiting factors in different regional contexts: Landscape genetics of the stone marten in the Iberian Peninsula. *Landscape Ecology*, 32(6), 1269–1283. <https://doi.org/10.1007/s10980-017-0512-0>



- Vergara, M., Cushman, S. A., Urrea, F., & Ruiz-González, A. (2016). Shaken but not stirred: Multiscale habitat suitability modeling of sympatric marten species (*Martes martes* and *Martes foina*) in the northern Iberian Peninsula. *Landscape Ecology*, 31(6), 1241–1260. <https://doi.org/10.1007/s10980-015-0307-0>
- Walsh, J., Rowe, R. J., Olsen, B. J., Shriver, W. G., & Kovach, A. I. (2016). Genotype-environment associations support a mosaic hybrid zone between two tidal marsh birds. *Ecology and Evolution*, 6(1), 279–294. <https://doi.org/10.1002/ece3.1864>
- Wan, H. Y., Cushman, S. A., & Ganey, J. L. (2019). Improving habitat and connectivity model predictions with multi-scale resource selection functions from two geographic areas. *Landscape Ecology*, 34(3), 503–519. <https://doi.org/10.1007/s10980-019-00788-w>
- Wasserman, T. N., Cushman, S. A., Schwartz, M. K., & Wallin, D. O. (2010). Spatial scaling and multi-model inference in landscape genetics: *Martes Americana* in northern Idaho. *Landscape Ecology*, 25(10), 1601–1612. <https://doi.org/10.1007/s10980-010-9525-7>
- Wasserman, T. N., Cushman, S. A., Shirk, A. S., Landguth, E. L., & Littel, J. S. (2012). Simulating the effects of climate change on population connectivity of American marten (*Martes Americana*) in the northern Rocky Mountains, USA. *Landscape Ecology*, 27(2), 211–225. <https://doi.org/10.1007/s10980-011-9653-8>
- Zeller, K. A., Jennings, M. K., Vickers, T. W., Ernest, H. B., Cushman, S. A., & Boyce, W. M. (2018). Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. *Diversity and Distributions*, 24(7), 868–879. <https://doi.org/10.1111/ddi.12742>
- Zeller, K. A., McGarigal, K., & Whiteley, A. R. (2012). Estimating landscape resistance to movement: A review. *Landscape Ecology*, 27(6), 777–797. <https://doi.org/10.1007/s10980-012-9737-0>

BIOSKETCH

Our research groups are interested in understanding the influence of landscape and environmental features on the evolution,

genetic structure and connectivity of carnivores, helping to determine conservation actions and clarify their taxonomy and evolutionary history. We also have great interest in understanding how the use of different data types on connectivity modeling analyses may impact management decisions, by producing distinct resistance layers.

Author Contributions: Caroline Charão Sartor, Tatiane Campos Trigo, Thales Renato O. de Freitas and Samuel Alan Cushman designed the research. Eduardo Eizirik and Javier A. Pereira provided the samples. Caroline Charão Sartor, Ho Yi Wan and Samuel Alan Cushman analysed the data. Tatiane Campos Trigo, Thales Renato O. de Freitas and Samuel Alan Cushman supervised the project. Caroline Charão Sartor led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Sartor, C. C., Wan, H. Y., Pereira, J. A., Eizirik, E., Trigo, T. C., de Freitas, T. R. O., & Cushman, S. A. (2022). Landscape genetics outperforms habitat suitability in predicting landscape resistance for congeneric cat species. *Journal of Biogeography*, 49, 2206–2217. <https://doi.org/10.1111/jbi.14498>