



UNIVERSIDADE FEDERAL DE UBERLÂNDIA
INSTITUTO DE BIOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E
CONSERVAÇÃO DE RECURSOS NATURAIS



DISTRIBUIÇÃO DE ONÇA-PINTADA NO BRASIL: INTEGRANDO
ASPECTOS DA PAISAGEM E DINÂMICA POPULACIONAL PARA
PREDIZER ÁREAS DE ADEQUABILIDADE AMBIENTAL

LETÍCIA BENAVALLI

UBERLÂNDIA, 2021

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PREDIZER ÁREAS DE ADEQUABILIDADE AMBIENTAL**

Dissertação apresentada à Universidade Federal de Uberlândia, como parte das exigências do Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais para a obtenção do título de mestre.

Orientadora: Natália Mundim Tôres

Coorientador: André Felipe Alves de Andrade

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RESUMO

Avaliações sobre a distribuição atual e adequabilidade ambiental para grandes carnívoros de distribuição geográfica abrangente tornaram-se uma demanda global como uma ferramenta importante para avaliar os requisitos ecológicos mínimos e o impacto dos fatores antrópicos críticos na ocorrência das espécies. No entanto, os modelos preditivos muitas vezes deixam de representar a realidade dos padrões observados na natureza. Nesse sentido, desenvolvemos modelos dinâmicos de distribuição geográfica da onça-pintada no Brasil, integrando os efeitos sinérgicos dos requisitos de adequabilidade ambiental e perda de habitat atual, bem como aspectos da dinâmica populacional em uma escala mais ampla. Além disso, objetivamos entender como a adequabilidade ambiental e diferentes limiares de cobertura vegetal afetam a conectividade da paisagem para esta espécie, sendo capaz de prever mudanças nas taxas de dispersão de onça-pintada como um proxy para sua vulnerabilidade na escala de fragmentos de paisagem. Nossos resultados destacam com maior detalhamento a perda de áreas adequadas em todos os biomas, especialmente para o Cerrado, ecótono Amazônia-Cerrado e Pantanal. Concluimos que a conectividade da paisagem é altamente sensível aos limiares usados para identificar áreas adequadas e recomendamos a necessidade de realizar análises com poder preditivo mais acurado, como a aqui apresentada, para fornecer informações precisas capazes de auxiliar na priorização e manejo em áreas cruciais para a persistência de onça-pintada.

Palavras-chave: Modelagem de distribuição de espécies, dispersão, conectividade, perda de habitat, fragmentação, *Panthera onca*

ABSTRACT

Assessments on distribution and environmental suitability for large and wide-ranging carnivores became a global demand as an important tool to evaluate minimum ecological requirements and the impacts of critical anthropogenic factors on species' occurrence. However, predictive models often fall short in representing the reality of the observed patterns in the landscape. In this regard, we developed dynamic models of jaguar's geographic distribution in Brazil, integrating the synergistic effects of environmental suitability requirements and current habitat loss, as well as aspects of population dynamics on a broader scale. Additionally, we aimed to understand how environmental suitability and different vegetation cover thresholds affect landscape connectivity for this species, being able to predict jaguar range shifts as a proxy for its vulnerability at the scale of landscape fragments. Our results highlight the loss of suitable areas across all biomes, especially for Cerrado, Amazon-Cerrado ecotone, and Pantanal. We conclude that landscape connectivity is highly sensitive to the thresholds used to identify suitable areas and recommend the urgent need of conducting more sensitivity analyses, as the one introduced here, to provide accurate information capable of subordinating on the prioritization and management in crucial areas for jaguar persistence.

Keywords: species distribution modelling, dispersal, connectivity, habitat loss, fragmentation, *Panthera onca*

Apresentação

Esta dissertação faz parte de uma iniciativa que compreende uma conflituosa relação dentro da biologia da conservação e pode ser elucidada por um antigo provérbio japonês:

“Vision without action is a daydream, action without vision is a nightmare”

Em tradução livre “visão sem ação é um devaneio, ação sem visão é um pesadelo”. Um dos aspectos mais desafiadores para aqueles que desejam trabalhar com conservação é colocar em prática aquilo que foi teorizado, o que corresponde à primeira parte do provérbio. Em contrapartida, ações devem ser baseadas em teorias, destacando que muitos modelos ecológicos ainda carecem em representar de maneira mais realística os padrões observados no ambiente. Partindo desse pressuposto e tendo em vista que a distribuição das espécies é um elemento fundamental para a elaboração de instrumentos conservacionistas, este trabalho apresenta implicações fundamentais para o estabelecimento de estratégias de conservação da onça-pintada em território brasileiro. Ao fornecer um mecanismo metodológico cujos resultados podem servir como ponte de cooperação entre pesquisadores e órgãos responsáveis pela elaboração de políticas públicas, buscamos compreender padrões de ocorrência dessa espécie considerando a integração de aspectos da dinâmica populacional em uma escala de paisagem e parâmetros mínimos de requisitos ecológicos.

Introdução geral

Ao longo das últimas décadas, um dos grandes desafios da biologia da conservação está relacionado com o estabelecimento de áreas prioritárias para a conservação da biodiversidade (Mittermeier et al. 2004; Brooks et al. 2006; Margules and Sarkar 2007), principalmente em vista das elevadas taxas de modificação da paisagem (Lindenmayer and Fischer 2013; Newbold et al. 2015) e expansão de áreas urbanas (Wood et al. 2013). Esses processos causam perda excessiva de habitat e diminuição das áreas de vida das espécies, as quais, por sua vez, tornam-se um dos principais fatores a serem compreendidos para mudar o paradigma tradicional da conservação (Ramirez-Reyes et al. 2016), buscando uma visão mais realista a respeito da capacidade de persistência de cada espécie (Miguet et al. 2016).

Dessa forma, em um ambiente dominado pelo homem, para reduzir o risco de extinção de uma espécie, são necessárias ações globais que considerem os requisitos ecológicos dos organismos (Reed 2004). Conectividade funcional e adequabilidade ambiental na paisagem podem aumentar a capacidade de sobrevivência dos indivíduos (Marinho-Filho e Machado 2006), especialmente em ocorrências de eventos extremos, como incêndios, doenças ou predação

(Clark et al. 2011; Azevedo 2017). Estes processos evitam o isolamento de populações e, conseqüentemente, mantêm a diversidade genética capaz que salvaguardar populações viáveis no ambiente - mecanismo importante para planos de conservação de longo prazo (Zetterberg 2010; Peterson et al. 2011).

Nesse sentido, estudos baseados na distribuição das espécies como uma ferramenta para melhorar a conectividade de habitats auxiliam a reconhecer áreas que detêm recursos ecológicos importantes para as mesmas, bem como em quais situações se faz necessário preservar vegetação remanescente (Peterson 2011; Powell 2012). Dentre os muitos fatores que podem impactar negativamente a disposição espacial das populações nos ecossistemas, a perda e fragmentação de habitat são os mais preocupantes (Koskimäki et al. 2014), assim como o crescente conflito com humanos (Carvalho Jr and Morato 2013; Castilho et al. 2017). Embora a perda e fragmentação de habitat sejam processos diferentes (Fahrig 2003), seus efeitos combinados podem causar diminuições expressivas na riqueza, abundância e densidade populacional das espécies (Koskimäki et al. 2014; Murphy and Romanuk 2014).

Para os grandes mamíferos carnívoros, a persistência de subpopulações geograficamente isoladas (i.e. sem conectividade) está diretamente relacionada com a movimentação de poucos indivíduos que se estabelecem em manchas de fragmentos (Saura et al. 2011). No entanto, na maioria dos casos, eles são incapazes de abranger fragmentos suficientes em suas áreas de vida (Thornton et al. 2011) ou mesmo de superar a distância entre áreas inadequadas. Esses empecilhos podem causar declínios demográficos acentuados que comumente resultam em processos de endogamia e deriva gênica (Lino et al. 2018). Ou ainda, a alteração na configuração espacial do habitat pode ser tão abrupta (Weiskopf et al. 2019) que a quantidade de fragmentos remanescentes pode não ser suficiente para auxiliar na dispersão ou refúgio da espécie em questão (Lees and Peres 2009, Mohamed et al. 2013). Como resultado dessas situações, podem ocorrer mudanças no comportamento de movimento dos indivíduos (Tucker et al. 2018; Ramos et al. 2020) e, conseqüentemente, diminuir a persistência das subpopulações em áreas fragmentadas (Watts et al. 2015).

Além disso, este grupo taxonômico representa um dos mais ameaçados, uma vez que seus representantes requerem áreas grandes e interconectadas para sobrevivência, juntamente com uma ampla disponibilidade de presas (Ripple et al. 2014; Ashrafzadeh et al. 2018). Assim, além da problemática da estrutura da paisagem, as conseqüências da perda e fragmentação de habitat também estão relacionadas aos traços ecológicos das espécies, como taxa de crescimento, tempo de vida (Henle et al. 2004) e capacidade de dispersão (Swihart et al. 2003). Nesse sentido, a onça-pintada, *Panthera onca* (Carnivora: Felidae), é uma boa espécie modelo para nos ajudar a

entender como predadores de topo interagem com características da paisagem em um padrão de dependência de escala, uma vez que é amplamente distribuída e ocorre em diferentes tipos de habitats (Sanderson et al. 2002; Petracca et al. 2018).

Apesar de ser um componente-chave na manutenção da biodiversidade dos ecossistemas pelo seu papel ecológico nas redes alimentares (Estes et al. 2011), a onça-pintada encontra-se classificada como quase ameaçada (Quigley et al. 2017). Além disso, estimativas de estudos recentes mostram que pelo menos 48% de sua área de distribuição geográfica original foi reduzida (Ramirez-Reyes et al. 2016; Quigley et al. 2017; de la Torre et al. 2017) – o que a torna suscetível a grandes declínios populacionais em um cenário de paisagens altamente modificadas (Zanin et al. 2015). No entanto, a intensidade dos impactos das ameaças varia em diferentes escalas (Alvarenga et al. 2021), então a integração de um plano abrangente que considere as prioridades ecológicas, demográficas e comportamentais pode potencializar significativamente os esforços para conservar esta espécie (Sanderson et al. 2002).

Nesse sentido, o ponto de partida inicial, que simultaneamente satisfaz múltiplos critérios de conservação (Zetterbeg et al. 2010) e gere resultados efetivos na discussão de ações conservacionistas para a onça-pintada, é o mapeamento da distribuição geográfica e os consequentes limiares ecológicos que essa espécie é capaz de suportar, indicando o momento no qual as mudanças na paisagem diminuem as chances de sua ocorrência. Atualmente, integrar efeitos de diferentes escalas nessa metodologia é uma tarefa árdua, considerando que se deve examinar a distribuição das condições ambientais abióticas e bióticas, bem como as restrições históricas de dispersão (Guisan and Thuiler 2005; Soberón 2007). Além disso, em território brasileiro, existe um agravante ainda maior para a onça: a ausência de proteção de grande parte das suas áreas de ocorrência (Sollmann et al. 2008), resultando em intensa sobreposição com áreas predominantemente utilizadas para o desenvolvimento econômico (Ellis and Ramankutty 2008; Boivin et al. 2016). Isso pode gerar efeitos idiossincráticos em modelos de distribuição que visem estabelecer padrões gerais de ocorrência.

Diante do exposto, nós buscamos desenvolver modelos dinâmicos de distribuição geográfica de onça-pintada no Brasil, integrando os efeitos sinérgicos dos requisitos mínimos de adequabilidade ambiental e a perda de habitat atual, além de aspectos de dinâmica populacional em uma escala de paisagem. Adicionalmente, visamos compreender como a adequabilidade ambiental e diferentes cenários de limiares de cobertura vegetal poderiam afetar a conectividade da paisagem para essa espécie. Para tanto, nos baseamos na metodologia de Modelagem de Nicho Ecológico (*Ecological Niche Models* – ENMs) (DeMatteo et al. 2017; Andrade et al. 2019), que estabelece relações entre pontos de ocorrência das espécies e diferentes condições ambientais.

Finalmente, predizemos a vulnerabilidade de onça-pintada em diferentes cenários de perda de habitat na escala de fragmentos da paisagem por meio de análises de autômatos celulares.

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CAPÍTULO ÚNICO

Este capítulo foi formatado para ser submetido à revista *Landscape Ecology* e, portanto, encontra-se de acordo com as normas exigidas pela mesma.

Jaguar distribution in Brazil: integrating landscape features and population dynamics to predict habitat suitability

Introduction

Distribution patterns of species have been inspiring and challenging ecologists for a long time (Wallace 1860; Grinnell 1917), but within the twentieth century, a new perspective in conservation biology is increasingly addressing the impact of human activities in species' occurrence predictions (Wikramanayake et al. 1998, 2004; New et al. 2000; Sanderson et al. 2002, 2006; Thorbjarnarson et al. 2006). This is especially important due to one demand for the creation of global actions capable to support range-wide mitigation strategies as a solution to avoid biodiversity loss under different scenarios of environmental suitability (Ferraz et al. 2002; Mumby et al. 2011), which comprehend conditional probabilities for species to occur in the environment (Elith et al. 2011). In this sense, mapping species distribution is a key element to identify, in a cheaper and faster way, basic information related to geographic distribution, abundance distribution in space, and environmental risks for a given species (Cavalcanti and Gese 2009).

The ecological Niche Modelling (ENM) approach has presented an exponential growth in its use (Lobo et al. 2010; Oliveira et al. 2020; Cheng et al. 2021; López-Tirado et al. 2021) as an efficient option to model complex relations between species and the environment due to its easy applicability in various fields (Pearman et al. 2010, Silva et al. 2014, Valladares et al. 2014; Tyberghein et al. 2012, Riul et al. 2013) and possible analysis at a geographical scale, rather than microenvironmental (Warren et al. 2008). By generating a measure of environment suitability (Peterson et al. 2011), these models can be used as a predictor of potential ecological, genetic, or even demographic occurrence thresholds (Colwell and Rangel 2009; Diniz-Filho et al. 2009; Nabout et al. 2011; Tôrres et al. 2012). In a practical view, presence-only data are used to estimate potential habitats based on biologically meaningful predictors variables (Pearson et al. 2007; Bradley et al. 2012), thereby, additional areas with similar environmental conditions can be identified (Ramirez-Reyes et al. 2016).

However, despite the huge amount of occurrence data freely available and gathered in biodiversity databases (Soberón and Peterson 2004), predictive models of species distributions have limitations to deal with processes that define the range at finer resolutions, such as biotic interactions, landscape dispersal, and occupation dynamics (Cabeza et al. 2010). So, regardless of the intensive exploration and the new applications of ENMs (Peterson 2011), there are still challenging issues to be addressed related to the dimensions of the ecological factors, which in

turn could be uncharacterized or even misunderstood in the process of shaping the distributions area (Wenger and Olden 2012). This gives space to discuss not only the uncertainty of these models' accuracy but also their (in)capacity to generate results that can represent reality as close as possible, especially considering the urgent need for a forecast regarding the actual and potential impacts of continued anthropogenic actions within species' range (Henriques et al. 2016; Sullivan et al. 2017).

A particularly new and promising approach that represents a methodological advance in this problem is the development of integrated models that encompass population dynamics in this process, helping us understand fundamental aspects of the real minimum requisites to one species not only occur but also persist in the environment (Guisan and Thuiller 2005; Franklin 2010). The incorporation of the population's estimative perspectives enable the focus on the limiting factors for the occurrence of species which is important when considering both anthropogenic and natural disturbance, especially because it's possible to simulate models that predict these impacts under different scenarios at large spatial scales (Gustafson et al. 2004; Scheller et al. 2005). In that case, linking species distribution, population dynamics, and landscape features provide a powerful framework to analyze how these synergetic factors affect species distribution by identifying suitable habitats and demographic parameters in these areas (Crooks et al. 2011). Furthermore, in the landscape attributes context, features such as reminiscent vegetation percentual and matrix quality (Pardini et al. 2010; Fahrig et al. 2011) are important topics to evaluate species dispersal ability as a proxy to identify more suitable areas and species migration possibilities in the future (Williams et al. 2008; Midgley et al. 2006; Early and Sax 2011).

This complex incorporation of finer-scale factors on landscape dynamics assesses potential changes in the distribution of suitable habitats taking into account several scenarios of extinction risk (Akçakaya et al. 2006) calculated from basic ecological requirements and simulations of demographic parameters thresholds such as colonization, dispersal, or extirpation indexes (Franklin 2010). In this regard, cellular automata (CA) modelling represents an alternative tool for spatially explicit simulations of dispersal and habitat suitability (Wilson et al. 2009), since it allows the simulation of metapopulation dynamics under realistic landscape scenarios (Nijs et al. 2004). One important support to understanding the ecological perspectives behind CA modelling is the habitat amount theory, which relates landscape features and habitat amount (Fahrig 2013) and predicts that this last one is a good proxy for species persistence (Mendes and De Marco 2017).

Several studies used CA models to integrate climate change and land use-induced changes in habitat suitability (Ostendorf et al. 2001; Dullinger et al. 2004; Iversen et al. 2004a; Engler and Guisan 2009; Vliet et al. 2009) to explore future scenarios and support the decision-making process in conservation by anticipating impacts caused in species' regional distribution, unraveling future patterns trends (Declerck et al. 2010; Melo et al. 2013; Beca 2016). This approach generates a more realistic view of the challenges that species face within natural ecosystems, once it considers resources dispersal and species' movement capacity to determine species occurrence and persistence (Fahrig 2001; Mendes and De Marco 2017).

This mitigation strategy for preventing biodiversity loss and increasing populations' persistence (Heller and Zavaleta 2009) can be improved by a multipurpose spatial analysis that identifies, for example (i) which areas should be priorities in terms of habitat quality and connectivity (Moilanen et al. 2005; Magris et al. 2015; Rayfield et al. 2016) or (ii) predict under which environmental conditions the extinction process should occur. For this last one, the theory of extinction thresholds, within the deterministic perspective, connects critical values of one or more parameters in which a population can't persist beyond or under them (Bascompte 2013). In the context of this work, a critical threshold is performed by a shift across the parameter of habitat loss, meaning that reached values above this threshold represent habitat destruction. This process is directly related to the loss of suitable habitat and can lead to the extinction of metapopulation (Zartman et al. 2006).

Regarding the landscape structure, the effects of the threshold can be discussed in both qualitative and quantitative terms, that is the production of various small and isolated patches (With and King 1999) and the reduction in the proportion of habitat (Bascompte and Solé 1996), respectively. Both processes reduce landscape connectivity (i.e fragmentation) through a disruption of the habitat's continuous clusters (With 1997), so, even in the presence of suitable habitat, a species can become extinct if the rate of local extinction exceeds the rate of colonization (Lande 1987). The ecological impacts of habitat loss at which this threshold in landscape connectivity influence species' dispersal abilities and behavior, therefore, it may interfere with their dispersal success (Fattebert et. al 2015). This means that a widespread population can be led to extinction if it reaches an abrupt decline in habitat occupancy (Fahrig 2001; Ficetola and Denoël 2009), in this sense, the prediction of thresholds is a major ally for conservation targets, especially when discussing the effects of habitat loss and land-use change (Groffman et. al 2006).

Thus, for rare or already threatened species, identifying sites where occurrence probability is high (Engler et al. 2004) and extinction thresholds should be driven by a full

understanding of how the interaction of biotic and abiotic variables operate on a landscape scale (Lawton et al. 2010; Mendes and de Marco 2017). In this sense, the jaguar, (*Panthera onca*), is found across different habitats, making this species a good model to study how apex predators respond to increased land-use (Morato et al. 2018). On top of that, land-use change causing habitat loss and fragmentation are particularly major threats to jaguar conservation in Latin America (Zimmermann et al. 2005), especially in countries where the human populations demand cause huge and unprecedented impacts on natural habitats (Ceballos and Ehrlich 2002; Ripple et al. 2014; de la Torre et al. 2018; Ceballos et al. 2020; Torres-Romero et al. 2020).

Jaguar habitats are being converted to agricultural lands, pastures, roads, and other human infrastructure (Conde et al. 2010; Haag et al. 2010; Colchero et al. 2011; Cullen et al. 2013, 2016; de la Torre et al. 2018; Thompson et al. 2020). Besides that, threats such as prey depletion, retaliatory killing, and diseases from domestic animals also represent synergic effects on jaguars' geographic range, reducing the habitat capacity to maintain jaguar populations (Sanderson et al. 2002; Quigley et al. 2017; Romero-Muñoz et al. 2019). As a consequence, effects related to the disruption of original occurrence patterns trigger off gene flow decreasing by both reduction of population and population fragmentation processes (Cardillo et al. 2005). Small and isolated populations become the main factors responsible to impede populations' genetic and demographic viability in a long-term and broader scenario (Janecka et al. 2007; Haag et al. 2010; Srbek-Araujo et al. 2018; Wulsch et al. 2016) thus causing a collapse to extinction after long periods of interbreeding (Yumnam et al. 2014) or other human-induced causes (Cardillo et al. 2005; Hill et al. 2019).

Given the above, we developed dynamic models of jaguar's geographic distribution in Brazil, integrating the synergistic effects of minimum environmental suitability requirements and current habitat loss, as well as aspects of population dynamics on a landscape scale. Additionally, we aimed to understand how environmental suitability and different vegetation cover thresholds affect landscape connectivity for this species. Our premise was that the results of the CA model would indicate a reduction in environmental suitability areas in general, but that this difference would be more accentuated in the scenario of maximum land-use conversion. Finally, we predicted jaguar range shifts as a proxy for its vulnerability in different scenarios of habitat loss at the scale of landscape fragments, which gave us aspects of habitat connectivity for this species.

Methods

Jaguar occurrence records and environmental information

Considering the 2000-2019 period, we gathered jaguar basic occurrence data within Brazil from (i) Global Biodiversity Information Facility (GBIF) and SpeciesLink online databases, (ii) scientific literature records, and (iii) Jaguar Conservation Fund dataset, obtained from field records and interviews with local residents, as well non published data from partners' researches. Raw information from online databases isn't systematically raised and may present some level of inaccuracy in their location (Giovanni et al. 2012) but these errors were overcome by the data dissipation considered on our broad scale (Tôrres 2010), aside of using the Google Earth program to confirm or search for lacked georeferenced information and for manual search for points allocated incorrectly. Besides that, to reduce possible sampling bias with autocorrelational occurrence data, we adopted one spatial filtering based on a thinning technique (Aiello-Lammens et al. 2015; Andrade et al. 2020) that considers pairs of occurrences as one within a distance defined by 2x the 10x10 cell size adopted in this study (Velazco et al. 2019). Finally, from a total of 1323 georeferenced records initially assembled, 981 unique occurrences were selected to fit our model.

We selected 4 environmental datasets according to their functional relevance to the jaguar (Valera-Aguilar 2010; Spangle et al. 2014) (Table 1). However, an experimental view of the variables showed us that watercourse, at our landscape scale, wouldn't be a good predictor due to its broader dispersal all over the country, so we deliberately choose to not use this. We used 19 bioclimatic variables and one of terrain elevation, all downloaded from WorldClim (Fick and Hijmans 2017), with 5 arc-minutes resolution, and SRTM (<https://www.usgs.gov/>, accessed on February 2021), with 1 arc-second resolution (~0.03 km), respectively.

Afterward, we resampled the topographic variable to the lowest resolution variables (i.e. 2.5 arc-minutes) performing a bilinear resampling method (Baboo & Devi 2010). Multicollinearity between independent variables could reduce the predictive capacity of our model (De Marco and Nóbrega 2018), so we performed a principal component analysis (PCA) which returned the most important correlations among the variables used. Based on this, we exclude explanatory variables with a variance inflation factor higher than ten ($VIF > 10$) (Queen et al. 2002). This test comprises the proportion of variance in one predictor explained by all the other predictors in the ENM model (Andrade et al. 2020) and reduced to ten variables to be

used in our ENM (Table 2). All variables were cropped to Brazil extent, from 5° to -34° in latitude and -75° to -34° in longitude.

Table 1. Environmental predictor datasets used in jaguar distribution models.

VARIABLES	SOURCE	DESCRIPTION
Bioclimatic	Worldclim	Bioclimatic variables map
Elevation	SRTM	Elevation map
Land cover	MapBiomias	Land cover map
Distance from water source*	IBGE	distance gradient map of the drainage network generated from the river vector map

*considered not suitable for our model.

Table 2. Non-correlated bioclimatic predictors used in our jaguar distribution model.

VARIABLES CODE	DESCRIPTION
BIO2	Mean diurnal temperature range (°C)
BIO3	Isothermality (°C)
BIO4	Temperature seasonality (°C sd)
BIO8	Mean temperature of the wettest quarter (°C)
BIO13	Precipitation of wettest month (mm)
BIO14	Precipitation of driest month (mm)
BIO15	Precipitation seasonality (mm)
BIO18	Precipitation of warmest quarter (mm)
BIO19	Precipitation of coldest quarter (mm)

Information on the 2019 landscape forestry cover was obtained from the MapBiomas platform (MapBiomas v.5), giving us land use and land cover data for all Brazilian biomes within a 30 meters resolution scale. The classification is submitted into an accuracy test that evaluates the pixels in each cell generating six different classes: forest, a non-forest natural formation, farming, non-vegetated area, and water. Furthermore, we attributed binary values (0 or 1) to each one of these classes and their subclasses (Table 3) in order to relate jaguar occurrence and its persistence ability. Thus, forest and non-forest natural formations were considered suitable (1) and all other classes non-suitable (0) (Sanderson et al. 2002; Morato et al. 2016). “Zero” does not mean that the species can’t move through this type of environment, but that it will not persist in an area with only this type of formation. Also, we are aware that persistence can be influenced by other factors, such as prey availability and conflict with humans, but we evaluate only in terms of forest cover, considering that better land-cover conditions are a requirement for landscape connectivity among populations (de Angelo et al. 2013; Olsoy 2016; Ramirez-Reyes et al. 2016).

Table 3. Land-use categories and their binary values attribution, according to jaguars’ habitat suitability. “1” was considered suitable and “0” was not suitable.

ID	CATEGORY	BINARY CODE
1	Forest	1
1.1	Natural Forest	1
1.2	Forest Formation	1
1.3	Savanna Formation	1
1.4	Mangrove	1
1.5	Forest Plantation	1
2	Non-Forest Natural Formation	1
2.1	Wetland	1
2.2	Grassland	1
2.3	Salt Flat	1
2.4	Rocky Outcrop	1
2.5	Other Non-Forest Formation	1
3	Farming	0
3.1	Pasture	0
3.2	Agriculture	0
3.3	Temporary Crop	0
3.4	Soy bean	0
3.5	Sugar Cane	0

3.6	Other Temporary Crops	0
3.7	Perennial Crop	0
3.8	Mosaic of Agriculture and Pasture	0
4	Non-Vegetated Areas	0
4.1	Beach and Dune	0
4.2	Urban Infrastructure	0
4.3	Mining	0
4.4	Other Non-Vegetated Areas	0
5	Water	0
5.1	River, Lake, and Ocean	0
5.2	Aquaculture	0

Environmental suitability modeling

In the first moment, we performed the ENM to evaluate the jaguar's suitable area using only bioclimatic and elevation variables. In a second moment, to better comprehend how anthropogenic factors influence this species' suitability area, we rescaled the binary classification for land-use from 30m to 2.5minutes, in order to obtain a percentual value of favorable habitat for the jaguar. Then, we explored three different scenarios of forest cover values to observe how different land-use prospects could affect jaguar distribution. In this way, we considered 40%, 48%, and 55% of forest cover values as maximum land-use conversion, median and minimum scenarios, respectively.

De Marco et. al (2020) and Mendes and De Marco (2017) used a general value of 50% as a threshold to determine whether areas are unlikely to support long-term populations for some mammal species in the Brazilian savannah and bats, respectively. This value represents a criterion of a minimal amount of natural vegetation to ensure species persistence. However, we don't know the exact value for the jaguar, hence we decided to explore different scenarios and our values were based on the assumptions that (i) according to their individual sensitivity to landscape connectivity, species may have different threshold values, and (ii) 42% is the value required for population persistence (Fahrig 2013). By using a conservative (i.e 55%) and a radical value (i.e. 40%) we captured different empirical responses of the jaguar through changes in the landscape. Importantly, this categorization of the scenarios was created by us, but in reality, these values can achieve even higher or lower percentages.

These scenario values represent thresholds of forest cover amount in each pixel. So, we created a new binary map for suitable areas, where pixels with lower values than the minimum

for the specific scenario received a null value (i.e. jaguar doesn't occur). On the other hand, pixels with equal or higher values than the minimum were attributed to value 1 (i.e. jaguar occur). Finally, we multiplied this new binary map by the first suitability map with only the bioclimatic and elevation variables used as predictors. The multiplication of pixels generates a new suitability value, which this time, considers all environmental variables attributed to this study.

Our model was constructed using four algorithms: (i) gaussian process (GAU), reporting the similarity between the occurrence points using a covariance function and interpolating observed data (Golding and Purse 2016); (ii) maximum entropy model (MXD), estimating the geographic distribution of the species concerning the environmental conditions and presence records also based on the maximum entropy principle (Phillips et al. 2017); (iii) random forest algorithm (RDF), using a random subset of the predictors to create and combine decisions trees (Liaw and Wiener 2002; Prasad et al. 2006) and (iv) maximum likelihood estimation (MLE), estimating parameters from given observations.

Notwithstanding the efficiency of these algorithms in predicting environmental suitability for species, it's required to use absence points to better adjust the model. We didn't consider absence information as these are hardly available in databases, in addition to the difficulty of differentiating between a true absence and a detection failure (Gu and Swihart 2004). As an alternative, we created an environmentally constrained allocation of the pseudo-absences in the region with lower suitability values for jaguar occurrence (Velazco et al. 2017), maintaining a 1:1 proportion with the presence records (Barbet-Massin et al. 2012). Additionally, our results could be influenced by the use of a pseudo-absence approach (Wisz and Guisan 2009; Lobo and Tognelli 2011), but we seek to diminish this bias by defining the whole Brazilian territory extent as the model' suitable adjustment.

Models were validated by block cross-validation with geographic partition structured as a checkerboard. The creation of binary maps to estimate potentially suitable areas is performed by the Jaccard, in which the threshold value is delimited by the Jaccard index. To evaluate the predictive capacity of each algorithm, ENM performance was appraised with the area under the receiver operating curve (AUC) and true skill statistic (TSS) (Allouche et al. 2006). Finally, to report our data's best performance, we created an ensemble model that considered suitable areas predicted by all algorithms, presenting TSS values greater than the mean between the models (Velazco et al. 2019). ENM analyses were conducted in the *ENMTML* R-package version 4.0.5 (Andrade et al. 2020).

Integrated model: incorporating populational dynamic into environmental suitability predictions

We incorporated a cellular automata approach to predict jaguar environmental suitability under simulations of population dynamics process, based on the previous ENM results related to jaguar responses to climatic and land-use conditions. Our general approach was to generate virtual simulations using the population's intrinsic growth rate (r), support capacity (k), and dispersal ability in addition to environmental features in the landscape (i.e. different scenarios of land-use change). So, differences in the jaguar' environmental tolerance and dispersal capacity represent variations in colonization and extinction process (Figure 1).

Populational data were obtained from the National Action Plan for Jaguar Conservation (ICMBIO 2013). This source gathers information for all biomes, but as our aim involved a broader scale, we reached a consensus to use values not so conservative or too exaggerated that could represent the mean for Brazil as a whole (Table 4). To begin with, we created a continuous map with different degrees of environmental tolerance by simulating the projection of the jaguar's distribution within all scenarios. This made possible observe how geographical distribution of suitable areas are affected by a range of the environmental tolerance.

Table 4. Values of the population parameters used in the integrated model, obtained from the National Action Plan for Jaguar Conservation (2013).

POPULATION PARAMETERS	VALUE
Growth rate (r)	0.058
Density (ind/100 km ²)	5
Dispersal ability (km)	40

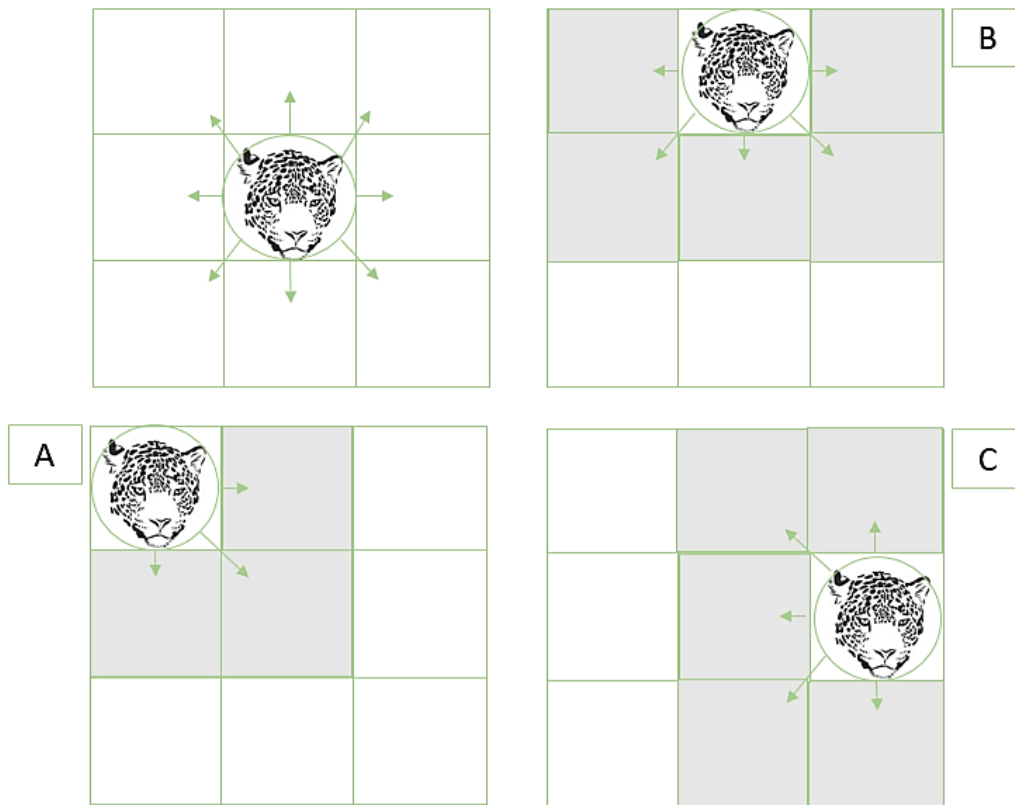


Figure 1. Overall scheme of new cells' colonization occurs in the integrated model. In the first quadrant, all white cells represent good values of environmental tolerance and therefore possible colonization for one individual. In the subsequent time evaluated, grey cells in the quadrants A, B and C represents all colonization options for the individual, accordingly to its position. Occupied cell provides propagules able to colonize neighboring cells.

The next step then was to incorporate population density per 100 km² as one of the parameters to be analyzed to represent long-term persistence in the distribution models. Importantly, we decided to use population density per 100 km² instead of support capacity, considering that our cell size had approximately the same area (9,2x9,2) and this measure can represent a more realistic view related to the number of individuals present in each cell. Finally, using the Matlab software to run 500 simulations, we analyzed dispersal, colonization, growth, and extinction rate of hypothetical populations within each cell in the subsequent time step. This process enabled to captured the variation on the logistical differential growth in the presence of different scenarios and values of habitat suitability. For example, the population growth rate is affected by cell suitability ($r \cdot S_{CELL}$) and the population density (or carrying capacity) is reduced by both habitat amount and suitability ($k \cdot S_{CELL} \cdot HA_{CELL}$) (Figure 2).

$$dN/dt = rN(1 - N/K)$$

Figure 2. Logistic differential equation proposed by Pierre Verhulst. Arrows represent the influence of (i) cell suitability on growth rate (r) and (ii) cell suitability and habitat amount on carrying capacity.

Furthermore, dispersal to neighboring cells was initiated when cell population density was higher than 60%. This generates a value for each cell that represents population abundance at the moment, indicating that when density value was high, dispersion process could occur. In this way, we used environmental suitability maps as a way to parameterize local population dynamics such as dispersion. Dispersal process occur in two levels: (i) landscape-cell, which individuals can move within landscape and locate their optimal habitats and (ii) habitat-cell, which is the smallest unit in the landscape and in this study, giving perspectives of how individuals can move within fragments. So, dispersion was considered within and between landscapes. With the dispersal ability of the jaguar being considered here as 40km, if one individual could reach a non-occupied cell with good suitability, this could be colonized. Therefore, occurrence probability was conceptually equaled to population persistence probability. For each cell, suitability is converted into the probability of persistence for the next interval. Based on these results, we evaluate the chance of extinction considering thresholds of each land-use simulated scenario, that is 40%, 48%, and 55%.

In cases in which its cells' value were bellow of the threshold, we considered that the jaguar cannot survive in the cell. In addition, even if a cell could house more individuals than the amount it already was, if the land-use threshold is below the stipulated, we considered that this cell couldn't sustain more individuals and, therefore, didn't present minimum requirements for jaguar occurrence. Finally, in order to better visualize the results of the integrated model and compared this with the initial ones, we treated CA results as a mask, considering that every cell with a value above 0 (i.e. some level of environmental suitability) was assigned a value of 1 (i.e. suitable). Then, we multiplied both results so that we could visually compare the lost percentage of suitable areas for the jaguar when we consider this integrated and more realistic model.

Results

Environmental suitability model

Regarding bioclimatic and elevation variables, our ENM showed that 82,16% (6.997.175 km²) of the Brazilian territory is capable of retaining suitable areas for jaguar occurrence. This ecological flexibility is shown in all models, but the one with the highest accuracy was the ensemble (AUC=0.983, TSS=0.896, Table 5). All parameters analyzed in our evaluation output result, as well as their standard deviation, were higher than the minimum requested to consider this as a good model to predict jaguar distribution. This can be confirmed with AUC, TSS, and Jaccard values higher than 0.9, 0.7, and 0.7, respectively; and Omission Rate (OR) close to 0 for all algorithms and ensemble (Table 5).

Table 5. Model evaluation for all four algorithms and ensemble. Parameters of AUC, TSS, JACCARD and OR values, as well as their standard deviation, are presented.

ALGORITHM	AUC (\pm SD)	TSS (\pm SD)	JACCARD (\pm SD)	OR (\pm SD)
MXD	0,964 (\pm 0,002)	0,867 (\pm 0,001)	0,875(\pm 0,003)	0,066 (\pm 0,015)
MLK	0,878 (\pm 0,075)	0,634 (\pm 0,170)	0,716 (\pm 0,089)	0,107 (\pm 0,033)
RDF	0,978 (\pm 0,003)	0,865 (\pm 0,012)	0,875 (\pm 0,011)	0,059 (\pm 0,006)
GAU	0,976(\pm 0,002)	0,861 (\pm 0,009)	0,870 (\pm 0,008)	0,067 (\pm 0,003)
ENSEMBLE	0,983 (\pm 0,000)	0,896 (\pm 0,019)	0,900 (\pm 0,018)	0,062 (\pm 0,015)

Despite this initial result, by integrating land-use aspects into the analysis, our findings showed that jaguar's environmental suitable areas were reduced within all three different forest cover thresholds analyzed (Table 6). For the maximum land-use conversion (Figure 3C), 25.6% of suitable areas will be lost, while for median (Figure 3B) and minimum (Figure 3A), this percentage increases to 33,67% and 34,86, respectively (Table 6). As expected, when selecting the maximum conversion scenario, we obtained relatively large and continuous suitable patches across our study area. In contrast, in the minimum scenario with a higher threshold of vegetation cover in the cell, we notice a more fragmented landscape, as well as an increase in the number of small patches. This shows that even cells with a higher percentage of forest cover can't guarantee possible habitat connectivity for the jaguar. This is especially more severe for the south and central region of the Cerrado biome, as well as the entire Atlantic Forest – that

presented minimal habitat suitability, besides being the region with the most isolated and smaller fragments. Further, the median scenario represented the middle ground between the two other scenarios.

In general, there is evidence for a common pattern in the concentration of areas considered unsuitable for the jaguar, in the south, southeast, the entire coast and the south of the central-west region. It is possible to observe this pattern in all the proposed scenarios, highlighting Amazon, Pantanal biomes as core zones of highly suitable habitat for jaguars. Although, some parts of the Cerrado, especially the Cerrado-Amazon ecotone, also presented large suitable vegetation blocks with suitable conditions for jaguar occurrence. Our predictions showed that the range limits are not expected to change within all scenarios, but a decrease in the most suitable areas in addition to the fragmentation increase seems to be a serious problem because many predicted areas to be suitable actually suffer from deforestation.

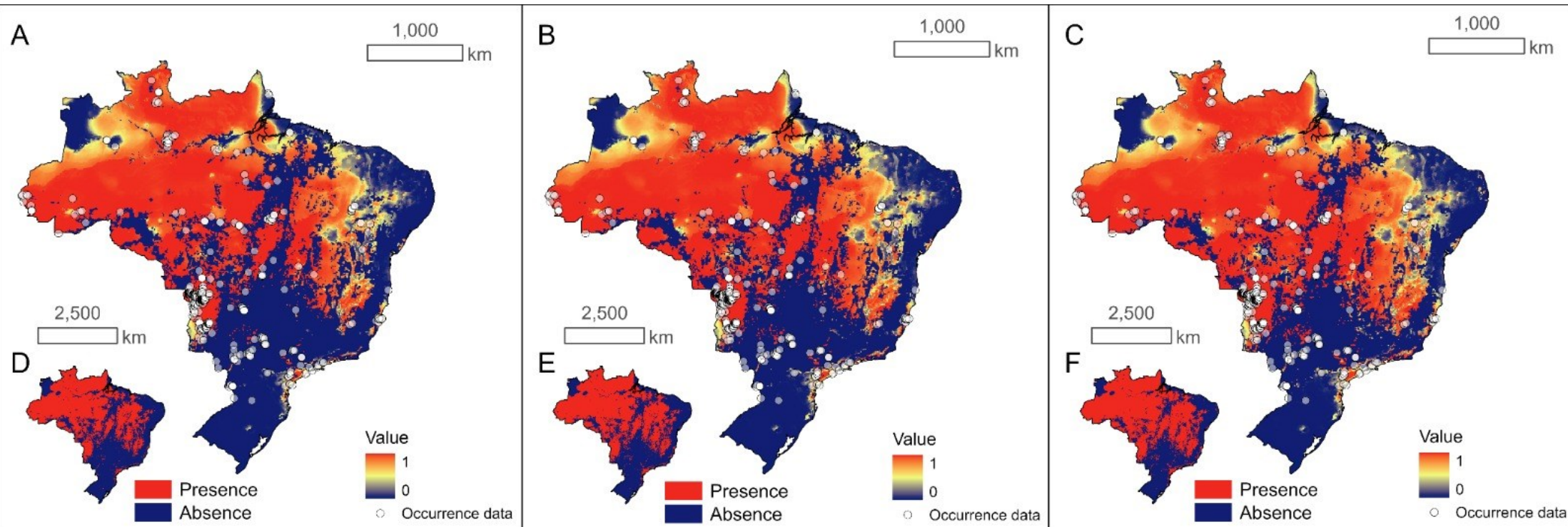


Figure 3. Considering the ENM modelling, the maps show suitable areas for jaguar occurrence based on a scenario of minimum land-use conversion (up to 55% forest vegetation in a cell), median land-use conversion (up to 48% forest vegetation in a cell) and maximum land-use conversion (up to 40% forest vegetation in a cell), respectively. “A”, “B” and “C” are a continuum map with darker red indicating progressively higher habitat suitability for jaguars, while higher darker blue indicates unsuitable areas. “D”, “E” and “F” is a binary map that indicates suitable (red) and non-suitable (blue) areas.

Integrated model: incorporating populational dynamic into environmental suitability predictions

By integrating factors of spatial needs and movements, as well as population' growth rate, the suitable areas for the jaguar has been reduced for all scenarios predictions (Table 7). This is especially seen on the maximum land-use conversion scenario, with a reduction of 9,75% of the total suitable area in relation to the first modeling that considered both environmental and land-use scenarios. For the median and minimum conversion scenarios these values reached 8,54% and 7,89%, respectively (Figure 4). Despite that, the overall view of suitable areas follows the same pattern as the initial modelling, but much more sensitive view of how land-use scenarios can affect jaguar distribution.

Table 6. Environmental suitable areas percentage lost under maximum, median a minimum land-use conversion in Brazil.

	INITIAL MODEL	INTEGRATED MODEL	
Scenario	Area (km²)		Lost areas (%)
Maximum conversion	5.206.462	4.698.544	9,75
Median conversion	4.851.818	4.437.072	8,54
Minimum conversion	4.558.228	4.198.575	7,89

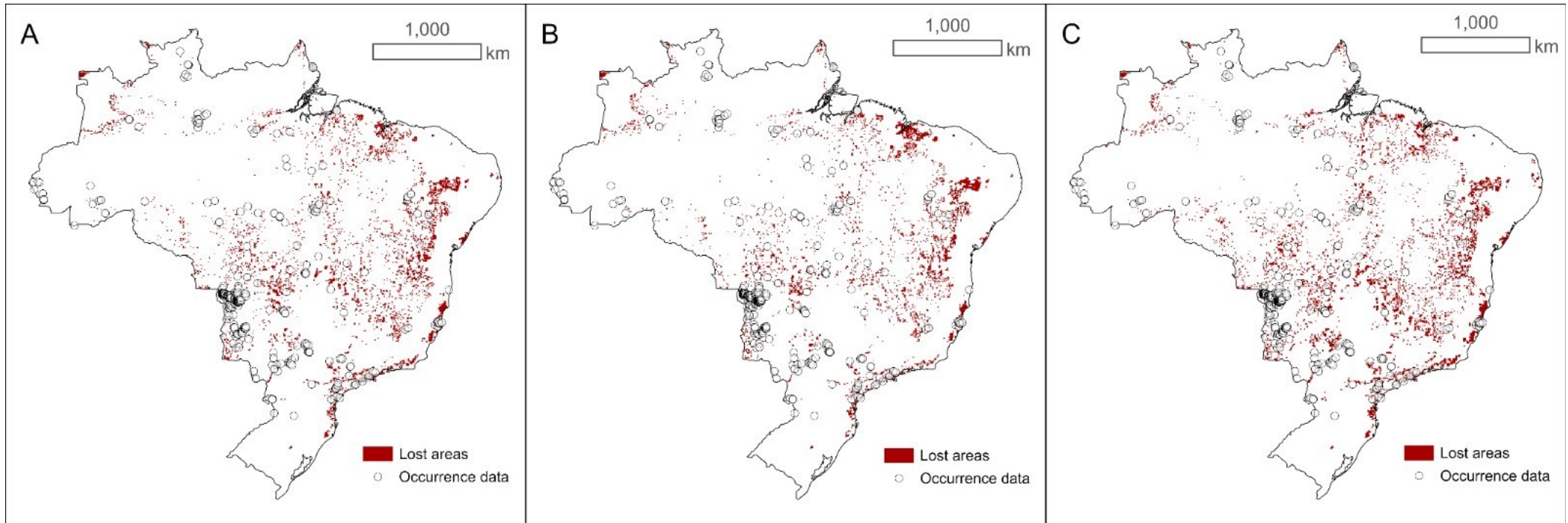


Figure 4. Loss of suitable areas (in red) when comparing results of both initial modelling and the integrated model, considering the maximum, median and minimum scenarios of land-use conversion, respectively.

Not surprisingly, in the maximum land-use conversion scenario (Figure 5C) and in the median one (Figure 5B), we found a more homogeneous scenario of suitable areas indicating that there is a higher level of habitat connectivity. But connection is maintained by minimum thresholds of suitable areas. Here, ecotone region between Cerrado and west Caatinga still present some level of habitat suitability. In addition, the maximum values of population density in a cell were lower in these scenarios of maximum and median land-use conversion. In contrast, in the minimum land-use conversion scenario we found a more fragmented landscape, suggesting that jaguar is highly associated with habitat suitability and low levels of anthropogenic impacts, since its distribution is restricted primarily to areas with larger patches of suitability index values (Figure 5A). In this sense, also in this scenario, we obtained the highest values of population abundance that a cell is capable of housing, indicating that higher values of jaguar density are closely related to higher rates of forest cover in large blocks, putting Amazon, Pantanal and the northeast of the Cerrado biomes as the core zones for jaguar persistence. In relation to jaguar dispersal range and population size, maximum land-use scenarios also showed the highest values, followed by median and minimum scenarios.

Table 7. Population size and jaguar range under maximum, median and minimum land-use conversion scenarios, considering the integrated model.

	Suitable area (km²)	Populational size	Range (km²)
Maximum conversion	4.698.544	107311	55704
Median conversion	4.437.072	101616	52580
Minimum conversion	4.198.575	96628	49729

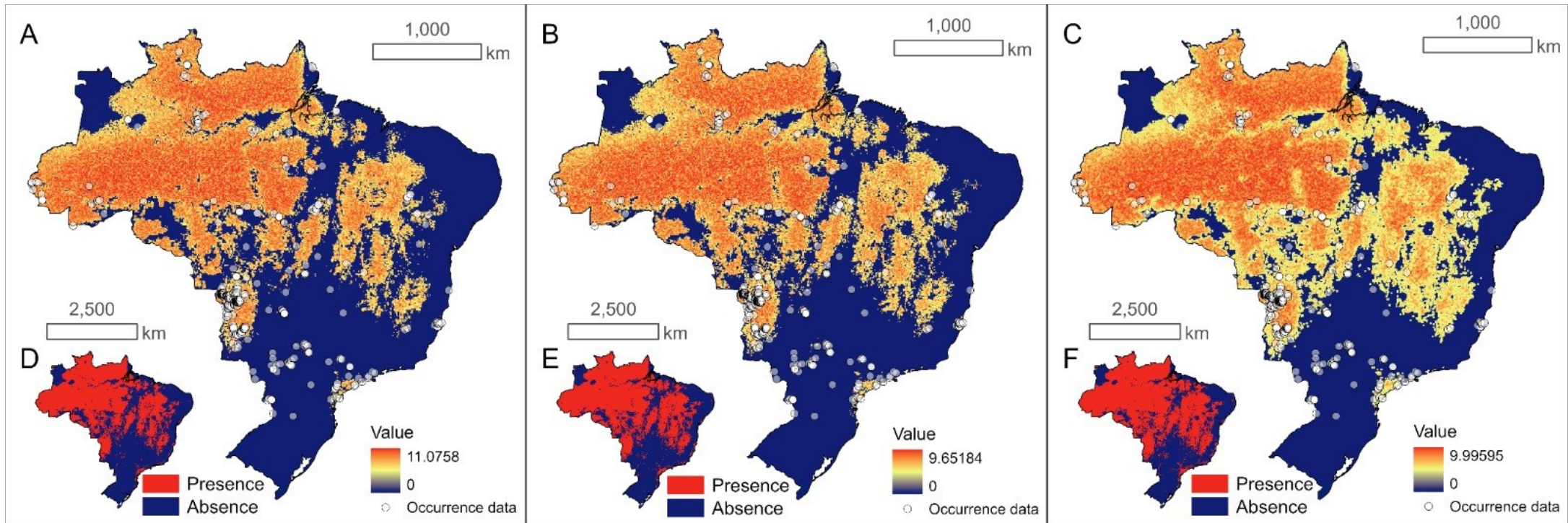


Figure 5. Predictions by the integrated model, showing suitable areas for jaguar occurrence based on scenarios of minimum land-use conversion (up to 55% forest vegetation in a cell), median land-use conversion (up to 48% forest vegetation in a cell) and, maximum land-use conversion, (up to 40% forest vegetation in a cell), respectively. A”, “B” and “C” are a continuum maps with darker red areas indicating indicate progressively higher habitat suitability for jaguars, while darker blue areas indicate unsuitable areas. D”, “E” and “F” is a binary map that indicates suitable (red) and non-suitable (blue) areas. Values from 0 to 9.99 indicate maximum population abundance in one cell.

Discussion

Species distribution modelling is a powerful tool for conservation, however, its limitations related to empirical modelling approach (Mod et al. 2020) often represent a mean to an end rather than an end itself (Franklin 2010). There will always be trade-offs when applying complex mechanistic models as a strategy to fully support actions aimed at protecting biodiversity (Dade et al. 2019) but specific suggestions (Pecchi et al. 2019) lead to a more efficient exploration on the possible methods that reduces the range of uncertainty of how realistic our data can be. Tremendous progress that addresses this problematic has been made, especially considering the control of data' spatial autocorrelation (Tôrres et al. 2012) and pseudo-absences, as well as their effect on the final result of the models (VanDerWal et al. 2009); inclusion of larger scales in the predictions (Allouche et al. 2008) and evaluation of the collinearity effect in the model (Kamino et al. 2012). Integration of these elements within the incorporation of population dynamics and landscape features can provide a powerful framework for linking species geographical distribution in suitable areas and vital rates effects on persistence (Franklin 2010).

In this regard, we have applied a specific rule-based CA model that imposes constraints for jaguar occurrence based on environmental variables, landscape barriers and population dynamics. We have presented a useful methodology to predict suitable areas and connectivity between populations in a broader scale depending upon species behavior and dispersal ability, providing a reference for monitoring future trends in jaguar populations. Thus, this can be applied to conservation planning strategies that actually consider the influence of anthropogenic factors and spatial movements of a species at the top of the food web in Brazil (Morato et al. 2018). Using an updated and reliable data set on jaguar presence and incorporating model uncertainties, we have demonstrated detailed dimensions of habitat loss and connectivity that can be included in a multifaceted and multiscale prioritization (Ewers and Digham 2006; Reino et al. 2013).

Our results followed a general pattern of what can be observed in the literature, this may be due to the well-known predictor variables that closely reflects environmental and geographical limits for jaguar occurrence (Tôrres et al. 2012; Spangle 2014), as well as its broader geographical range (Alvarenga et al. 2021). Despite that, there are interesting insights that detail (i) subtle differences if we relate to our results obtained through modeling suitable areas considering the current jaguar distribution and (ii) differences more accentuated if we relate to our dynamic model results. These differences can be attributed by the incorporation of

changes in land-use for the first case and combination of land-use conversion and population dynamics characteristics for the second, making our estimation of environmental suitability more reliable and consistent, once using actual data from jaguar occurrence. Also, by our specific index of suitability loss simulations, we provide additional interpretation to discuss jaguar' vulnerability within all scenarios, especially for the one related to maximum land-use conversion.

Environmental suitability model

In fact, among our results from the environmental suitability model, the median land-use conversion is the scenario with most similarity when compared with ones already published by other researchers (Tôrres et al. 2008; Ferraz et al. 2013). However, with the increase in deforestation rates over the last few years (Austin et al. 2017; Mammadova et al. 2020), it is possible to adopt a more extreme and restricted view, indicating that this median modeling, in reality, is no longer consistent with what is found in nature, since many areas previously considered suitable were converted into areas for agriculture and pasture, mainly in the arc of deforestation (Garcia et al. 2019) and in the west of the Cerrado, a region under strong pressure from the conversion of natural areas for sugarcane and soy plantations (Strassburg et al. 2017).

Thus, when we consider the scenario of maximum land use conversion, more faithfully close to the mischaracterization of habitats and jaguar populations isolation (Roques et al. 2016; Srbek-Araujo et al. 2018; Piña 2019), our results demonstrate a visible loss of suitable habitat for this species, as long as fragmentation within suitable areas, for some parts of the amazon biome: in the Rondônia state, due to expansion of soybean farming (Amaral et al. 2021), rural population and networks of unofficial roads (Jusys 2016), leading to an isolation of jaguar population in this state; in the extreme northeast of the Amapá and Pará state, with high rates of agriculture expansion and cattle ranching (Cattaneo 2008; Reydon et al. 2019). There is room for an increase of up to 20% in the expansion of traditional economic activities, such as livestock and agriculture, to the Legal Amazon region (Ferreira et al. 2005), bringing us that this reality may be even more dramatic in the future. However, also for this biome, our model could present a limitation related to the northwest of the Amazonas state. It showed us that this area is considered highly unsuitable for jaguar occurrence, but this can be justified by the lack of primary occurrence data (probably due to the inaccessibility of field validation of this species), since environmental conditions and even vegetation cover, are similar to other regions considered suitable.

In the Cerrado biome, which reached alarming deforestation rates in recent years (Strassburg et al. 2017; de Arruda et al. 2019), over 20.400 km² of its native vegetation were suppressed between 2017 and 2019 (Assis et al. 2019). This corroborates our results related to the loss of suitable habitat in the Cerrado-Amazon ecotone region, where between the state of Maranhão and Pará, studies have indicated that the main factors associated with this deforestation are high human population density (Trisch and Torneau 2016), agriculture (Laurence et al. 2014) and road proximity (Barber et al. 2014). In addition, Goiás (in Federal District surroundings), and Northern Cerrado (MATOPIBA region - Bahia, Piauí, Tocantins and Maranhão states) were the regions that most demonstrated fragmentation of suitable areas and this may be associated with deforestation rates 241% higher than in any other Cerrado area, being considered as the last agricultural frontier of this biome (Graesser et al. 2018; Trigueiro et al. 2020).

This could also explain our results related to the Caatinga biome, since jaguar populations within Piauí and Bahia, mainly from National Parks, could face an isolation in the future, considering actual rates of deforestation (Antongiovanni et al. 2018). This result represents a trend already described (Roques et al. 2016), but it is much more worrying because it demonstrates that measures are not being adopted to prevent an even greater isolation of Caatinga jaguars from other populations (Morato 2014). This suggests that the only feasible possibilities for jaguars in Caatinga will be extinction through a process of population isolation, since the Cerrado, the most feasible connection of suitable areas for this biome (i.e. in the Cerrado-Caatinga ecotone), is suffering from a large mosaic of deforestation on remaining natural areas.

Finally, Pantanal and Atlantic Forest biomes were the one that presented most similarity with the information already described in the literature. For all scenarios, Atlantic Forest represents the biome in which we found most areas with lowest values of habitat suitability, excluding some regions from the São Paulo and Paraná states, which represents conservation units (Paviolo et al. 2016; Diniz et al. 2018). However, for Pantanal, we alert that although we observed a good environmental suitability for jaguar occurrence, only 9.3% of this area is protected by conservation units (Alvarenga et al. 2021), indicating that future monitoring should be a prioritization, especially in the largest continuous portions of northwestern of the Mato Grosso do Sul state.

Integrated model: incorporating populational dynamic into environmental suitability predictions

Our initial hypotheses were corroborated with the reduction of the total suitable areas for all scenarios, especially, being higher for the prediction that considered maximum land use conversion value. This demonstrated the effectiveness of the dynamic model in better explaining multiple factors that threaten jaguar distribution in Brazil, since the areas with the highest probability of occurrence are regions where this species is more likely to persist (Moilanen et al. 2005). In this way, by simulating different forest cover thresholds in synergy with dispersion metrics (as a proxy of colonization) and habitat suitability (as a proxy of extinction) in each grid cell, we could capture the variation of hypothetical population viability within all study area – crucial parameters to be considered in a long-term conservation plan (Rabinowitz and Zeller 2010).

Firstly, in relation to the differences between the scenarios of land-use conversion, by increasing the conversion threshold for 55%, we realize that there is greater isolation between the suitable areas. While decreasing, the environmental suitability in the landscape becomes more homogeneous and connected. At first sight this may seem positive, but is very alarming, once this connectivity is associated with areas of low quality and with lower carrying capacity values capable of maintaining the persistence of jaguar populations. These results can be discussed from the point of view of the habitat amount theory, as they relate the survival probability of a species considering different ecological thresholds, such as reproductive and dispersal rates, habitat loss and matrix quality (Fahrig 2001; 2003). Also in this topic, our unexpected result regarding the carrying capacity estimate for the maximum land-use conversion scenario was higher than that for the median scenario. However, it is important to emphasize that new individuals have the ability to colonize a new cell, but it may be that in the subsequent time this would generate greater mortality in the cell. This is a methodological aspect that can be better analyzed in the future, as several studies show that higher density of individuals is related to prey availability and vegetation cover (Karanth et al. 2004; Ramalho 2012).

Additionally, many studies highlight the importance of quality and spatial arrangements of habitats as structural features enabling species to persist or even change their distributions in response to landscape changes (Early and Thomas 2007; Hodgson et al. 2009; Doerr et al. 2011; Frey-Ehrenbold et al. 2013; Alagador et al. 2015; Rayfield et al. 2016). For the jaguar, large and high-quality habitats are the main determinants for population' dispersal ability (Thompson

et al. 2021), so that new areas can be colonized by source populations and establish a successively persistence in natural environments. Roques et al. (2015) found evidence that habitat deterioration has a huge impact on jaguar genetic patterns, demonstrating that, for all biomes in Brazil, genetic diversity is higher within the largest and continuum habitat and lower when populations are isolated. However, we must be aware that there are other factors besides only vegetation cover linked to the quality of the matrix, such as prey' quantity and environmental productivity (Karanth et al. 2004, 2006; Jędrzejewski et al. 2018). In this matter, our model can generate source-sink situations for some areas where we found good parameters of habitat quality, especially because those could influence growth and fecundity of resident jaguars. So, sink areas represent in the space new chances for individuals arrive (Guisan and Thuiller 2005).

For all scenarios, the results were accurate mainly for the Cerrado, Caatinga and Atlantic Forest biomes. We provide a broad overview of factors that can influence jaguar connectivity, indicating that, with few exceptions, these biomes neither capture the highest suitability for jaguars nor the most important patches for habitat connectivity able to maintain natural heterogeneity between them. Thus, the Amazon and Pantanal represent the largest blocks of suitable areas, followed by smaller blocks east of the Cerrado (Maranhão and Tocantins States), as well as west of the caatinga (Cerrado-Caatinga ecotone and Piauí state).

More isolated, when considering the scenario of maximum land-use conversion and its different effects on suitability for each biome, as well as the pressures to convert natural areas for various economic purposes previously described, several studies help us to understand the effects of land-use alterations in jaguar distribution. For the Atlantic Forest and the Cerrado, the biomes with high levels of deforestation and high human population density (Mello et al. 2016), males present greater home range because they have to travel greater distances to obtain resources and find females (Morato et al. 2016). However, traveling greater distances across less or unsuitable habitats increases the risk of individual's death, mainly to poach or in road-crashes (Fahrig 2007).

Another clear and direct indication of how forest loss and fragmentation in the Atlantic Forest biome can affect jaguar occurrence is its association with almost exclusively medium and large patches of the largest protected areas (Mazzolli 2009; de Angelo et al. 2011). Habitat recovery and connectivity are necessary to increase dispersal between populations as a measure to reduce genetic loss in these regions (Haag et al. 2010), but poach and prey depletion are local threats that also depend upon urgent implementation of conservation actions (Srbek-Araujo and Chiarello 2016). As a measure to improve mitigation in relation to these impacts is the

proposition of spatial prioritization based on population status within key areas, but only 2.8% of this biome is suitable for jaguar persistence, even with low densities rates (Paviolo et al. 2016). Our results of apparent extinction in suitable areas across the northern and southern coastal extremes, with populations currently confined only in São Paulo and Paraná extremely small patches, show that the situation for jaguars in Atlantic Forest can be much more delicate.

For Cerrado, Portugal et al. (2019) also prioritize key areas for jaguar persistence based on high environmental habitat suitability areas, describing that less than 1% of these units fall within protected areas. Our more refined results indicate that there are still suitable areas, but highly suitable are scarce and under isolation, especially for the Mato Grosso state, and for the Bahia and Tocantis states, suggesting that critical ecotones between Cerrado-Amazon and Cerrado-Caatinga can be much more relevant for jaguar persistence than previous described (Morato et al. 2014; Roques et al. 2014; Diniz-Filho et al. 2018). The same trend can be discussed for the northern part of Caatinga, since the contact of populations is disrupted with individuals from the Amazon and the Atlantic Forest, because movement in this landscape seems to be unfeasible (Sanderson et al. 2002). In this sense, feasible habitat connectivity is also restricted to a large mosaic of remaining natural area, especially for the western region of this biome.

In our model, Amazon is the most important biome in terms of quality and suitable area for long-term survival of the jaguar in Brazil, as well as housing a higher density of jaguars in terms of continuous area, as well as described in other studies (de Oliveira et al. 2012; Lorenzana et al. 2020; Menezes et al. 2021). In relation to the result of higher support capacity found only within this biome (i.e. 9.99), we can attribute to the productivity of this region, being one of the highest in Brazil (Silva 2013) and to low human population densities, generating consequently, greater amount of vegetation cover (Jędrzejewski et al. 2018) and smaller rates of prey depletion. However, hunting is an aggravating threat that can influence the number of individuals in the region, especially if we consider key-zones of conflicts with humans (de Carvalho and Desbiez 2013; Jędrzejewski et al. 2017). In addition, continued loss of habitat in the arch of deforestation (Nogueira et al. 2008) - east and southeast limits of this biome – can be the main factor that explains the loss of quality for habitat connectivity and them, diminishing the chances of the jaguar to colonize new cells in our model.

Finally, for Pantanal ecosystem, the worrisome implications of our findings complement information on the National Action Plan for Jaguar Conservation (Desbiez et al. 2013) and Alvarenga et al. (2021), indicating that high human impacted areas are strongly avoided by jaguars and in the absence of actions to mitigate the effects of habitat loss in this biome,

dispersal and gene flow are faded to highly reduce until total isolation of this population. Unfortunately, future projections indicate this pattern (Miranda et al. 2018) due to recent policy changes in the Brazilian forest code (Souza et al. 2020), which legalizes and enhances deforestation rates in areas considered non-forested, such as the Cerrado (savanna) and Pantanal (flooded areas). Another aggravating factor that can reduce the occurrence and connectivity in suitable areas in this biome are current fires, which doubled in 2020 (INPE, 2020). Also, private areas such as private ranches play a major role in jaguar conservation, since it can enhance habitat connectivity. Although the effectiveness of these areas is strict related to building good relation between land-owners and conservationists, long-term jaguar conservation in priority areas may assist even in reducing illegal hunting beyond reserves, with a beneficial conservation agreement for both (Gutiérrez-González et al. 2015).

In conclusion, our general results were successful in mapping environmentally suitable areas for jaguar occurrence, indicating that the effects of land-use conversion are more decisive with regard to shaping the distribution of this species than other environmental variables. Using the different thresholds approach, we can particularly predict the effects of landscape connectivity as a predictor of jaguar vulnerability across different biomes. In this sense, our maps and analyzes with greater predictive power can help to design more efficient conservation strategies that consider the context in which the jaguar is inserted, in addition to acting as a regional and site-based platform for jaguar distribution. The methods developed here can easily be applied to other species, especially large carnivores, as a way to detail accurate understanding of the process and responses of this species under different landscape patterns.

Data limitation

The option to generate a dynamic model at the national level allows a broader view of the main favorable regions for the jaguar, making it easier to direct the allocation of (i) research efforts to areas where basic information is still lacking, such as the case from the extreme west of the Amazon, and (ii) public policies that enable the persistence of this species in the long term throughout the national territory. However, for the next steps, this approach can bring even more interesting and important results if observed at the level of biomes, or even, on an even smaller scale, among the areas already considered as priorities for the conservation of the jaguar. These analyzes can demonstrate, with even more sensitivity, the real conservation status of this species, as well as the main threat factors at local scales, in areas inside and outside of environmental protection, considering that conservation units represent only 12% of the Brazilian territory. Thus, we can identify primary targets for jaguar movement and thus

maintenance of ecosystem functioning (Bauer and Hoye 2014) and determine the extent to which jaguar can persist in human-dominated areas.

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Considerações finais

A onça-pintada é considerada uma espécie-chave para a manutenção da biodiversidade, visto que exerce controle populacional de suas presas e, portanto, participa de processos importantes na paisagem. Apesar disso, suas populações vêm sofrendo grande declínio e a perda de habitat e fragmentação da paisagem representam umas das principais ameaças para a conservação a longo prazo dessa espécie. Nesse sentido, a disponibilidade de áreas adequadas para sua sobrevivência, bem como a conectividade da paisagem, pode atuar como fontes mantenedoras da qualidade genética. Dessa forma, a modelagem de distribuição de nicho e conectividade da paisagem é uma abordagem promissora que apresenta uma forma mais abrangente de compreender, por exemplo, a relação entre distribuição geográfica e requisitos ecológicos mínimos necessários para a persistência dessa espécie (e tantas outras).

Apesar de inúmeras aplicações para a biologia da conservação, muitas pesquisas carecem em apresentar resultados próximos da realidade que as mesmas procuram analisar. Portanto, as limitações dessa metodologia, como métricas de avaliação, dados de ocorrência de qualidade, entre outras, devem ser consideradas para incrementar o desempenho dos modelos. Além disso, as características ecológicas, bem como as ameaças para sua sobrevivência, podem influenciar a performance dos resultados. Assim, nesse trabalho apresentamos um modelo dinâmico que integra as características ambientais, aspectos de dinâmica populacional e ameaças atuais para detalhar, em uma escala de paisagem, a distribuição atual de onça-pintada no Brasil. A partir do resultado inicial, convertermos os valores de adequabilidade ambiental em parâmetros demográficos, demonstrando, de maneira clara, como as alterações antrópicas na paisagem afetam a ocorrência dessa espécie.

Embora o padrão seja o mesmo já discutido na literatura, nossos resultados demonstraram com maior acurácia as regiões que limitam a ocorrência, conectividade e, conseqüentemente, persistência da onça-pintada, com destaque para o arco do desmatamento na Amazônia, ecótono entre Caatinga-Cerrado e, finalmente, áreas isoladas da Mata Atlântica.

Essa interface teórica de identificar quais e a intensidade de fatores preocupantes deve ser avaliada por programas de conservação de longo prazo. Entretanto, destacamos que as avaliações de distribuição das espécies em grandes escalas são importantes para estudos que visem orientar o estabelecimento de estratégias de conservação, sendo também de extrema importância compreender os mecanismos que influenciam a mesma em menor escala. Para a onça-pintada, por exemplo, deve-se considerar ainda aspectos de outras ameaças antropogênicas, como o conflito com humanos e a caça de presas e, se esses mecanismos atuam de maneira diferenciada para cada bioma. Apesar das limitações, a metodologia aqui empregada demonstra ser uma boa alternativa para obtenção de predições mais acuradas, de forma que pode ser uma aliada fundamental para pensarmos em medidas mais direcionadas às ameaças atuais e às características ecológicas específicas da onça-pintada, podendo ser aplicada para outras espécies e para estudos mais robustos.