
**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, EVOLUÇÃO E
BIODIVERSIDADE**

**THE IMPACT OF CLIMATE AND LANDSCAPE ANTHROPIZATION ON
CARNIVORE MOVEMENT: A MULTI-SCALE APPROACH**

Marina Furlan Giubbina

**Rio Claro – SP
2023**

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CARNIVORE MOVEMENT: A MULTI-SCALE APPROACH

Marina Furlan Giubbina

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de doutora em Ecologia, Evolução e Biodiversidade.

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Dedico esta tese à todas as mulheres mães cientistas.

Ao meu companheiro Cauê

E às minhas piticas Luna e Flora, sem as quais nunca

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Resumo

O planeta Terra está atualmente enfrentando desafios sem precedentes decorrentes de mudanças induzidas pelos seres humanos, especialmente a antropização da paisagem e as mudanças climáticas, que resultaram na perda de habitat, fragmentação, poluição, espécies invasoras e eventos climáticos extremos. Esses fatores estressantes colocam em perigo a biodiversidade terrestre e perturbam o funcionamento dos ecossistemas. Entre os mais afetados estão as populações de animais, especialmente os carnívoros, cujos padrões de movimento são diretamente influenciados por esses fatores estressantes cumulativos, moldando a distribuição e as interações das espécies. Esta tese de doutorado tem como objetivo compreender o impacto do clima e da antropização da paisagem sobre a movimentação de carnívoros. O primeiro capítulo fornece uma revisão bibliográfica evidenciando a necessidade de uma análise integrada de clima e paisagem para planejamento de estratégias de conservação de carnívoros em uma escala global. Esta revisão culmina em um framework conceitual que conecta sistematicamente os diversos aspectos climáticos e de paisagem afetando a movimentação e uso do espaço por carnívoros. O segundo capítulo explora o impacto do clima e da paisagem na adequação do habitat e no movimento da *Panthera onca* no bioma do Pantanal Brasileiro e também é explorado a influência da sazonalidade, da precipitação e do uso da terra no comprimento de passo das onças-pintadas. Os resultados obtidos indicaram as regiões mais adequadas para a espécie, bem como mostraram a sensibilidade das onças às interações entre clima e paisagem, e a influência da precipitação e da sazonalidade no movimento. Considerando as evidentes mudanças climáticas, medidas regenerativas de conservação, como agrofloresta e sistemas de integração Lavoura, Pecuária Floresta (LPF), que integram a produção de recursos para os humanos e proporcionam um ecossistema saudável para a vida selvagem, são estratégias que indicam ser eficazes dentro do nosso contexto atual. Portanto, essa tese gera dados empíricos demonstrando quais fatores devem ser considerados para conservação da onça-

pintada e conseqüentemente para o bioma Pantanal, já que a onça atua como uma espécie chave mantendo o equilíbrio do bioma.

Palavras-chave: *Clima, Sazonalidade, Pantanal, antropização da paisagem, onça-pintada, Modelagem de distribuição de espécies, movimento animal, comprimento de passo.*

Abstract

The Earth is currently facing unprecedented challenges arising from human-induced changes, notably landscape anthropization and climate change, which have led to habitat loss, fragmentation, pollution, invasive species, and extreme climate events. These stressors endanger terrestrial biodiversity and disrupt ecosystem functioning. Among the most affected are animal populations, particularly carnivores, whose movement patterns are directly influenced by these cumulative stressors, ultimately shaping species distribution and interactions. This doctoral thesis aims to comprehend the repercussions of climate and landscape anthropization on carnivore movement. The first chapter provides a review of the influence of climate and landscape anthropization on animal movement, with a specific focus on carnivore mammals. It was evidenced that there are few studies analyzing the effects of climate and landscape on carnivore movement, and the combined analysis of these factors is of utmost importance to plan conservation strategies in a scenario of constant climate and landscape changes. The second chapter explores the impact of climate and landscape on habitat suitability and movement of *Panthera onca* in the Pantanal biome and we also explore the influence of seasonality, rainfall and land use on Step Length of jaguars. The results obtained indicated the regions most suitable for jaguars, as well as showing the sensitivity of this species to the interactions between climate and landscape and the influence of rainfall and seasonality in the movement. Considering the evident climate changes, regenerative conservation measures, such as agroforestry and agro-silvopastoral systems, which integrate resource production for humans and provide a healthy ecosystem for wildlife, are strategies that appear to be effective within our current context. Therefore, this thesis generates empirical data demonstrating which factors should be considered for jaguar conservation and consequently for the Pantanal biome since the jaguar acts as a keystone species maintaining the biome's balance.

Keywords: Climate change, seasonality, Pantanal, landscape anthropization, jaguars, Panthera onca, species distribution modeling, animal movement, step length.

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1. General Introduction

The Earth is facing unprecedented challenges as a result of human-induced changes, such as landscape anthropization caused by land use and climate change (Newbold et al., 2015; Crowther et al., 2014; Aycrigg et al., 2021; Wolf et al., 2020). These stressors, including habitat loss, fragmentation, pollution, invasive species, and extreme climate events, are threatening terrestrial biodiversity and disrupting ecosystem functioning (Newbold et al., 2015). Among the various impacts, the movement patterns of animal populations, particularly carnivores, are directly affected by these cumulative stressors, ultimately influencing species distribution and interactions (Tucker et al., 2018; Yackulic et al., 2011; Gaynor et al., 2018).

Carnivores, as large-bodied predators, play critical roles in ecosystems functioning, regulating their prey population levels and sometimes acting as seed dispersers (McColgin et al., 2017; Symes et al., 2017; Silveira et al., 2016). However, they are highly susceptible to the effects of landscape anthropization due to their needs for extensive living areas and their solitary or small group behavior. Another challenge that the carnivores are facing is related to climate modifications, once it is undeniable that the Earth's climate has been changing due to human activities (Wolf et al., 2020).

To persist in these rapidly changing climate condition environments, much of today's biota will need to traverse human-dominated landscapes (Gaynor et al., 2018). Therefore, understanding how climate variables, such as temperature, precipitation, and seasonal variations, interact with habitat loss and fragmentation to influence carnivore movement is essential to develop more effective conservation strategies (Ausband et al., 2016; Droghini & Boltin, 2018).

Animal movement is driven by factors like thermoregulation, resource availability, and seasonal changes, which directly impact foraging and dispersal movements (Inman et al., 2020; Farhadinia et al., 2020). The animal movement is a multifaceted process that operates across various spatio-temporal scales and shapes biodiversity patterns (Schweiger et al., 2012), thus affecting genetic diversity, metapopulation and metacommunity dynamics (Blaum et al., 2012; Vanschoenwinkel et al., 2008). Consequently, elucidating the relationship

between landscape attributes and habitat distribution is crucial for assessing species survival and conservation planning (Jennings et al., 2016; Hämäläinen et al., 2017).

To address these pressing ecological challenges, the main objective of this doctoral thesis is to understand the effects of climate and landscape anthropization in the movement of carnivores. The first chapter aims to provide a comprehensive conceptual synthesis of climate and landscape anthropization on animal movement, with a focus on carnivore mammals. By examining the responses of carnivores to climate variables and anthropogenic landscape attributes, this research contributes to a better understanding of species distribution, genetic structure, and population viability (Karelius et al., 2019; Aycrigg et al., 2021).

The second chapter aims to understand the impact of climate and landscape alterations in the habitat suitability and movement behavior of *Panthera onca* in the pantanal biome and the influence of seasonality in the movement patterns shaped by rainfall and land use. Ultimately, our findings are crucial to carefully implement conservation measures and strategies to safeguard ecosystems and the diverse fauna they support in the face of rapid global changes.

2. Objectives

Our main objective in this research was to understand the influence of climate and landscape anthropization on carnivore movement. More specifically our objectives were:

In chapter 1, *An overview on climate and landscape anthropization impact on carnivore movement*: to perform a conceptual research of the influence of climate and landscape anthropization on carnivore movement and provide a framework with the findings.

In chapter 2, *The impact of climate and landscape on jaguar's movement*: we intended to answer the questions:

1. How does climate influence the habitat suitability of *Panthera onca* in Pantanal biome?
2. How does Landscape variables influence the habitat suitability of *Panthera onca* in Pantanal biome?
3. How the movement of jaguars is affected by habitat suitability?
4. How does the rainfall influence seasonality movements of jaguars?
5. How does seasonality influence the movement of jaguars in different land uses?

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CHAPTER I - An overview on climate and landscape anthropization impact on carnivore movement

An overview on climate and landscape anthropization impact on carnivore movement

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Abstract

Climate change, habitat loss, and fragmentation are concurrent processes that have synergistic effects on wildlife. These stressors are of great importance for species persistence within their current geographical range and significantly impact animal dispersal. The ability of species to move within the landscape is crucial for individual survival. Anthropogenic habitat loss and fragmentation result in spatial alterations of the environment, affecting species' perception of the landscape, which, in turn, influences their movement capacity. This can have serious consequences for ecosystem dynamics, such as the disruption of trophic chains, seed dispersal, gene flow, and natural regeneration. Additionally, climate factors, such as temperature, precipitation, and seasons, play a significant role in influencing these movements. The combined effects of climate change and landscape anthropization on animal movement, particularly for carnivores, remain uncertain. Understanding the factors that influence the space requirements of fauna is essential for implementing effective conservation measures in a changing climate. To address this, we conducted a comprehensive review of scientific papers focused on landscape topics, climate topics, and their influence on carnivore movement. Through our review and summarization of these papers, we have developed a conceptual framework that enhances our understanding of how landscape anthropization and

climate impact carnivore movement. Our findings demonstrate that specific factors, such as habitat type, cultivated lands, human activity, precipitation, temperature, and others, influence the foraging and dispersal patterns of carnivores. Habitat loss and fragmentation strongly influence species movement and, consequently, their ability to adapt to climate change by searching for habitats with suitable conditions for survival. Establishing a clear link between land use change, climate, and animal movement is crucial to improve our understanding of ecological processes and to develop more effective conservation and management strategies for fauna and ecosystems.

Keywords: climate, habitat loss, fragmentation, animal movement, seasonality, precipitation, temperature, connectivity, landscape structure, land use.

Main text

One of the most important questions in ecology and conservation is how cumulative stressors — such as habitat loss and fragmentation, climate change, pollution, invasive species and diseases — impact ecosystems and its fauna. Despite these stressors occurring simultaneously and posing threats to ecosystem and their functioning, they are often studied in isolation [56; 18]. Climate change, habitat loss, and fragmentation are prime examples of co-occurring processes that have synergistic effects on wildlife [56]. These stressors play a significant role in the persistence of species within their current geographical range and can impact species dispersal [39].

Climate variables, such as temperature, precipitation and seasonal variations of the environment affect ecological processes such as animal movement [26, 71]. For instance, these factors influence the period of time and which resources are available, such as water, preys and forage patches [21, 30]. Thus, the wildlife activity patterns will depend on their adaptations to climate variations. The species respond to environmental temperature by thermoregulating with physiological and behavioral strategies, thus the temperature is a crucial climate factor that determines movement patterns [4]. The precipitation influences water and food resources availability, hunting visibility, which directly affect movement decisions of animals [4]. In addition, seasonal variations influence both temperature and precipitation, thus many species exhibit seasonal changes in behavior [99; 59; 98]. Therefore, understanding how climate factors influence habitat use is crucial to understand species distribution, species interactions and how wildlife respond to climate change [94].

The human-induced habitat loss and fragmentation are the main factors that cause global climate change and biodiversity loss [10]. The landscapes resulting from fragmentation as a process (*sensu* Fahrig 2003 [29]) changes the distribution of resources such as habitat, water, forage patches [22], feeding resources, such as preys [31] and consequently affect species decision movements. In the anthropocene, a fragmented landscape is characterized by the presence of patches of natural habitats surrounded by human modified land cover [59].

The landscape connectivity is a multi-scalar concept that allows us to investigate how the interaction of landscape elements influences animal movement capacity, and consequently affect species survival [54]. Thus, the landscape connectivity is shaped by both the availability and spatial configuration of the habitat (i.e. land cover types, anthropogenic or natural barriers; [13]). The ability of organisms to inhabit and navigate in these environments is crucial for the survival of the species [15;88]. Therefore, understanding how functional connectivity affect animal movements are of utmost importance to elaborate conservation planning since it strongly affects animal dispersal, habitat selection, genetic structure and viability of populations [5].

The movement of an organism is driven by processes that act across multiple spatio-temporal scales. It plays a key role in biodiversity patterns, which directly and indirectly determines species distribution and species interactions [90]. Furthermore, the animal movement shapes species genetic diversity [7, 92; 61], metapopulation dynamics [82], potencial seed dispersal [87; 37, 80] and linkage on metacommunity dynamics [101, 23, 59].

There are several types of movement categories: migratory resident (including dispersion) and nomadic. Within these categories there are movements to find mates, defend territory, and the most studied with carnivores, foraging and dispersal [6]. The foraging movements occur within home ranges and may take place repeatedly at the same day, while the dispersal are movements that occur away from the birthplace towards another location (e.g. for reproduction), with peaks occurring in specific seasons [42].

Carnivore mammals (order Carnivora) are excellent models to comprehend how landscape anthropization and climate variations affect their movement, since they generally require large living areas, they are solitaires or live in small groups and suffer with hunting pressure [3; 29; 75; 56]. Large-bodied carnivores also tend to be in high levels of threat in places with human contact, since they may represent a risk to livestock and/or people, thus they are killed [84]. These carnivores have a great importance for the maintenance of trophic

chain, acting as predators and seed dispersers (i.e. some carnivore-frugivore species such as some Canidae consume fruits and disperse intact seeds [37]; and provide important benefits to humans, such as food, recreation and income [89]. Over 26% of all carnivore species are threatened (IUCN 2020), mainly by the anthropization of the environment that has been considered new drivers of mass extinction events [30]. The extinction of this group may cause serious disruption in ecosystem processes, such as cascade effects, since they act as regulators of population in low levels of trophic chain [85]. Thus, they are excellent models to understand how landscape anthropization and climate variables affect animal movement.

The combined effects of climate variables with habitat loss and fragmentation in animal movement are poorly known, being extremely relevant to comprehend the persistence, movement and distribution of species across the globe [76; 56]. Understanding the space requirements of wildlife is crucial to implement efficient conservation measures for the ecosystem and its fauna [49]. In order to fulfill this gap, our aim here is to provide a conceptual synthesis of how climate and landscape anthropization influences animal movement, particularly carnivores.

In this paper we reviewed studies relevant to these topics and derived a conceptual framework based on reported data. For this, we considered the most studied subjects of landscape alterations (i.e. land use, landscape structure, connectivity) and climate variables (i.e. precipitation, temperature and seasonality), summarized and organized the papers published with these topics and carnivore movement.

Materials and methods

We conducted a search of research on carnivore movement between January 2000 and December 2020 using the scientific citation index "Web of Science®". We used specific keywords to search for papers related to landscape topics, including land use, landscape

structure, or connectivity, as well as foraging or dispersal in relation to carnivores. Additionally, we searched for papers that examined climate variables such as seasonality, precipitation, rainfall, or temperature, along with foraging or dispersal in relation to carnivore taxa. To be eligible for inclusion in our review, the papers needed to be based on empirical data from GPS or radio telemetry experiments. We applied exclusion criteria to remove papers that solely relied on data from camera traps, sightings, expert opinions, genetics, capture-mark-recapture studies, reviews, or traffic road measures, aquatic carnivores. Subsequently, we analyzed the conclusions of the studies regarding the influence of climate or landscape on carnivore movement (Table S1). Using the reported data, we constructed a conceptual framework for further understanding.

Results

We found 213 papers with our survey, with 68% being related to landscape and 32% related to climate variables (Figure 1). After applying the exclusion criteria, the total number of papers examining the effects of climate variables was 16, while 27 papers focused on the effects of landscape variables on carnivore movement (Table S1). The Figure 2 displays the locations where data from all the studies were collected.

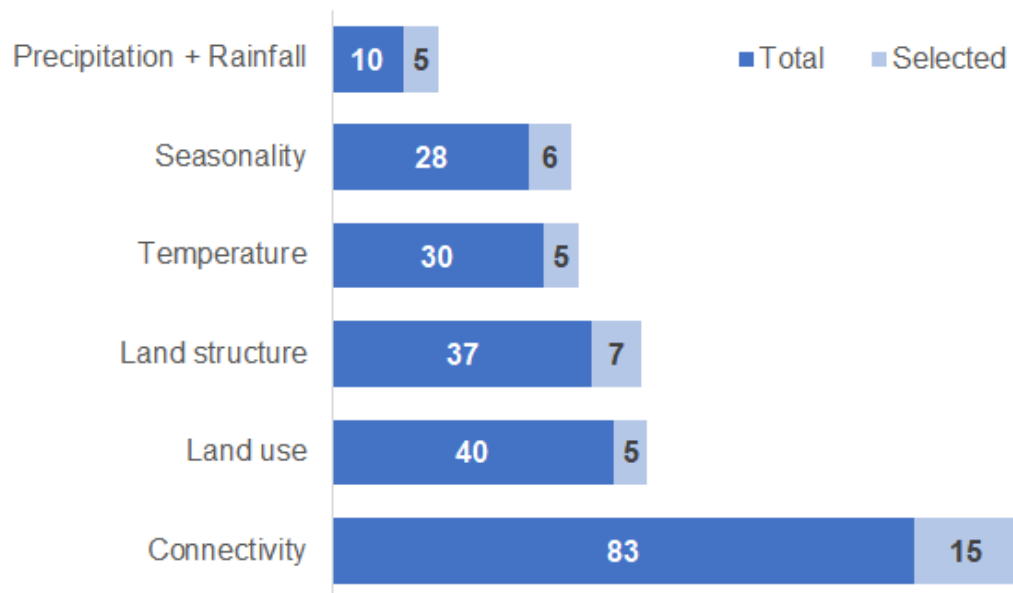


Figure 1. Total publications found (dark blue) in the portal Web of Science before the application of exclusion criteria; issues selected for review after the application of exclusion criteria (light blue) in each topic of climate (seasonality, temperature, precipitation+rainfall) and landscape (landscape structure, land use, connectivity). The exclusion criteria were papers with trap cameras, sightings, expert opinions, occurrence data, genetics, capture-mark-recapture, reviews and traffic road measures exclusively.

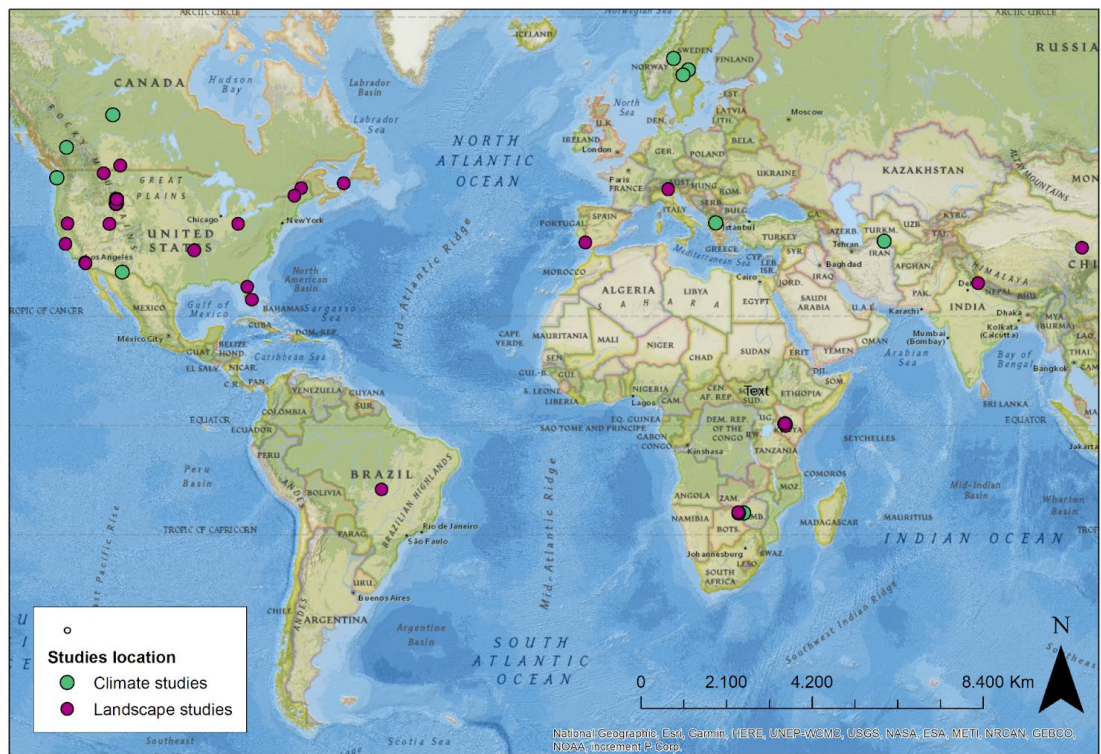


Figure 2. Map representing the locations where the data of all studies were collected. The green dots represent the studies that analyzed climate variables and the red dots represent papers that examined landscape variables.

After reviewing the selected papers, we developed a framework that illustrates the relationship between climate variables and landscape variables and their effects on carnivore movement (Figure 2). This framework aims to enhance our understanding of the factors derived from landscape changes and climate factors that influence carnivore foraging and dispersal decisions. Climate factors refer to the abiotic aspects of the environment that directly or indirectly affect movement patterns. Temperature, precipitation, and seasonality were found to influence step length, dispersal capacity, home range size, and foraging behaviors. Land use changes resulted in alterations in the spatial configuration and composition of the landscape. Consequently, the percentage of natural habitats [33], anthropogenic features [33], habitat types [63, 69, 25], and cultivated lands [63] affected the movement patterns of the

studied carnivores. The landscape structure, including the presence and arrangement of natural and anthropogenic features (e.g., crop types, urban areas, rangelands), habitat distribution, type, and amount, influenced dispersal capacity [97, 69], foraging behaviors [22, 30], and daily movements [16, 72]. Landscape connectivity was influenced by the presence of urbanized areas, roads, and cultivated lands, which in turn affected movement decisions. The majority of studied species avoided these areas [43, 62, 78, 81, 46, 27, 32], while others used them solely for passage [22, 51, 35]. Therefore, the presence of anthropogenic features had an impact on the functional connectivity of carnivores. Human activity directly influenced movement decisions, as some species avoided suitable habitats during periods of human activities [72, 97]. Other species perceived these areas as barriers to dispersal [81, 43, 62].

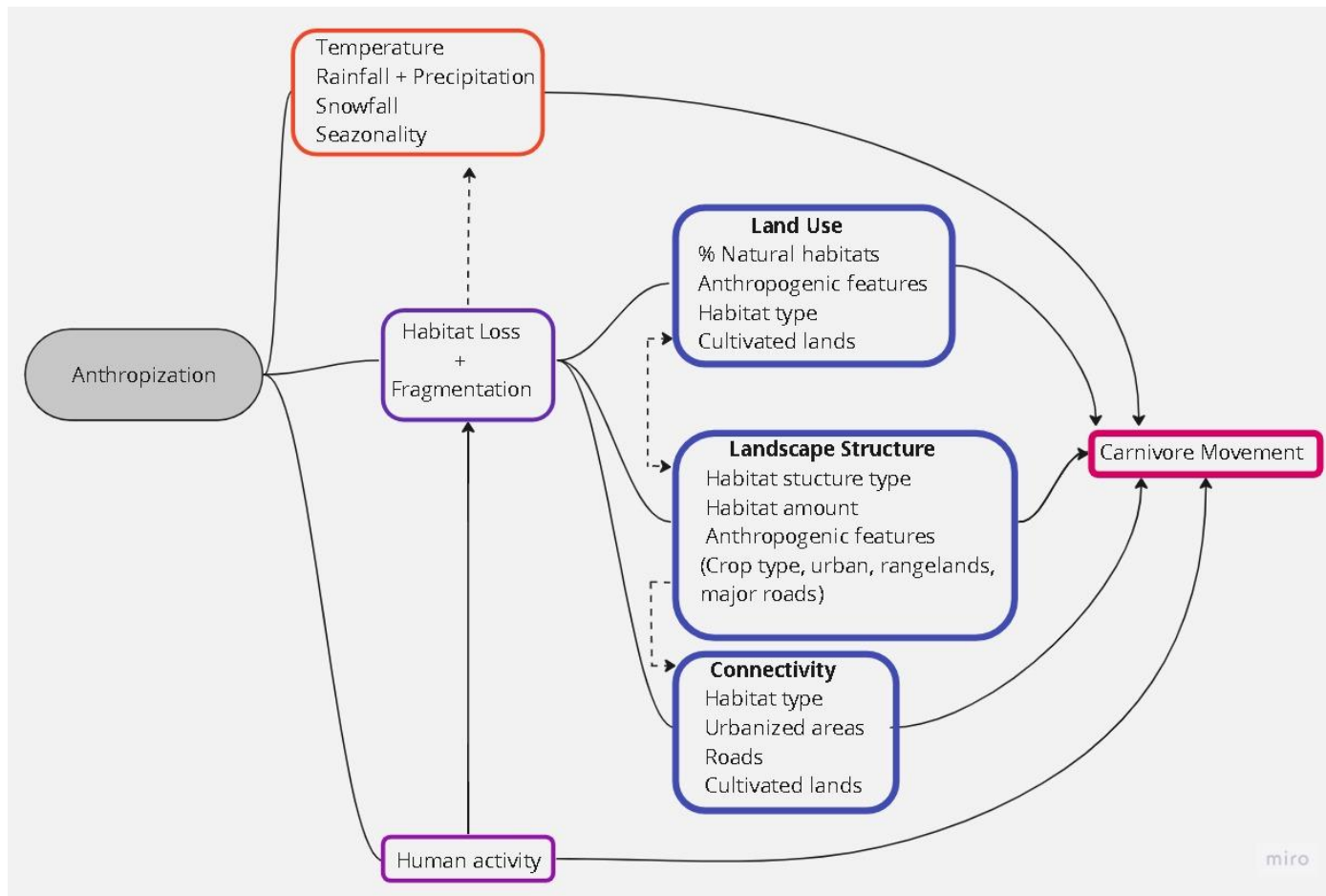


Figure 2: Framework derived from the findings of the reviewed publications. The anthropization of the environment is characterized by human activity, habitat loss, and fragmentation. It also influences climate variables (orange box), such as temperature, precipitation, and season length, which in turn affect carnivore movement. The landscape variables (blue boxes) resulting from habitat loss and fragmentation lead to changes in land use, alterations in landscape structure, and connectivity of the environment. All of these factors impact home range size, dispersal capacity, and foraging behavior.

3.1. Climate influences on movement patterns

Seasonality

Climate seasonality plays a significant role in ecosystem dynamics, and many species exhibit behavioral and life history changes throughout the seasons [99]. For instance, the predation patterns of large carnivores can vary based on prey vulnerability during different

seasons. Omnivorous carnivores can also adjust their activity patterns, home range size, and movements in response to seasonal variations in resources. An example of this is observed in *Nasua narica* in the Chiricahua Mountains of southeastern Arizona, where home range sizes and movement speed increase from winter to spring and summer in both males and females due to seasonal changes in resource availability [58]. In British Columbia, Canada, the North American badger (*Taxidea taxus*) exhibits significant differences in winter and summer home ranges. Both male and female badgers have considerably smaller winter home ranges compared to summer home ranges [98]. The authors report a reduction of 98% in home range size during winter, whereas in summer, the male's home range is larger than that of females. During winter, all individuals move less, while in summer, daily movements are 80% greater than in winter, with males showing a 94% increase in movement [98]. In the Scandinavian peninsula, the dispersal of wolves (*Canis lupus*) from the Scandinavian population to the Finnish population is influenced by several factors. The absence of ice in the Bothnian Bay during spring and summer, which coincides with the peak of dispersal, limits the movement of wolves. Furthermore, mortality in reindeer (*Rangifer tarandus*) management areas restricts dispersal, with 100% of collared wolves being shot in those areas [50].

For omnivorous brown bear *Ursus arctos* in Sweden the observed patterns were different: in winter, their movement patterns are already influenced by hibernation, resulting in distinct behavior. However, during the other seasons, there is no significant difference in home range size, movement, and activity [38]. During summer and early fall, brown bears primarily rely on berries and tend to be more diurnal, while in spring, they predominantly prey on ungulates during the night. In a north-west population, bear movements increase from early spring to summer, and the intensity of human disturbance affects their movement patterns [71]. A study analyzing movement data for *Canis mesomelas* and *Canis adustus* found that their home range size is larger during the cold, dry winter due to the mating season, compared to the hot, dry summer [53]. Seasonality directly or indirectly affects the movement patterns and home range size of these species. Some species adjust their home range according to

the seasons, with generally an increase from winter to summer [58, 98, 50]. However, further studies are needed to gain a clearer understanding of the contribution of seasonality to carnivore movement in order to implement effective conservation strategies for species and habitats.

Temperature

Decisions regarding movement across the landscape are influenced by various intrinsic and extrinsic factors. Environmental temperature plays a crucial role in determining movement patterns, and animals respond to temperature changes through physiological adaptations and behavioral strategies [8].

For instance, in Yellowstone, USA, wolves (*Canis lupus*) make decisions about moving their pups based on environmental temperature. On hot days, individuals move their pups less frequently compared to colder days [4]. In Iran, dispersing leopards (*Panthera pardus*) remain inactive during high temperatures and exhibit increased movement during colder temperatures, indicating a direct influence of environmental temperature on their dispersal capacity [28]. In Greece, *Ursus arctos* (brown bears) make fewer movement decisions on hot days and have smaller home ranges compared to northern populations. The authors concluded that temperature and human activity are the main factors contributing to this difference [20]. Cold climate species, such as wolverines (*Gulo gulo*), have a preference for snow-covered territories. The presence and persistence of snow during spring significantly impact the species' global distribution. Wolverines have large feet that enable them to navigate through deep snow in winter. In higher temperatures, they select altitudes above tree lines, where snow remains, to establish their territories. Wolverines also exhibit large home range sizes and are capable of dispersing to areas located at least 170 km away from their mother's home range [39].

Based on the reviewed research, it becomes evident that environmental temperature plays a crucial role in determining territory size [65, 20, 40], daily movements [4], and dispersal

capacity [28, 40]. Therefore, temperature is a significant factor influencing carnivore movements.

Precipitation + Rainfall

Rainfall levels can have an impact on various factors such as predator visibility, prey densities, vegetation cover, and water availability [4], thus this climatic variable influence animal movement. In the case of wolves (*Canis lupus*) in Idaho, Montana, and Yellowstone National Park, rainfall is a significant factor influencing their decisions to move pups from one site to another, primarily due to water availability [4]. Similarly, in Zimbabwe, the movement decisions of lions (*Panthera leo*) are influenced by rainfall. They exhibit slower and shorter movements with increased precipitation, and females specifically reduce their path length and speed [27]. A similar pattern was observed for lions in Kenya, where increased rainfall resulted in reduced speed and increased turning angles [72]. In the State of Washington, USA, rainfall can also impact the home range size of *Ursus americanus* [48]. Snowfall, on the other hand, influences the movement of cold climate animals. For instance, in Alberta, Canada, increased snowfall reduces the movement of *Canis lupus* compared to days before or after the event [24]. Therefore, it can be concluded that precipitation affects the movement decisions [4, 24], home range size [48], and movement patterns [26, 72] of carnivores, although only a limited number of studies were included in this review. Further understanding of the influence of precipitation on carnivore habitat selection and movement, especially for tropical species, is necessary. Considering the potential shifts in rainfall and snowfall regimes due to global warming, it becomes crucial to acquire more knowledge on this topic in order to understand and address the impacts on carnivore movement patterns.

Remarks on climate variables influences on movement patterns

The size of home ranges, dispersal patterns, and foraging movements of individuals are directly or indirectly influenced by seasonal variations in the environment. In general, movements [50] and home range sizes are larger in summer compared to winter [58, 98].

Seasonality directly impacts climate variables, including temperature and the presence of dry or wet seasons, which in turn affect resource productivity, prey availability, and water accessibility. For instance, temperature influences thermoregulation, which affects dispersal capacity [40, 28], daily movements [4], and territory size [40, 20, 66]. Rainfall affects resource production, water availability, visibility, and prey density, thereby influencing movement decisions [4, 24], movement patterns [27, 72], and home range sizes [48]. Therefore, climate variables play a significant role in shaping carnivore movement, as individuals adjust their ranges and movements in response to these variables. However, only a limited number of studies have considered climate variables as influencing factors of carnivore movement. Out of the 68 identified studies, only 23 (33%) were selected for review. Thus, there is a crucial need to pay more attention to climate factors, particularly considering that climate change is a global phenomenon already impacting the persistence of species within their current geographical ranges and influencing species dispersal [39], which consequently affects global biodiversity [77].

3.2. Landscape influences on movement patterns

Landscape structure

The landscape structure denotes the pattern of a landscape, determined by its use type and by its structure, i.e. shape, size, arrangement and distribution of landscape elements [102]. Humans have reshaped the landscape structure through landscape modification [64] since the beginning of agriculture and animal domestication (~12,000 yr ago, [79]). The landscape alterations by agriculture and urbanization are the main cause of extinctions and biodiversity decline worldwide [57; 45]. The species living in wildland-urban gradients are shaped by their capacity to exploit anthropogenic resources, as well as tolerance to human proximity and disturbed landscapes [68]. For instance, the dispersal direction of Swift foxes (*Vulpes velox*) in Texas was influenced by land use. They dispersed toward rangelands and away from crop lands, towns and a forest Reserve [69]. The authors explained the direction of dispersal as the

reason that swift foxes prefer areas with short-structured vegetation, therefore, avoiding tall-structured vegetation such as Conservation Reserve Program (CRP) lands and crop lands.

For *Puma concolor* in Utah, the habitat structure influenced the distances traveled, natural (i.e. desert) and anthropogenic obstacles, such as agriculture, thus modifying landscape permeability [97]. In that case, the dispersal distances were smaller in fragmented habitats and higher in remote areas. In a study conducted in Portugal, individuals of *Canis lupus* avoided potential sources of human disturbance. The resident wolves restricted their movements to mountainous areas less used by humans and presented resistance to move in dense human-populated lowlands. The dispersers presented a higher tolerance to humans when compared to residents. Both presented more avoidance to anthropogenic features during daytime than twilight and night, showing a resistance to human presence. Resident wolves selected areas with mean patch size larger than disperser wolves, indicating a more restricted perception of the landscape [83]. In Florida, percent forest cover had no influence on home range size of *Puma concolor* [16]. The absence of cougars in some sites was associated with human disturbance in managed landscapes (e.g. intensive agriculture, urban, major roads) presenting a barrier to dispersal. However, panthers selected resting at larger forest patches, and also selected interior forest at daytime in plots with 10% forest cover, thus demonstrating avoidance to human presence [16]. In California, cougars moved with high speed in grassland, woodland and urban areas, indicating that these areas are used only for passage. The individuals moved slower in riparian vegetation, indicating a preference for riparian areas as resting sites and foraging [22]. Canada lynx (*Lynx canadensis*) in Maine, USA, showed strong habitat selection by selecting patches within their home range that enhanced foraging opportunities. They preferred habitats with intermediate prey (hare) density and structure vegetation with easier access and visibility to hares (i.e. intermediate densities of understory stem cover), also changed their movement tortuosity to move from higher to lower quality patches. The authors highlight that these results showed strong evidence of resource preference, which corresponded to patch and landscape scales [30].

The lions in Kenya showed partial avoidance of pastoral land, despite similar prey densities to natural lands, indicating this limitation by people's influence. They used the preferred areas at night, when human activity ceased [72]. They moved faster and straighter near human habitation and in pastoral land when compared to natural habitats, indicating an adjustment of their movement in response to humans.

Based on the literature presented, we can conclude that habitat type and anthropogenic features, such as agricultural and urban areas, have an impact on the dispersal direction [69], distances traveled [97], movement patterns [22], and movement speed [22] of carnivores. Certain species require a minimum presence of natural habitats within their range [16] and exhibit a preference for patches with diverse vegetation structures [30]. Furthermore, human activities and human presence influence movement decisions, with some species avoiding areas with human activities and others adjusting their movements based on the reduction of human activities during nighttime [83, 72, 16].

Land use type

The habitat loss and fragmentation are among the main threats to biodiversity decline across the globe [11; 45]. These processes reduce the persistence of the species in the landscape, thus it is important to know which elements of the habitat must be preserved [34]. The response of Iberian Lynx (*Lynx pardinus*) in Portugal and Spain to agriculture depends on the crop type and on the presence of remaining natural habitat [33]. These animals avoided intensive cultivation areas (i.e. irrigated arable lands) when establishing home ranges, but frequently selected permanent crops such as olive groves and/or heterogeneous agricultural lands.

Puma concolor in The Cypress Hills Uplands, located in southwest Saskatchewan and southeast Alberta, selected rugged terrain and proximity to water and avoided open cover types. These processes negatively impact the persistence of species within the landscape, highlighting the importance of identifying and preserving key habitat elements [34]. The

response of the Iberian Lynx (*Lynx pardinus*) in Portugal and Spain to agriculture is influenced by the type of crops and the presence of remaining natural habitat [33]. These animals tend to avoid areas of intensive cultivation, such as irrigated arable lands, when establishing their home ranges. Instead, they frequently select permanent crops like olive groves and/or heterogeneous agricultural lands.

In Kenya, African wild dogs (*Lycaon pictus*) selected their home ranges in areas characterized by low human population densities and proximity to rivers and roads. They also exhibited a preference for habitats with a lower percentage of tree cover. However, habitat selection varied significantly among different life stages, with dispersal groups showing greater tolerance for higher human population densities, while denning and pregnant individuals were least tolerant of such areas [70]. Coyotes (*Canis latrans*) in Nova Scotia, Canada, during the snow-free season and snow season preferred heterogeneous landscapes due to their generalist foraging behavior. During the snow-free season, coyotes preferred open patches during the day but avoided open landscapes at night. In deep snow, they tended to forage in forested areas. These findings indicate that coyotes exhibit a complex response to land cover, and their movement patterns may also vary based on behavioral factors [25].

In conclusion, the presence of natural habitats is a crucial factor for the movement of carnivores [25, 33, 70, 2]. In addition, some species prefer to move in heterogeneous landscapes [25, 63, 33] and present a certain avoidance to anthropogenic features [33, 70]. Therefore, we presume that the presence and percentage of natural habitats, habitat type, anthropogenic features and cultivated lands influence habitat selection and the movement of carnivores.

Landscape connectivity

Habitat fragmentation and human disturbance have been recognized as factors that negatively impact the long-term survival of species, as it relies on their ability to navigate and inhabit altered landscapes [15; 88]. Landscape connectivity is influenced by the physical characteristics of the habitat, including land cover types, as well as the behavioral movement responses of the species [5]. Therefore, effective conservation management of human-

modified landscapes necessitates a comprehensive understanding of wildlife's movement capacity within the landscape and how these anthropogenic features influence their movement decisions [16; 5].

Urbanized areas, human activities, the presence of roads, and cultivated lands are examples of anthropogenic features that impact habitat and functional connectivity. Evaluating the influence of the landscape on cougar (*Puma concolor*) movement in southern California, it was observed that individuals traveled at a slower pace and followed meandering paths through riparian habitats. In contrast, they moved more quickly through human-dominated areas, while avoiding paved roads as much as possible, as dirt roads may have facilitated their movement. Among different habitat types, riparian vegetation was the most preferred during movement, while woodland, grassland, and urbanized areas were least selected [22]. Another study conducted with *Puma concolor* in California found that cougars utilized landscapes with moderate disturbance levels, proximity to low-traffic roads, and intermediate to medium-sized patches of land. These areas provided an abundance of prey and made catching them easier. Highly disturbed areas, on the other hand, were not utilized by the cougars [35]. Similarly, in Southern California, *Puma concolor* avoided grasslands, areas with sparse vegetation cover, barren and desert scrub habitats, as well as private unprotected lands, exurban, suburban, and urban housing areas [42]. Human-dominated areas, paved roads, and open spaces directly influenced the movement decisions of cougars, affecting the functional connectivity of the species. However, in areas with low to intermediate human disturbance, certain human features, such as dirt roads, facilitated their movement.

The bush dog (*Speothos venaticus*) in Mato Grosso, Brazil, exhibited a preference for moving through native vegetation, while moving at a faster pace in cultivated lands, suggesting that these areas are mainly used as corridors for passage [51]. In Lassen National Forest, California, *Martes caurina* (Pacific marten) selected areas with complex structural vegetation, resulting in sinuous and slower movements. They avoided areas with simple vegetation structure, which led to intermediate movement patterns, as well as open areas where their

movements became more erratic and linear. Fuel treatments, such as canopy management to prevent forest fires, had a negative impact on their movement and habitat connectivity [62].

Brown bears (*Ursus arctos*) in the Italian Alps exhibited a preference for areas located far from main roads, with an average distance of approximately 2,500 meters. Additionally, they avoided bike trails, maintaining a distance of around 5,000 meters, which suggests their avoidance of areas associated with human recreation. Their habitat ranges were characterized by wetland and shrub complexes, orchards, and deciduous forests. On the other hand, they avoided cultivated lands and areas dominated by human activities, which directly influenced habitat connectivity [78].

In the Northern Rocky Mountains of Canada, *Lynx canadensis* (Canada lynx) established their home ranges in mid-elevations characterized by low surface roughness, high canopy cover, minimal open grassland vegetation, and high values of greenness. The study revealed that the connectivity between lynx habitats in Canada and the United States is facilitated by a few corridors located south of the international border. Interestingly, a portion of individuals (27%) were observed crossing highways, emphasizing the need for mitigation efforts such as land purchases and conservation easements to preserve connectivity among lynx populations. This becomes increasingly important due to anticipated growth in traffic and urbanization in these areas [96].

Bobcats (*Lynx rufus*) in New Hampshire, USA, face barriers to movement in major roads and urban developments. These landscape disruptions create bottlenecks in their movements, and the individuals show sensitivity to the resulting impacts on landscape connectivity [80]. In Florida, *Ursus americanus* (American black bears) exhibit avoidance behavior towards urban areas and major roads. They prefer to move through forested wetlands rather than human-modified lands, indicating an active avoidance of highly modified areas within the landscape [45]. In the Kavango-Zambezi Transfrontier Conservation Area (KAZA) encompassing Angola, Botswana, Namibia, Zambia, and Zimbabwe, dispersing male African lions (*Panthera leo*) avoid agro-pastoral lands, highways, and areas dominated by human

activities [26]. Therefore, human activities and human-dominated land cover types have a direct impact on the functional connectivity of these species.

Gantchoff et al. (2020, [32]) conducted a study characterizing land use differences in a recolonizing population of black bears (*Ursus americanus*) in the Ozark Highlands, Missouri, USA. Through their movement routes, they identified linkages that connected core areas, which are patches larger than the median annual range for each sex. These core areas and linkages predominantly consisted of pasture and grass covers, as well as annual crops such as soy and corn. In the case of male grizzly bears (*Ursus arctos*) in the Greater Yellowstone Ecosystem and the Northern Continental Divide Ecosystem, the authors used GPS data to derive potential corridors. The results indicated a low potential for movement between the two ecosystems, mainly due to wide, open inter-mountain valleys that encompass human settlements and agricultural areas. Fragmentation also limited the available path options [74].

Sarkar et al. (2018) [86] used GPS locations and landscape variables to identify priority conservation areas to leopard (*Panthera pardus*) conservation in the Kailash Sacred Landscape, India. Leopards are known to frequently share habitats with human-dominated landscapes, which often leads to conflicts between humans and leopards [93]. The results of habitat suitability modeling revealed the influence of various environmental features, landscape characteristics, and topography combined with the spatial organization within the landscape at different scales. The study identified suitable areas that leopards frequently utilize, which are associated with primary forests that are interconnected. However, fragmented forest patches affected by intensive human activities such as open pastures, agricultural fields, and secondary forests are occasionally used by leopards and are more susceptible to human-leopard interactions. The authors emphasize the need for immediate attention to leopard conservation in this area, proposing the implementation of landscape-level management strategies due to the recent high levels of mortality resulting from human-leopard conflicts.

Avoidance to human infrastructure, such as roads, settlements, trails, open agricultural lands, high livestock density areas, constraint the movement of *Canis latrans* residents in

Portugal [83]. The presence of these human features strongly constrains suitable habitats and functional connectivity for the wolves, limiting their movements to mountainous areas with lower human occupation. While dispersing individuals display less wariness towards humans, they still avoid areas associated with human activity. The authors identified potential corridors that offer dispersal opportunities among five wolf packs within the study area [80]. Similarly, dispersing wolverines (*Gulo gulo*) in Yellowstone National Park and Grand Teton National Park demonstrate a similar movement pattern. They have the ability to navigate through lower-quality habitats that connect higher-quality patches. As a result, these individuals exhibit greater flexibility in their movements compared to their routine movements within their home range [14].

The presence of anthropogenic features, including paved roads, cultivated lands, and urbanized areas, has a significant impact on movement patterns and the ability of species to navigate their environment [22, 35]. It was found that the majority of studied species actively avoid these areas [43, 62, 78, 81, 46, 27, 32]. Some species utilize anthropogenic features, such as cultivated lands and dirt roads, solely for passage purposes [22, 51, 35]. Conversely, others demonstrate a preference for moving through native vegetation rather than anthropogenic lands [62]. Thus, human-dominated areas pose challenges and heavily influence carnivore movement, thereby affecting both structural and functional connectivity. Understanding how these features influence species' movement decisions is crucial for implementing effective conservation measures tailored to the specific requirements of each species in different areas.

Remarks on landscape influences on movement patterns

The movement decisions and patterns of species are directly influenced by their perception of the landscape [83]. Changes in land use, the presence of anthropogenic features such as crop lands, urban areas, and roads, as well as human activities, have a significant impact on individuals' movement behaviors [43, 62, 77, 80, 46, 27, 32]. For some species,

these factors can act as barriers to foraging and dispersal [81, 43, 62]. Dispersing animals exhibit different habitat use compared to resident individuals, displaying less wariness towards human features [83, 14]. This finding has important implications for effectively implementing conservation measures to ensure the long-term success of metapopulations. Understanding the landscape structure requirements of species is crucial for maintaining global biodiversity, as the movement capacity of wildlife plays a vital role in species survival [54]. This is particularly significant for carnivores, as their survival is essential for maintaining balance within trophic chains. Carnivores act as predators, regulating populations, and some species also contribute to seed dispersal through consumption of fruits [37].

Discussion

Carnivore species alter their home range [58, 98] and dispersal movements [50] in response to seasonal changes, which are influenced by temperature, snow, and rainfall patterns. However, global climate change is causing alterations in the length of seasons, resulting in modifications to species' dispersal and foraging behavior [76]. It is expected that biological life will track the thermal changes of the environment across seasons and geographic spaces [12]. We presume that species will adapt to warming temperatures by shifting their biogeographic ranges to maintain their thermal niches [52, 1], as thermal conditions influence territory size [66, 20, 40], daily movements [4], and dispersal capacity [28, 40]. Changes in rainfall patterns, another climate factor, can also affect species' movement behavior as it directly influences water availability, hunting visibility, prey density, and resource production, consequently impacting movement decisions [4, 24], home range size [48], and movement patterns [26, 72]. Therefore, warming temperatures and changes in rainfall patterns serve as mechanisms driving ecological changes in fragmented landscapes.

On a global scale, human activities such as habitat loss, fragmentation, greenhouse gas emissions from forest fires, and pollution have altered Earth's energy balance, directly

impacting its climate [104]. Rigorous analysis of data and evidence has revealed that since the 1950s, global warming cannot be solely explained by natural causes, as human activities have had a significant influence [104]. In the month of July 2023, the Earth experienced unprecedented temperatures that surpassed any recorded in history, it was the hottest month on record [105]. The frequency and intensity of extreme weather events have increased across much of the Earth and are projected to worsen in the coming decades. In regions where the planet's temperature could rise by 4°C, the number of extreme weather events may be up to 9 times higher [41].

More than 4.12 million hectares of primary tropical forest were lost in 2022, 10% more than 2021, based on information presented in the Global Forest Review by the World Resources Institute [103]. Brazil possesses the highest quantity of primary forests globally, yet it also holds the unfortunate record for the highest deforestation rates. In the year of 2022, over 40 percent of the global loss of primary tropical forests took place within the country, primarily attributed to non-fire causes such as extensive deforestation through clear-cutting. These losses reached their highest level since 2005 [103].

Tropical forests are essential to maintain Earth's climate by acting as carbon sinks, sequestering large amounts of carbon dioxide from the atmosphere]. Furthermore, habitat fragmentation reduces the species capacity to track rapid climate change due to changes in the habitat configuration which compromises the dispersal capacity to habitats with optimal climate conditions [9], increasing the susceptibility of biological populations to stochastic extinctions [19; 44]. Some species can tolerate human features [22, 51, 35] using it just for passage. Although, the presence of anthropogenic features and human activities act as barriers and the majority of carnivore species studied avoid those lands [43, 62, 78, 81, 46, 27, 32]. The species ability to move in the landscape plays a key role in the survival of organisms [39], and changes in animal movement patterns may cause serious consequences for the ecosystem dynamics, such as rupture of trophic chains, seed dispersal, gene flow and natural regeneration of environments [65, 47, 100]. Although, the combined effects of climate and habitat loss and fragmentation, are uncertain in animal movement, especially carnivores,

because of the lack of empirical evidence presented in this review. It is extremely relevant to comprehend the persistence, movement and distribution of species across the globe [76; 56], because understanding the space requirements of fauna is crucial to implement efficient conservation measures for the ecosystem and its fauna [49].

Conclusions

In this review, we found that 22% of the published papers on climate variables were conducted in the southern hemisphere, while 78% were conducted in the northern hemisphere. Similarly, 20% of the published papers on landscape variables were conducted in the southern hemisphere, while 80% were conducted in the northern hemisphere. Some significant studies on the impact of landscape and climate on carnivore movement in the southern hemisphere are available in grey literature sources such as dissertations, book chapters, conference proceedings, magazine articles, reports, newsletters, blogs, wikis, and preprints [36]. However, searching for such literature can be challenging, despite the increased accessibility of the internet and online bibliographic databases. It is also challenging to provide specific details on how the search for grey literature was conducted and how the results were included in the review process. Transparency and reproducibility are crucial for the methodology in order to address this factor [55]. After conducting this review, we discovered that several available studies use different keywords than the ones we selected to describe landscape anthropization []. This discrepancy contributes to the scarcity of studies in the southern hemisphere.

Only a few studies have analyzed the effects of climate on carnivore movement [17], indicating the need for further research to understand how these factors influence carnivore dispersal and foraging behavior. And also, the combined effects of climate and landscape anthropization. The quantification and prediction of landscape alterations, resulting from habitat loss and fragmentation, primarily rely on data collected at local scales [67]. However,

climate change operates at a broader scale, necessitating the integration of data from different scales to better understand its impacts. This integration is crucial for improving biodiversity conservation and ensuring the provision of vital ecosystem services that contribute to human well-being and a high quality of life [73]. While there are some studies that utilize modeling to predict biodiversity patterns by considering landscape modification and climate variables [67; 95], the literature still lacks comprehensive modeling of the combined effects on animal movement.

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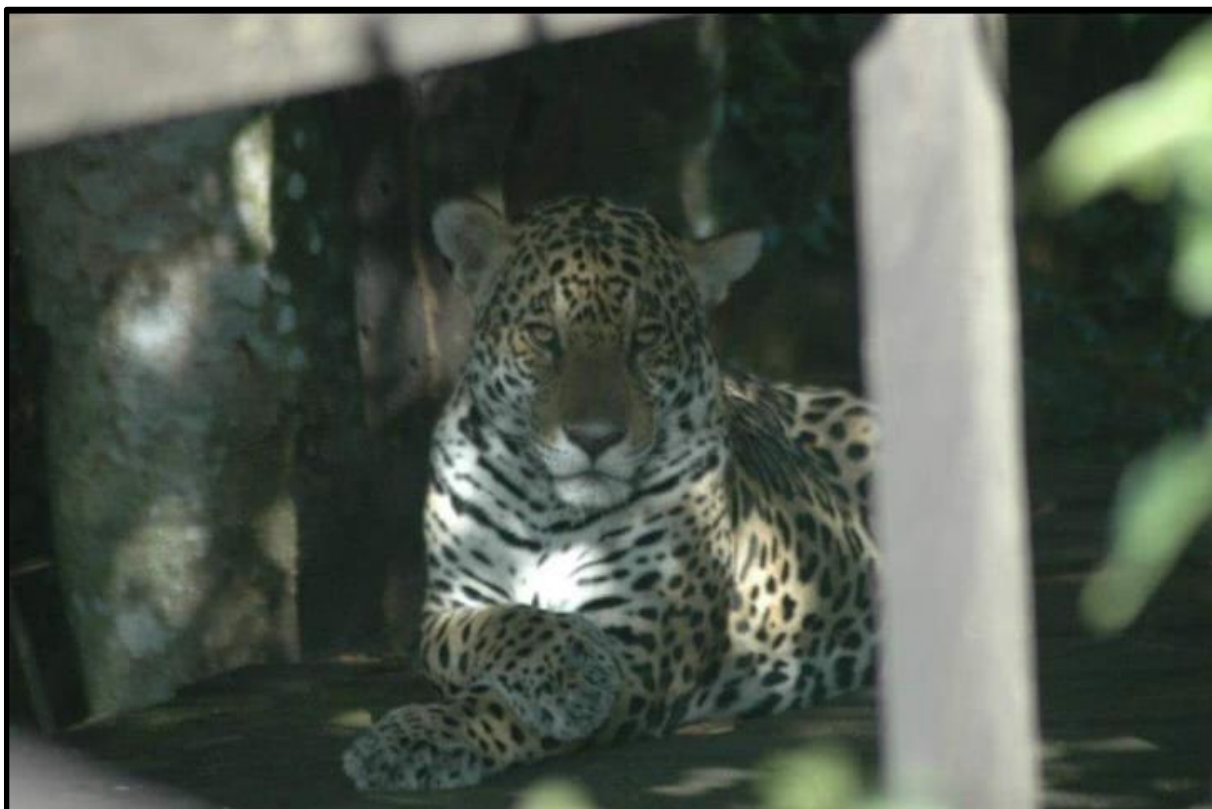


Foto: Marina F. Giubbina

CHAPTER II - The impact of climate and landscape on jaguar's movement, the neotropical apex predator

The impact of climate and landscape on jaguar's movement, the neotropical apex predator

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ABSTRACT

Currently, the Earth is facing unprecedented challenges due to human activities such as landscape alterations and climate change. These alterations have resulted in the deterioration of habitats, their fragmentation, and also the occurrence of extreme weather events. These pressures pose a significant threat to land-based biodiversity and interfere with the proper functioning of ecosystems. Among the most affected are animal populations, particularly carnivores, whose movement patterns are directly influenced by these cumulative stressors, ultimately shaping species distribution and interactions. This study aims to analyze the habitat suitability of *Panthera onca* (jaguar) and assess the influence of landscape and climate on the species' habitat selection. We conducted a Species Distribution Modeling (SDM) for jaguars using climate and landscape variables and employed a Step Selection Function to understand the impact of seasonality and land use on *Panthera onca*'s movement. Our findings indicate that climate and landscape variables are a different scale complement to predict habitat suitability for jaguars and directly shape their movements. The seasonality was a great factor influencing the Step Length with rainfall and land use contexts. Jaguars tend to shape their movements comparing wet and dry seasons, thus our results highlight the direct influence of climate and landscape on jaguar movement. We also encourage regenerative measures of conservation, such as agroforestry and agrosilvopastoral, that integrate the production of resources for humans and provide a healthy ecosystem for wildlife.

Keywords: Landscape anthropization, climate, jaguar, species distribution modeling, animal movement.

1.INTRODUCTION

Landscape anthropization caused by land use change is reducing terrestrial biodiversity globally (Newbold et al., 2015). Habitat loss and fragmentation are directly or indirectly the main causes of biodiversity loss globally. Land use alterations can affect movement (Tucker et al 2018), range (Yackulic et al., 2011) and activity patterns of animal populations (Gaynor et al., 2018), especially mammals. The climate is also an important factor that influences habitat selection of fauna (Crowther et al, 2014; Aycrigg et al, 2021). Although, species responses to climate combined with landscape anthropization are still unclear. Currently the central challenge in conservation biology is to monitor and predict the influence of the multi-scale approach of climate and habitat loss and fragmentation on animal distribution and persistence (Hannah et al. 2011).

The animal movement affects directly and indirectly biodiversity by determining species distribution and interactions (Schweiger et al 2012). Furthermore, the animal movement shapes genetic diversity (Blaum et al. 2012, Shafer et al. 2012; Moraes et al. 2018), metapopulation dynamics (Revilla et al. 2004), potencial seed dispersal (Silveira et al. 2016; Hämäläinen et al. 2017, Ramos et al. 2020) and linkage on metacommunity dynamics (Vanschoenwinkel et al. 2008, Driscoll et al. 2009, Mokany et al. 2012). The movement decisions and movement patterns are directly affected by landscape perceptions of the species. The land use, the presence of anthropogenic features such as crop lands, urban and roads, and human activities affect movement decisions (Jennings et al, 2016; Karelus et al 2019; Gantchoff et al 2020) and may present a barrier to movement of some species (Reed et al 2016, Jennings et al 2015, Moriarty et al 2016).

In the past, the climate of Earth changed. Some species adapted to the new climate conditions, others moved to track suitable climate and others went extinct (Alroy et al., 2008; Gill et al., 2009; Harnik et al., 2012). Rigorous analysis of data and evidence reveal that since

the 1950's the Earth's climate has been changing due to human activities and not because of natural causes (Wolf et al. 2020). To persist in this rapidly changing climate conditions environment much of today's biota will need to traverse human-dominated landscapes. Thus the species survival will depend on their ability to move in different anthropogenic landscapes (Hirschfeld & Rödel, 2017).

Carnivore species alter their home range (McColgin et al. 2017, Symes et al. 2017) and dispersal movements (Kojola et al. 2009) according to seasons (McColgin et al. 2017, Symes et al. 2017, Kojola et al. 2009), temperature (Ausband et al. 2016, Farhadinia et al. 2020, Inmann et al. 2012), snow (Droghini & Boltin 2018) and rainfall events (Ausband et al. 2016, Droghini & Boltin 2018, Elliot et al. 2014a, Orioll-Cotterill et al. 2015). The temperature affects the thermoregulation, which interferes the dispersal capacity (Inman et al. 2020, Farhadinia et al. 2020), daily movements (Ausband et al. 2016) and also territory size (Inman et al. 2020, De Gabriel Hernando et al. 2020, Nel et al. 2012). The rainfall affects resource production, water availability, influences the visibility and prey density affecting movement decisions (Ausband et al. 2016, Droghini & Boltin 2018), movement patterns (Elliot et al. 2014, Orioll-Cotterill et al. 2015) and home range size (Koehler & Pierce 2003). Therefore, the climate variables are of great importance influencing carnivore movement, once the individuals shift their ranges and movements according to it.

Global warming has been causing a series of extreme climate events, such as heat waves in temperate zones (Schiermeier, 2021), extreme cold and dry in tropical regions (CPTEC/INPE, 2021). These changes in climate combined with landscape anthropization directly influence animal movement behavior (Goswami et al., 2021). Currently one of the major challenges is to understand how these two different scale processes, climate and landscape anthropization, affect animal's movement and how we can provide conservation strategies for the species and the ecosystem. Therefore this study aims to understand the impact of climate and landscape alterations in the movement of jaguar (*Panthera onca*). More specifically we intend to answer the following questions:

1. How does climate influence the habitat suitability of *Panthera onca* in Pantanal biome?

Hypothesis 1. The habitat suitability of jaguars will be restricted to areas with high average rainfall and more stable temperature variation.

2. How does Landscape variables influence the habitat suitability of *Panthera onca* in Pantanal biome?

Hypothesis 2. The habitat suitability for jaguars will depend on factors such as water availability, presence of forests, and absence of significant human disturbances.

3. How the movement of jaguar is affected by habitat suitability?

Hypothesis 3. Jaguars are expected to exhibit increased mobility in areas where Species Distribution Modeling predicts higher habitat suitability.

4. How does the rainfall influence seasonality movements of jaguars?

Hypothesis 4. Rainfall will affect jaguar movements with an expectation that they will move more during dry seasons rather than the wet season.

5. How does seasonality influence the movement of jaguars in different land uses?

Hypothesis 5. Jaguars will exhibit a preference for movement in areas with water and forest cover then in anthropogenic land use, and they are expected to be move more during the dry season compared to the wet season.

2. MATERIAL AND METHODS

Several steps were necessary to answer the previous questions. In a nutshell, we overlapped two different Species Distribution Models (SDM) considering (1) climate variables (1km resolution), and (2) landscape variables (30 m resolution), which generated a final map overlapping both climate and landscape models. The final map was associated with Step

Selection Function analysis (Thurfjell et al., 2014) to observe the effects of climate and landscape acting synergically in the movement of jaguars. We also used the same approach to comprehend the influence of seasonal rainfall and landscape in step lengths of *Panthera onca*. All the models are explained in detail in the sections below.

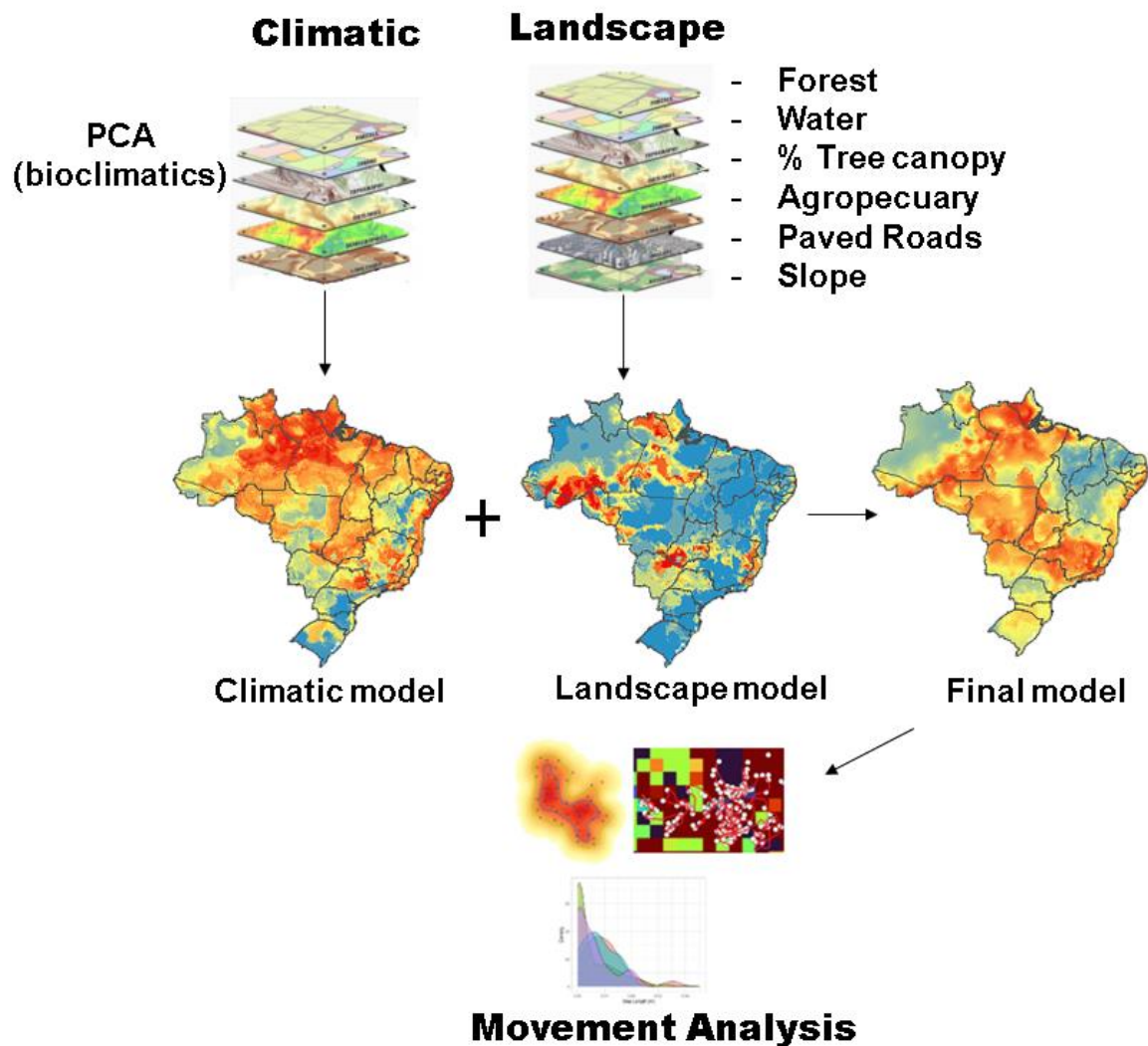


Figure 1. Method used for SDM of jaguars involved a three-step process. First, climate variables were utilized to create a climate model. Next, landscape variables were used to build a landscape model. Finally, a map was created by overlaying both layers of the previous models, which was used to analyze jaguar's movement.

2.1. Model species

The jaguar, the largest felid and carnivore in the Neotropics (Silver et al., 2004), is currently facing a severe decline in its population (Galetti et al., 2013; Morato et al., 2016). Its natural range distribution covers from the southern United States, throughout Central and South America, to Argentina (Eizirik et al., 2001; Morato et al., 2018). Classified as "Near Threatened" by the IUCN (2022), the species is experiencing a decline primarily due to habitat loss and fragmentation (Haag et al., 2010; Galetti et al., 2013), reduced prey populations in its natural habitats (Salom-Pérez et al., 2007), and human conflict (Zimmermann et al., 2005). Given its current threats and ecological importance, the jaguar serves as an excellent model to understand the influence of climate and landscape alterations on animal movement.

2.2 Environmental predictors

We selected four environmental categories to model habitat suitability for jaguar: 1) bioclimatic; 2) landscape (habitat diversity, tree cover, water frequency, forest, agriculture, pasture); 3) topographic (slope) and 4) anthropogenic (paved roads and human density). The assessments methods to each one of these predictors are explained below:

2.2.1 Bioclimatic variables

The bioclimatic variables were produced using the R software (version 4.2.1) with the bioclim package. Precipitation and temperature data from the years 2000 to 2016 were collected from WorldClim (Fick and Hijmans, 2017) to generate 19 bioclimatic variables using the function biovars from package dismo (Hijmans et al., 2017) in R software (version 4.2.3). After generating the bioclimatic variables, a Principal Component Analysis (PCA) was conducted to reduce the dimensionality of the dataset while retaining most of the original variation. The first six axes, which had eigenvalues greater than one and explained approximately 90% of the environmental variation were selected (**Table S1**). The

eigenvectors of each cell for each axis were used as variables in the models, resulting in sets of six climatic variables.

2.2.2 Landscape attributes

Habitat heterogeneity data were obtained from the Global Habitat Heterogeneity database (Tuanmu and Jetz, 2015), accessed through EarthEnv (<https://www.earthenv.org/texture>). The database utilizes the Enhanced Vegetation Index (EVI) derived from Moderate Resolution Imaging Spectroradiometer (MODIS) imagery. The metric used for analysis was Homogeneity, a second-order texture metric based on the similarity of EVI values between adjacent pixels, which is negatively correlated with habitat heterogeneity. Additionally, the percentage of tree canopy cover data for the Brazilian territory was downloaded from the Global Forest Change databank (Hansen et al., 2013). The features water, forest, agriculture and pasture were acquired from MAPBIOMAS (<https://brasil.mapbiomas.org/>), and the rasters for each variable for the Pantanal territory in the year 2016 was downloaded using the toolkit available in the Google Earth Engine (Souza et al., 2020). A kernel density calculation was performed to determine the distance of water bodies and flooded areas across the Pantanal territory.

2.2.3 Topography

The terrain slope data were obtained from the SRTM derivative data available in the TOPODATA databank, which is a Brazilian Geomorphometric Database (de Morisson Valeriano and de Fátima Rossetti, 2012; Valeriano, 2008). This dataset can be accessed on the Ambdata website (<http://www.dpi.inpe.br/Ambdata>) provided by the Brazilian Institute of Space Research (INPE).

2.2.4 Anthropogenic information

Two anthropogenic layers, human density and density of paved roads, were utilized in the study to represent human disturbance and accessibility. The human density information was derived from the Brazil 2010 census spatial data provided by the Brazilian Institute of Geography and Statistics (IBGE, 2023). This information was downloaded as a vector file, which we rasterized to create a final mosaic with human density information per square kilometer for the entire Brazilian territory.

The density of paved roads raster was based on the vector dataset of existing roads downloaded from the Departamento Nacional de Infra-estrutura de Transportes (DNIT, <http://servicos.dnit.gov.br/vgeo/>). A kernel density calculation was performed to determine the density of existing paved roads across the entire Brazilian territory.

To ensure compatibility among all layers, each dataset was rescaled and/or calculated at a resolution of 30 m and projected onto the WGS 84 geographic coordinate system using ArcGIS 10.2 (Esri, Redlands, CA). Collinearity among the predictor variables was examined using bivariate Pearson correlation (correlation coefficient > 0.7) and the layers correlated were removed from the suitability modeling (**Table S2**). The variable habitat diversity was correlated with human density (Cor.coeff = 0.856) and paved roads (Cor.coeff = 0.980), and paved roads with human density (Cor. coeff = 0.966) suggesting that areas with greater habitat diversity tend to have higher human population density and consequently paved roads. Thus we decided to exclude habitat diversity and human density from the modeling analysis and maintain paved roads, because jaguars tend to be attracted to roads (Alegre et al., 2023)

2.3. Spatial and environmental rarefaction of occurrence data

To model climate and landscape suitability for *Panthera onca*, we acquired 227 records from online databases, such the Global Biodiversity Information Facility (GBIF), VertNet, *Panthera onca*'s dataset (Morato et al., 2016) and personal observations by M.F. Giubbina

(12 visualizations of *Panthera onca*'s individuals registered by GPS locations in the wet season of 2012 and 2013 in Miranda and Aquidauana - MS) from the years 2000 until 2016. To eliminate spatial clustering and duplicate entries in the occurrence data, we utilized the SDMtoolbox in ArcGIS 10.2 (Esri, Redlands, CA). To address potential issues with autocorrelation arising from sampling bias, which could significantly influence our model predictions (Fourcade et al., 2014; Merow et al., 2013; Redding et al., 2017), we implemented a filtering process. Our filtering criteria included applying a minimum distance of 5 km radius, and excluding all the records within this radius. This distance was chosen based on the assumption that data points with similar environmental characteristics would tend to be within 5 kilometers from each other (**Figure 2**).

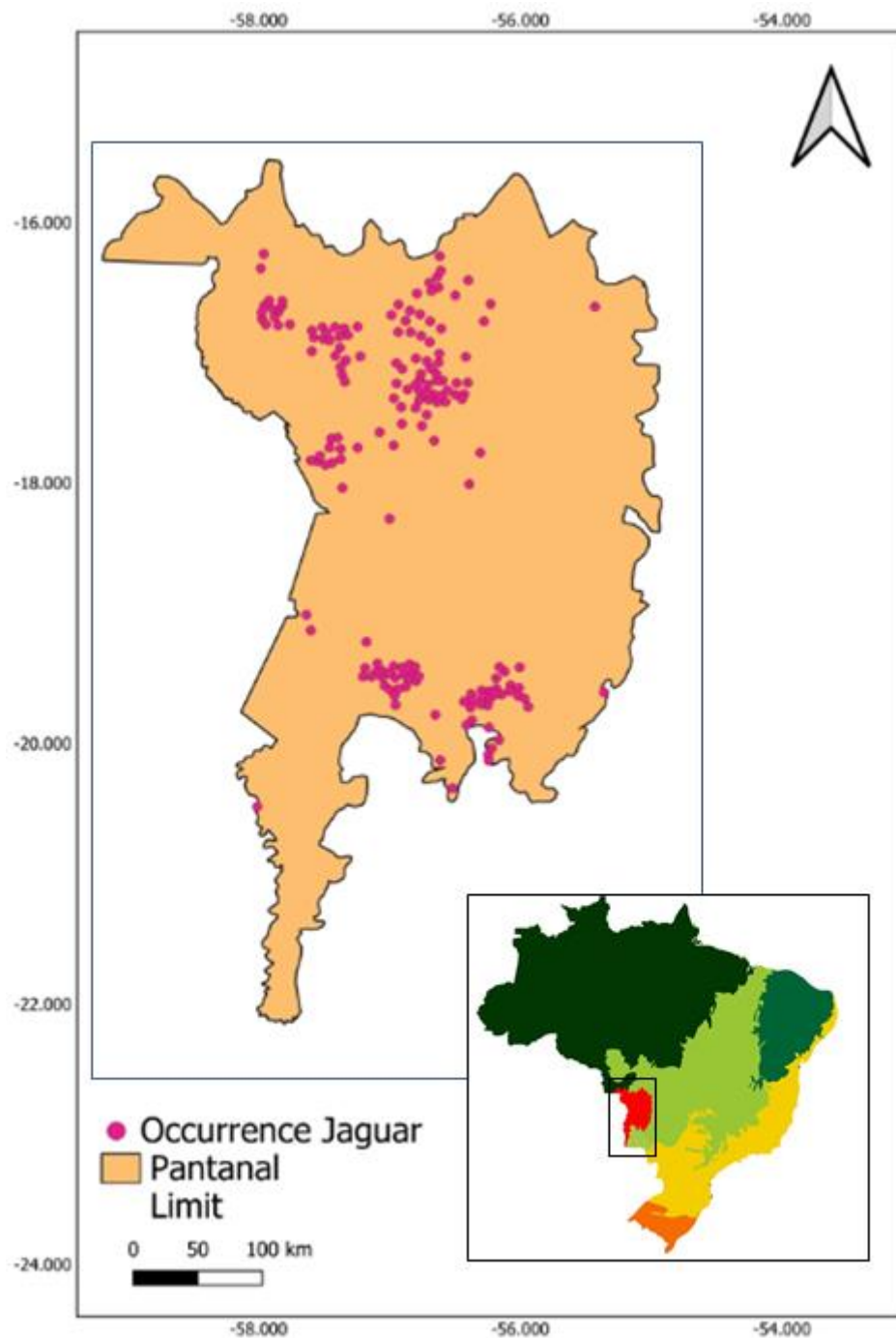


Figure 2. Occurrence registers of *Panthera onca* used after the filtering criteria was applied (excluding the records with minimum distance of 5km radius) to Model the Species Distribution in the pantanal biome.

2.4. Climate and Landscape modeling

Climate and landscape modeling were made separately. We selected four algorithms to generate climate and landscape suitability for the species based on presence-only and presence/pseudo absence data using the packages *dismo* (Hijmans et al., 2017) and *kernlab* (Karatzoglou and Feinerer, 2010). The algorithms chosen were: (1) Bioclim (Hijmans et al., 2017); (2) Domain (Hijmans et al., 2017); (3) MaxEnt - Maximum Entropy v3.3 (Elith et al., 2011; Phillips et al., 2004), (4) Random Forest (Breiman et al., 2001). We opted for these methods since we utilized two techniques focusing on presence-only data (Bioclim and Domain), alongside two machine learning strategies (MaxEnt and RandomForest) using presence and background data (Li, Guo, & Elkan, 2011; Phillips, Aneja, Kang, & Arya, 2006).

To evaluate the models, we employed the True Skill Statistics (TSS) method (Allouche et al., 2006), which provides a more comprehensive measure of model performance. To calculate the TSS index we used the “maximum training sensitivity and specificity” threshold, where 75% of the data was randomly selected for training the models, and the remaining 25% was used for testing the models. This process was replicated 10 times to ensure robustness of the results and to avoid autocorrelation.

We combined all the replicated maps using a frequency ensemble approach, applying the “maximum sensitivity and specificity” threshold value for each model. As a result, the final distribution maps were generated, including a standardized frequency map representing a habitat suitability map (**Figure 1**).

2.5 Movement analysis

2.5.1 Landscape movements with models layers

After generating both climate and landscape models, we used the minimum presence threshold (LPT) of 0.25 to convert the frequency maps of climate suitability and landscape models into binary maps. This threshold represents the lowest suitability value linked to a species presence record, and it is a valuable tool to evaluate the influence of the landscape and climate in the movement of *Panthera onca*.

To analyze jaguar's movement, we used the dataset available in Morato et al. (2018), which includes GPS data from 51 jaguar individuals across the Brazilian Pantanal biome, spanning the period from 1999 to 2016. Then, we applied a Step Selection Function (Thurfjell et al., 2014) to compare the Step Lengths in Habitat and Non-habitat predicted by the SDM ensemble using the R package *amt* (Signer et al., 2019). The Step Lengths were calculated with standardized fixes to occur at 12-hour intervals for all individuals. Thus, to verify the difference of the step lengths between habitat and non-habitat classes we conducted a Kruskal-Wallis test.

2.5.2 Climate movements

To evaluate the influence of rainfall in Jaguar's movement using the Step Length of individuals, comparing data between wet and dry seasons, we employed Step Selection Functions (SSF). Additionally, we standardized the fixes to occur at 12-hour intervals for all individuals. We conducted the analysis for 8 individuals acquired from Morato et al. (2018; ids: 13, 25, 27, 30, 59, 60, 81, 111), which presented enough records for three months in wet season (december, january and february) and dry season (june, july and august). To calculate the Step Lengths, we used the *amt* R package (Signer et al., 2019).

The tested variables included the mean precipitation of every month of the wet season and dry season by year that each individual was tracked (2008, 2009, 2010, 2011, 2012, 2013

and 2015). The layers were downloaded from the WorldClim 2.1 historical monthly weather data (Fick and Hijmans, 2017). To test the hypothesis that jaguars adjust their movement patterns in response to seasonal changes in precipitation, we conducted a Mann-Whitney analysis using the step length as the response variable, and the mean precipitation by month in both the wet and dry seasons as predictor variables.

To estimate accessible resources based on potential steps that could have been taken by the jaguars, we calculated random steps, which allowed us to assess the influence of precipitation variations during wet and dry seasons on jaguar step lengths. By comparing actual step lengths with these random steps generated from precipitation data, we could interpret behavioral decisions of how jaguars modulate their movement patterns in response to precipitation dynamics.

2.5.3. Landscape analysis

To assess the impact of seasonality and landscape on jaguar's movement, with the same 8 individuals used in rainfall analysis, we calculated the Step Lengths for different land uses in wet season (december, january, february) and dry season (june, july, august). To calculate the Step Lengths we standardized the fixes to occur at 12-hour intervals for all 8 individuals using the *amt* R package.

The land use variables included forest, agriculture, pasture, grassland, water (euclidean distance to water) and were acquired from MAPBIOMAS (<https://brasil.mapbiomas.org/>). The rasters for each variable for the Pantanal territory was downloaded using the toolkit available in the Google Earth Engine (Souza et al., 2020). All these layers were rescaled and/or calculated at a 30-meter resolution and projected onto the WGS 84 geographic coordinate system using ArcGIS 10.2 (Esri, Redlands, CA).

To determine significant differences in step length between different land use classes, we conducted a Kruskal-Wallis and a Dunn-test with Bonferroni adjustment for land use types

and a Mann-Whitney test to verify the differences of Step Lengths between wet season and dry season.

To estimate available resources, we employed random alternative steps that could have been chosen by the individual, allowing us to estimate accessible resources through this alternative step approach. The strength of selection for environmental covariates associated with movement decisions was evaluated by comparing each actual step with these random steps, facilitating an interpretation of behavioral decisions within a habitat selection analysis (Thurfjell et al., 2014). Consequently, to assess the statistical significance of landscape variables in explaining step length variability, we generated random steps, enhancing the accuracy of our analysis (Avgar et al., 2016; Signer et al., 2019). A Kruskal-Wallis test was conducted to verify the statistical relevance of random steps compared to actual steps.

2.5.4 Random Steps

To estimate available resources, we employed random alternative steps that could have been chosen by the individual, allowing us to estimate accessible resources through this alternative step approach. The strength of selection for environmental covariates associated with movement decisions was evaluated by comparing each actual step with these random steps, facilitating an interpretation of behavioral decisions within a habitat selection analysis (Thurfjell et al., 2014). Consequently, to assess the statistical significance of landscape variables in explaining step length variability, we generated random steps, enhancing the accuracy of our analysis (Avgar et al., 2016; Signer et al., 2019). A Mann-Whitney test was conducted to verify the statistical relevance of random steps compared to actual steps.

3. RESULTS

3.1. Climatic Models

We used the climatic modeling to answer our first question: How does climate influence the habitat suitability of *Panthera onca* in Pantanal biome? The model showed a large prevalence of suitable areas in the Pantanal Biome, with AUC values ranging between 0.655 and 0.999, and the minimum sensitivity thresholds ranging between 0.268 and 0.995 among the four algorithms tested. The AUC values were lower for Bioclim, similar for SVM and MaxEnt and higher for randomforest (**Table 1**). Besides the values of AUC, the algorithms presented different suitable areas for the species, with the Random Forest predicting higher suitable areas than the other algorithms.

Table 1. Thresholds, TSS and AUC average values from the habitat suitability models for *Panthera onca* in Pantanal biome. N = 10, significant TSS and AUC (>0.7) in bold.

Algorithm	Threshold	TSS	AUC
Climate			
<i>Bioclim</i>	0.0321	0.2681	0.6553
<i>Domain</i>	0.5122	0.6034	0.8677
<i>Maxent</i>	0.5363	0.7363	0.8350
<i>Random Forest</i>	0.4850	0.9983	0.9999
Landscape			
<i>Bioclim</i>	0.0647	0.1651	0.5717
<i>Domain</i>	0.2711	0.3506	0.7252
<i>Maxent</i>	0.6211	0.7401	0.8080
<i>Random Forest</i>	0.4713	0.9962	0.9999

The climatic models predicted areas where conditions are more likely to favor the occurrence of *Panthera onca* based on climate, with factors like temperature and precipitation attributes contributing to the identification of suitable habitats. Through **Figure 3** we can notice highlighted areas with optimal climatic attributes for the species, indicating favorable locations for *Panthera onca*'s presence in nearly the entire Pantanal biome, with only a small portion being less suitable.

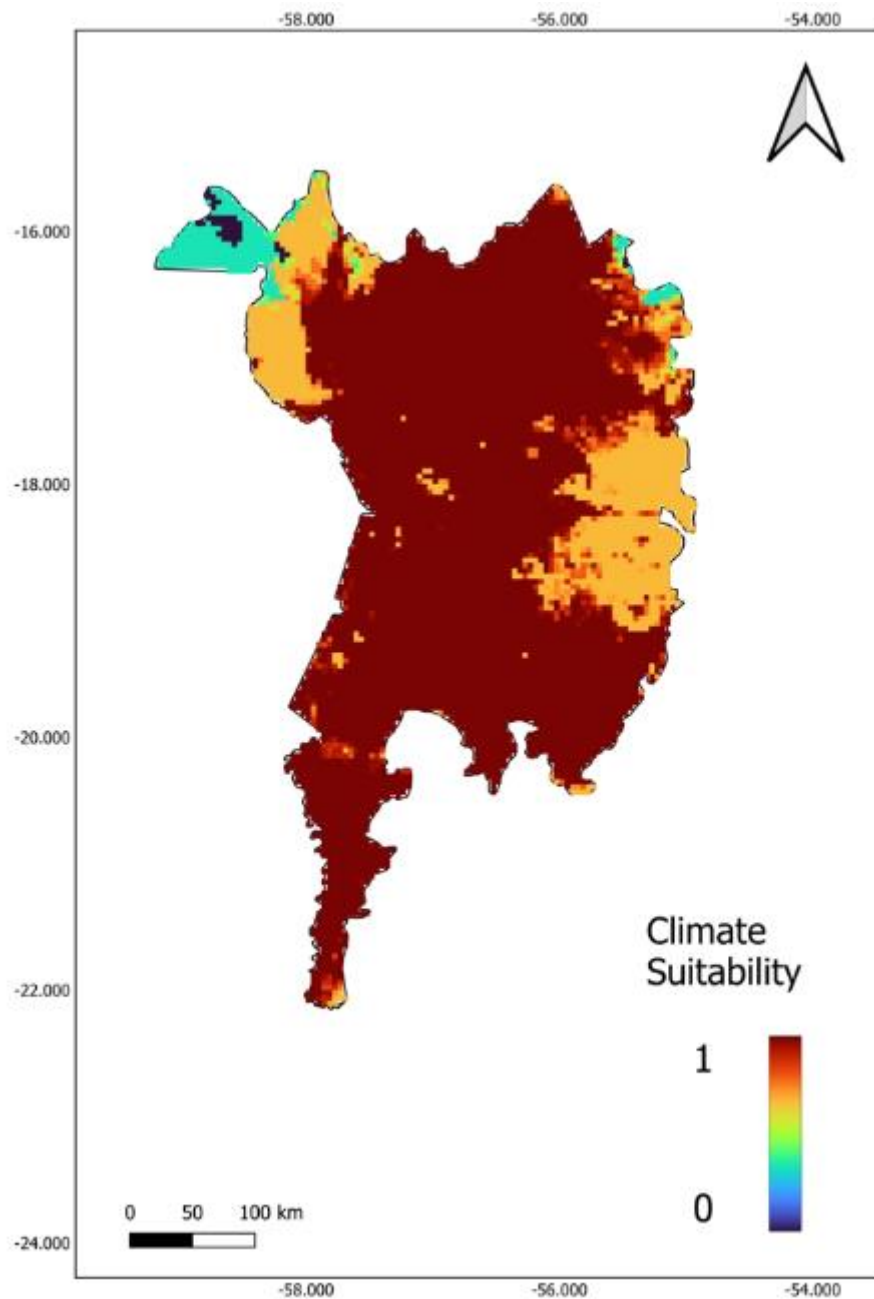


Figure 3. Ensemble frequency of Species Distribution Modeling for *Panthera onca* in the Pantanal biome using bioclimatic variables. Red colors indicate high habitat suitability for the species, while blue color indicates the absence of habitat suitability according to climate.

3.2. Landscape Models

Using landscape modeling, we could answer our second question: How does Landscape variables influence the habitat suitability of *Panthera onca* in Pantanal biome?. Similar to the climatic modeling results, the Random Forest algorithm also had higher values of TSS (0.9962406015) and AUC (0.9999856512) scores within the landscape modeling approach, emphasizing its capability to provide precise predictions based on landscape variables. SVM (TSS 0.350617284; AUC:0.725211761) and Maxent (TSS: 0.3401825174; AUC: 0.7080152672) also had satisfactory performance and showed their relevance predicting habitat suitability using landscape data. In the landscape modeling context, the GLM algorithm presented variable outcomes, indicating a tendency towards relatively modest performance compared to the other modeling techniques.

The model prediction result can be seen in **Figure 4**. The red zones are characterized by qualities aligned with *Panthera onca*'s habitat preferences. The map delineated geographic areas where landscape attributes corresponded to the species' needs, emphasizing potential habitats. Key factors such as distance of water, distance of paved roads and agriculture+pasture contributed significantly to recognize suitable habitats (**Figure 5**).

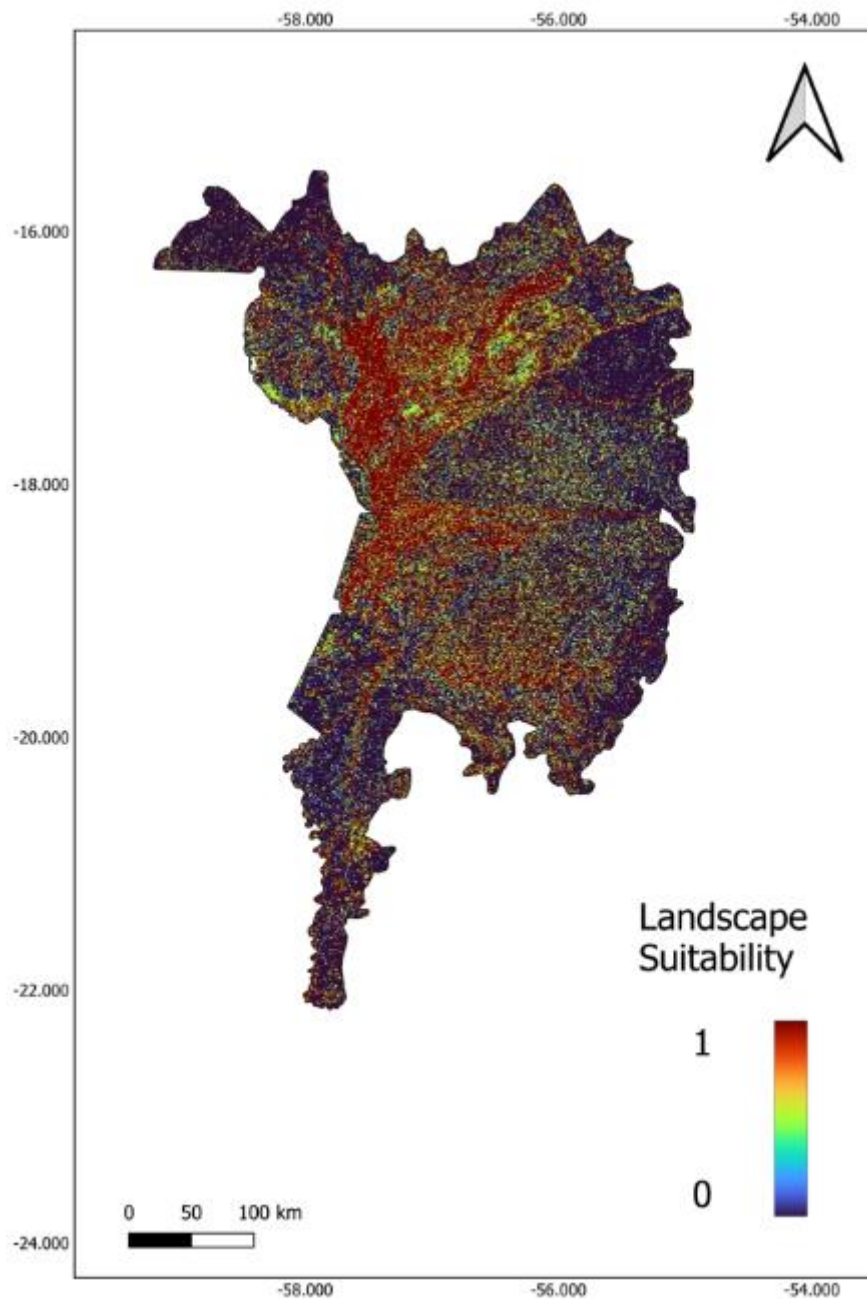


Figure 4. Ensemble frequency of Species Distribution Modeling for *Panthera onca* in the Pantanal biome using landscape variables. Blue represents areas with zero habitat suitability, red indicates high habitat suitability, and green denotes moderate habitat suitability for the species based on landscape characteristics.

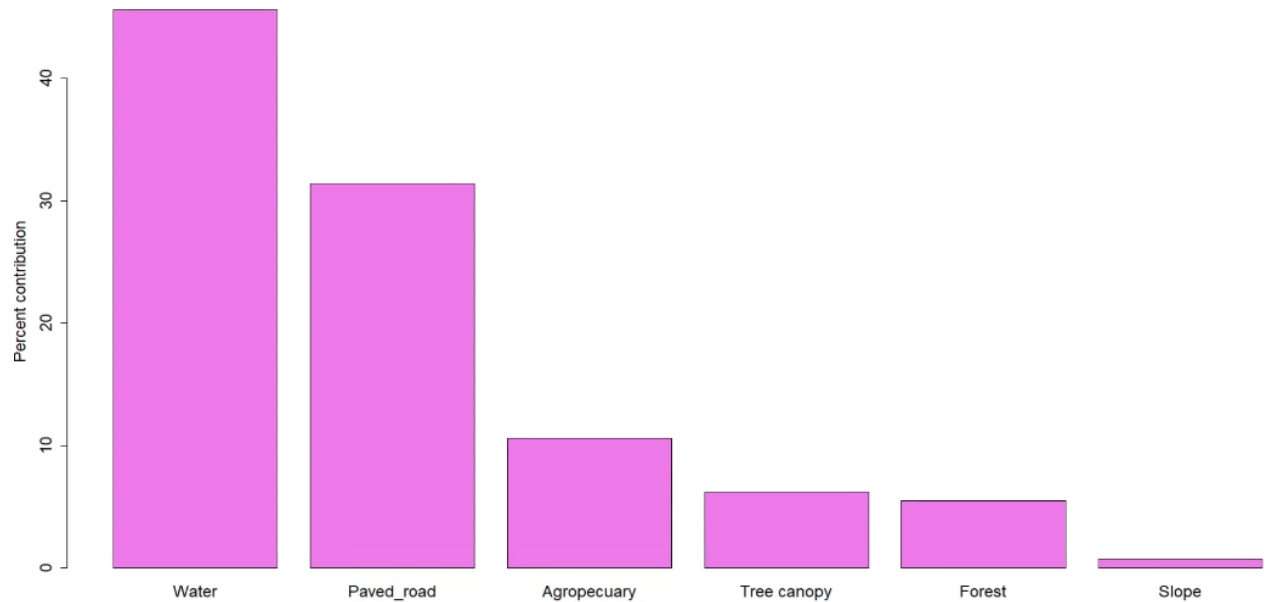


Figure 5. Percentage of contribution in the construction of Jaguar SDM model of each Landscape variable. Water distance, paved road distance, presence of Agropecuary, % Tree canopy, presence of Forest, Slope.

3.3 Final map combining climate and landscape suitability

To answer the question “How is the movement of jaguar affected by habitat suitability?”, we needed the final map, which was obtained by overlapping landscape and climate ensemble frequency models (**Figure 6**). This merged map indicates the most suitable areas for *Panthera onca*, considering the impact of the weather associated with a refined perspective on their landscape requirements. Moreover, this approach is more realistic, once it considers a broader view on the jaguar’s different resources needs and preferences

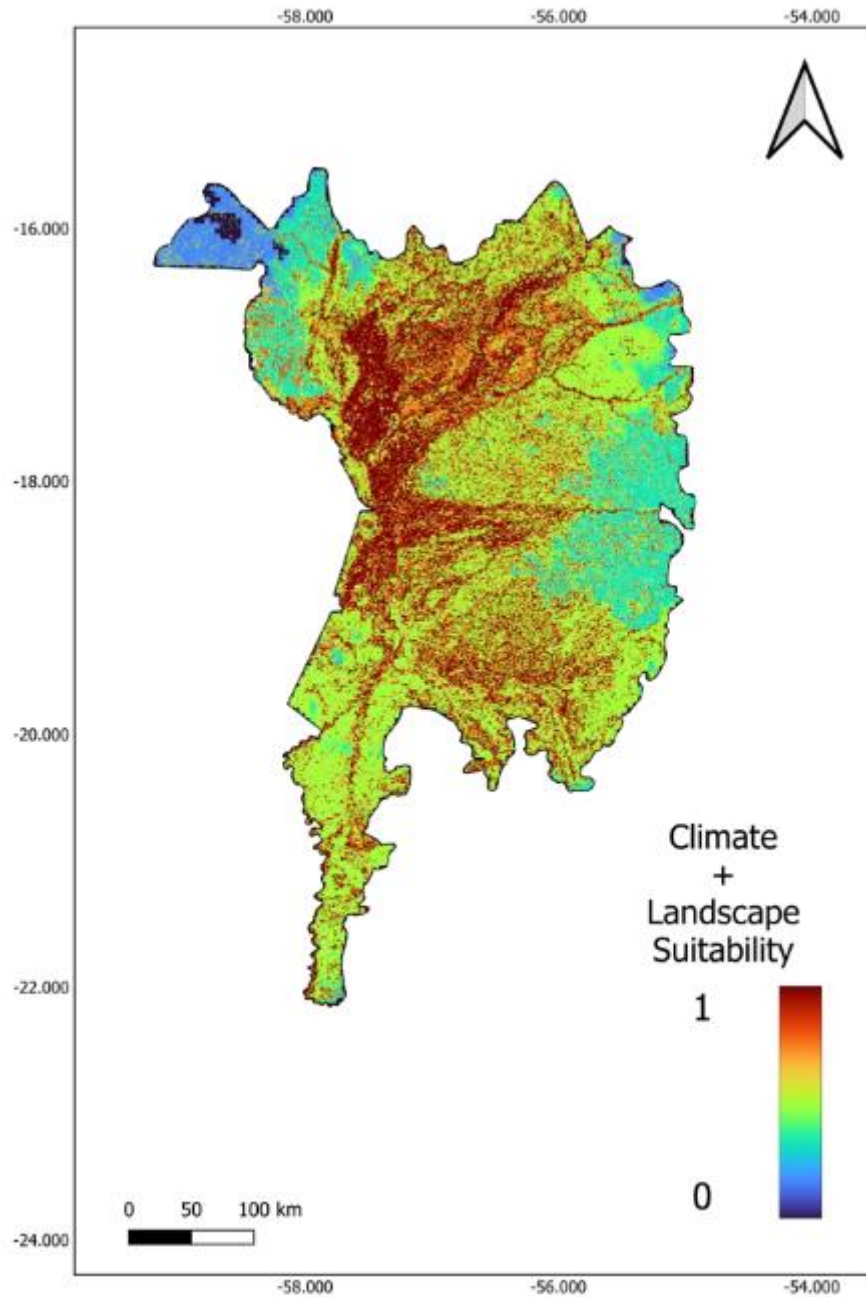


Figure 6. Ensemble frequency of *Panthera onca* Species Distribution Models in the Pantanal biome integrating both climate and landscape variables. Blue denotes areas with zero habitat suitability, red signifies high habitat suitability, and green represents regions with moderate habitat suitability for the species according to climate and landscape.

3.3. Movement

3.3.1 SDM movements

Using the final map obtained in the previous section, we could answer the question “How is a model of habitat suitability effective to understand the movement of jaguars?”. We could only provide results of the influence of landscape in the Step Length of jaguars by a landscape approach, once the climate SDM did not present enough difference in the jaguar GPS locations. The Step Length (SL) were statistically different in "Non-Habitat" and "Habitat" classes ($W = 42003.35$; $p\text{-value} = 2.2e-16$; Std. deviance = 1.168542). This can also be noticed observing the density of steps between classes (**Figure 7**), where the density of steps was more observed in Habitat areas. When assessing the influence of landscape variables in explaining step length variability using random steps, we found significant distinctions between step length of random steps and Habitat areas ($W = 6102$; $p\text{-value} < 0.001$); and between random and non-habitat areas ($W = 11130.2$, $p\text{-value} < 0.001$).

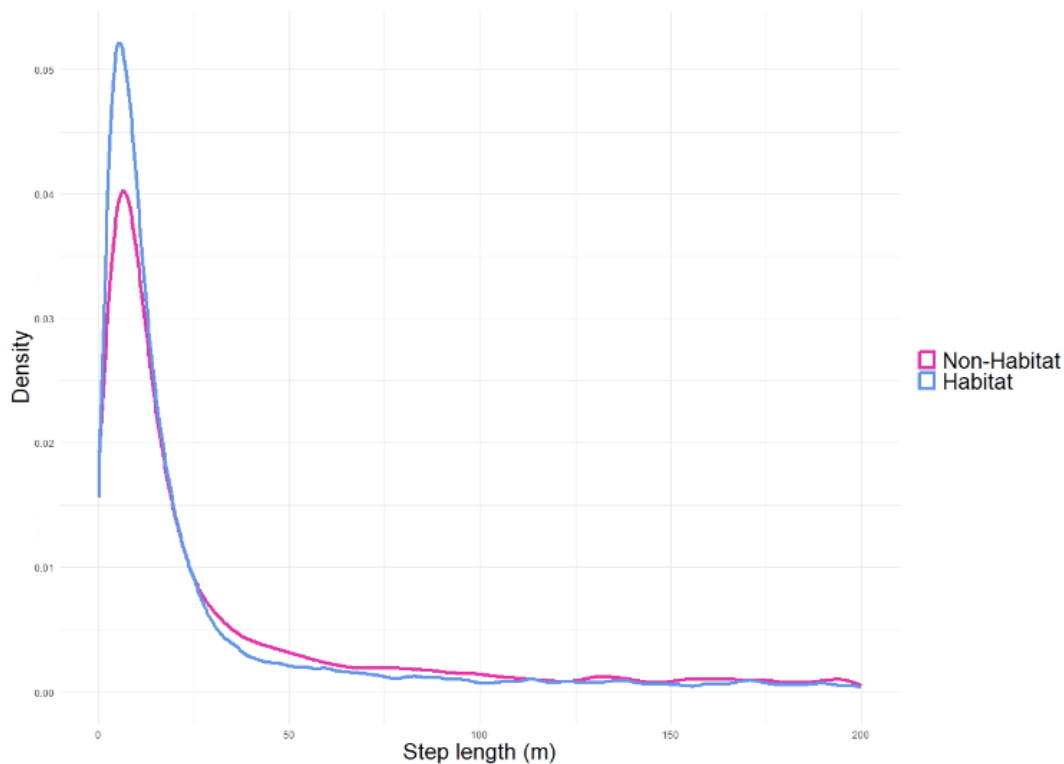


Figure 7. Step Density of Jaguars in Habitat (blue line) and Non-Habitat (pink line) categorized by Step Length (m).

3.3.2 Climatic movements

Answering our question “How does the rainfall influence seasonality movements of jaguars?”, we found variation on the step length of the individuals between the dry and wet seasons (**Table 3, Figure 9**). Notably, one single individual (Ind. 60) did not display differences between seasons ($p\text{-value} = 1$, $W = 43$), which can be attributed primarily to substantial data gaps in the records. In contrast, all the other individuals exhibited a significant difference of step lengths between seasons, with more variation and variability in wet season than in the dry season (**Figure 9**).

Table 3. Statistics calculated to assess the differences in the step length between seasons.
Values of W (Mann-Whitney), and p-value.

	W (Mann-Whitney)	p-value
Id. 13	227193.5	<<0.0001***
Id. 25	248476.0	<<0.0001***
Id. 27	1509.0	0.0024**
Id.30	171.0	0.02424*
Id. 59	57.0	0.01375*
Id. 60	43.0	1.0000
Id. 81	13235.0	0.0022**
Id.111	220.0	0.0032***

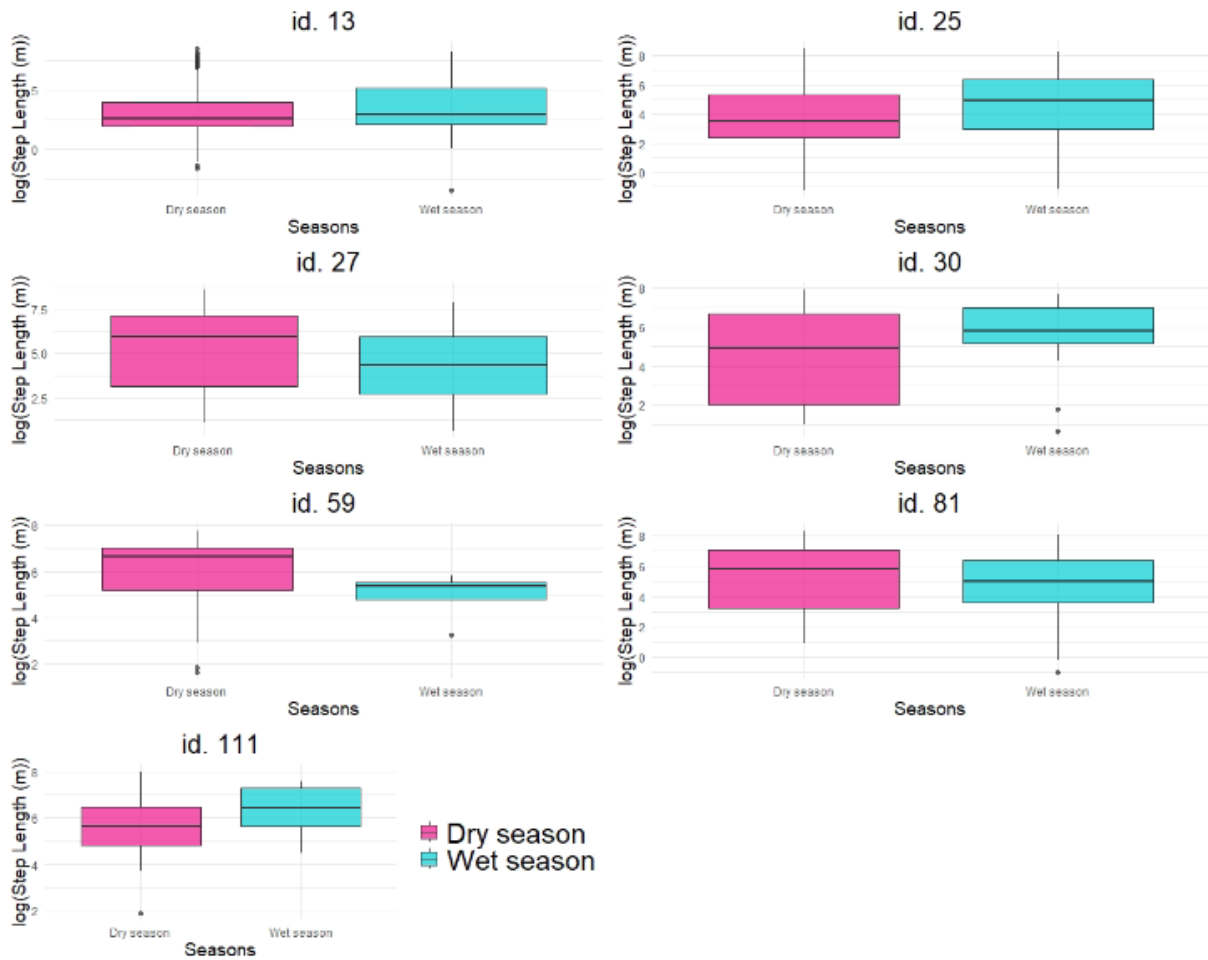


Figure 9. Influence of rainfall on step length (in meters, logarithmic scale) for individual jaguars (ID: 13, 25, 27, 30, 59, 81, 111) during the dry season (pink box) and wet season (purple box) in the Pantanal biome.

At a population level, we can notice some differences in step lengths on the different seasons ($W = 1324558$, $p\text{-value} < 2.2e-16$), with steps showing more variation and variability in wet than in the dry season (**Figure 10**). Moreover, the density of steps is higher in the dry season, indicating a clear influence of the rainfall on jaguars movement (**Figure 11**). The random steps were generated and presented significant differences between the actual steps (**Table 4**).

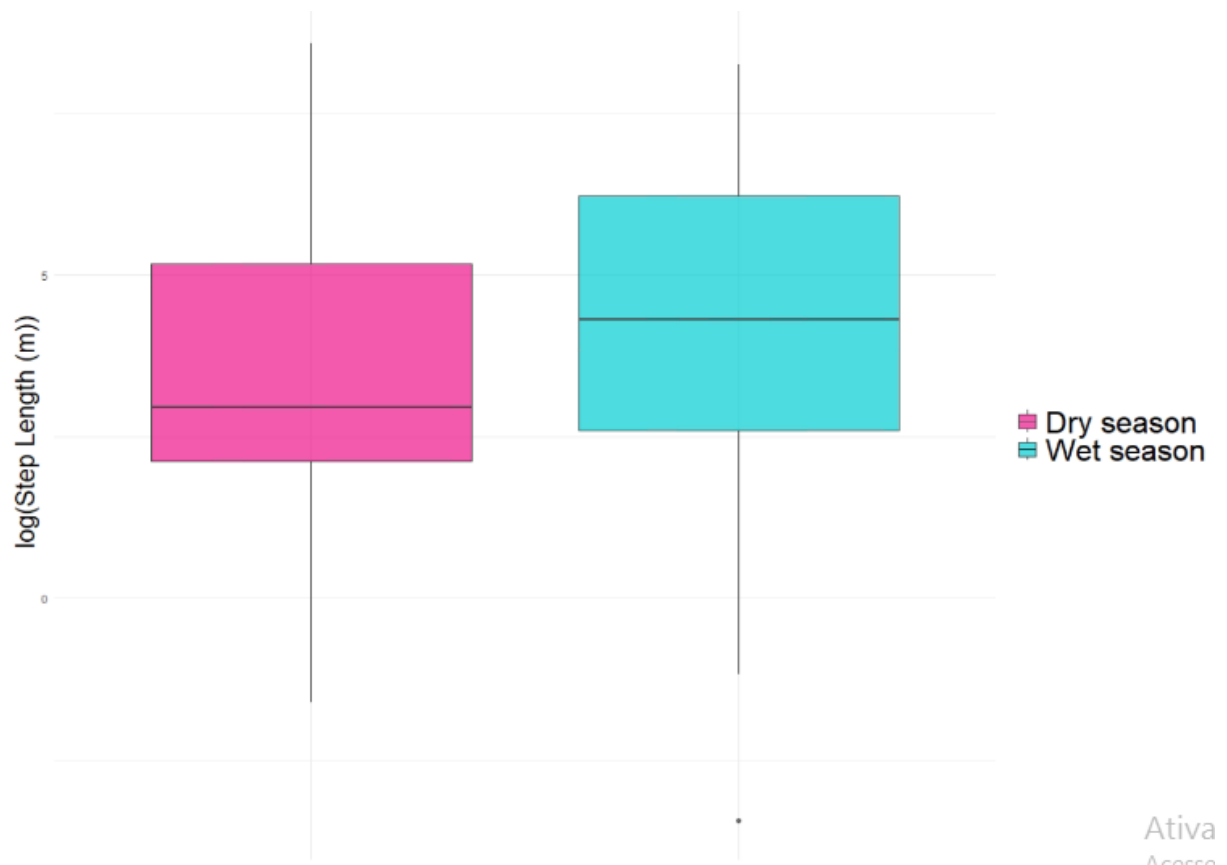


Figure 10. Box plot representing the variation of step lengths (meters, in logarithmic scale) between dry season (pink box) and wet season (purple box) in population level.

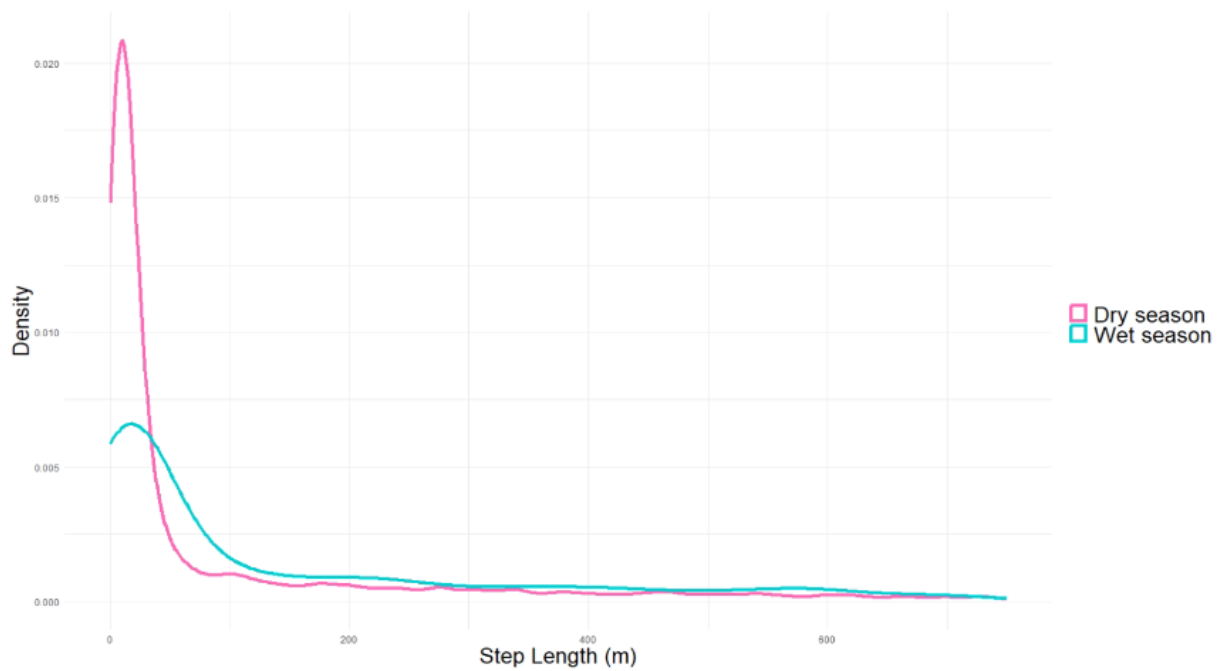


Figure 11. Influence of rainfall on the density of Step Lengths of *Panthera onca* at population level. The pink line refers to the step lengths in the dry season and the purple line represents the wet season.

Table 4. Mann-Whitney results between random steps and real steps with rainfall variable of each individual.

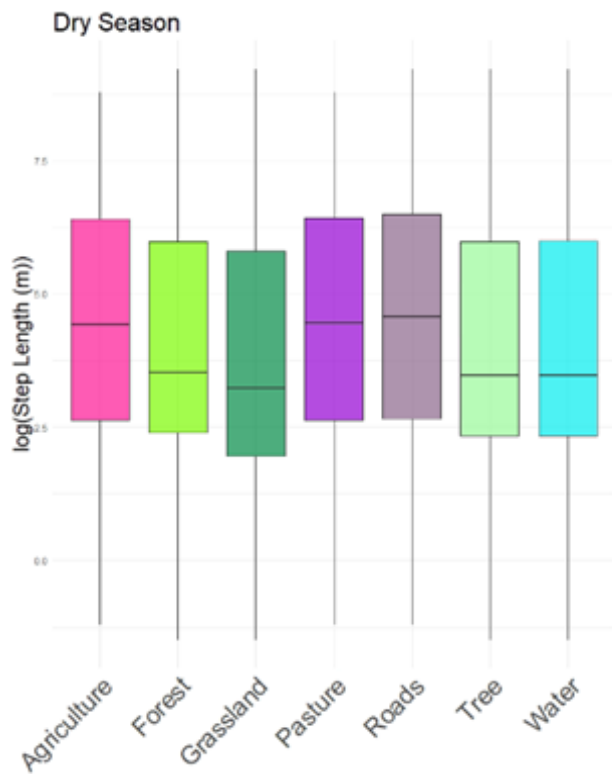
id	W	p-value
(Mann-Whitney)		
13	30978	<<0.001***
25	1737	<<0.001***
27	1836	<<0.001***
30	846	<<0.001***

59	414	<<0.001***
60	396	<<0.001***
81	5490	<<0.001***
111	288	<<0.001***

3.1.3 Landscape seasonal movement

Answering the question “How does seasonality influence the movement of jaguars in different land uses?”, we analyzed the differences in step lengths between land use classes and between the dry and wet seasons (**Figure 12, Table 5**). We observed a statistical difference in all land use classes between the seasons, with a higher density of step lengths in the dry season when compared to the wet season (**Figure 13**).

A.



B.

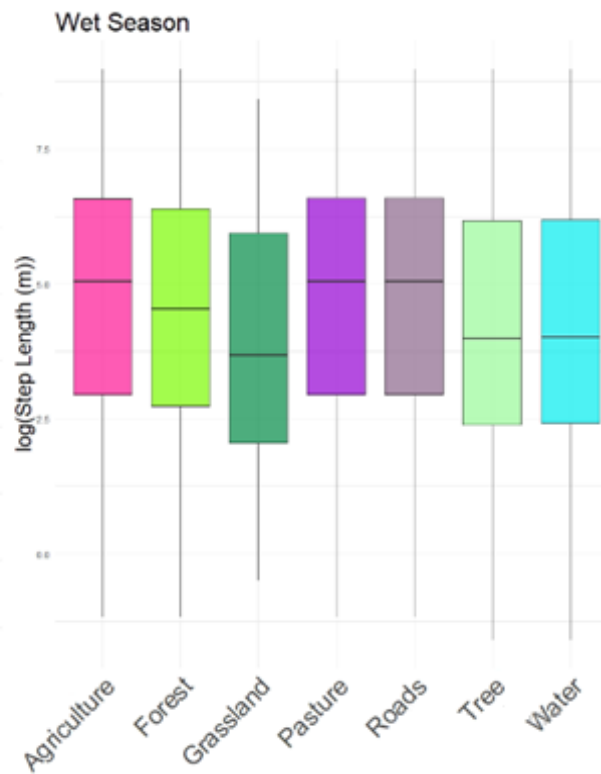


Figure 12. Influence of land use classes by season on the step length (m, logarithmic scale) of jaguar's individuals. The **A** plot refers to step length in Dry season (june, july and august) and the **B** plot refers to Wet season (december, january and february).

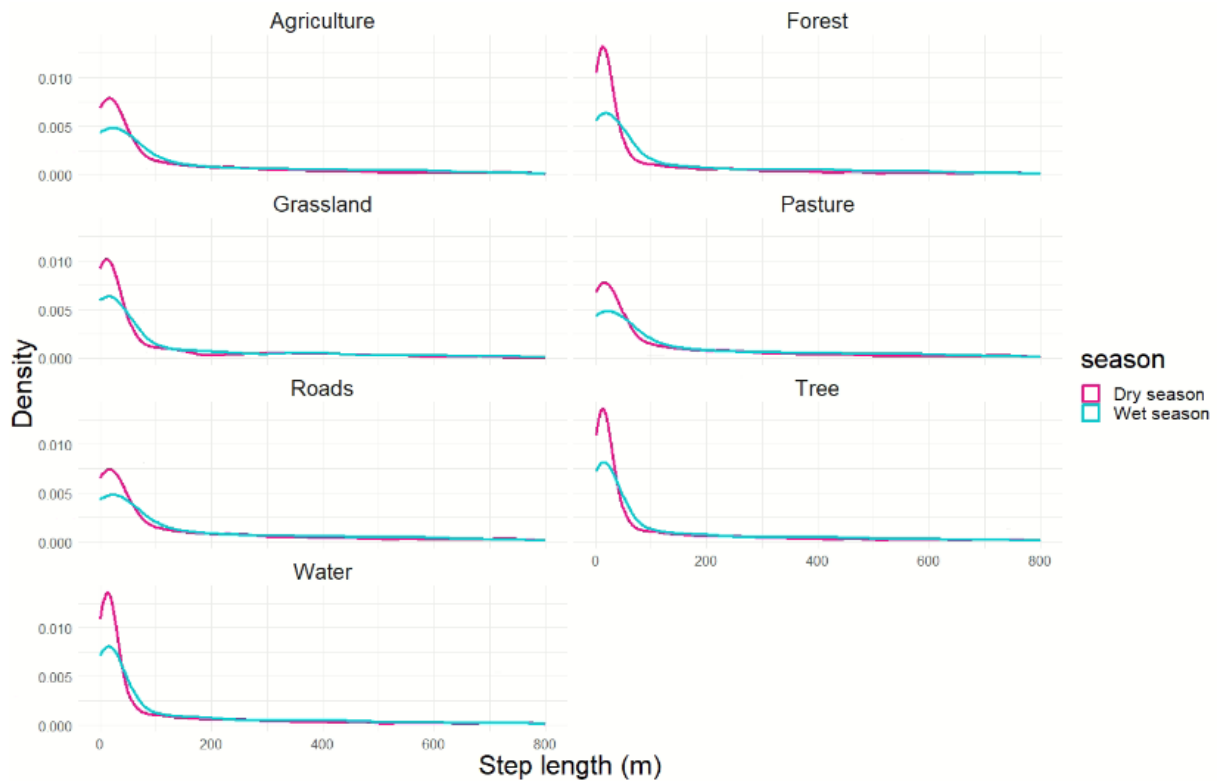


Figure 13. Density of Step Length (m) of land use classes between seasons. Dry season in pink line and wet season in blue line.

Table 5. Mann-Whitney and p-values calculated comparing Step Length between wet season and dry season by land use class. P-values >0.05 show no statistical significance of season difference.

Variable	W	P-value
Mann-Whitney		
Agriculture	1406840	<<0.001***
Forest	2607344	<<0.001***
Grassland	140728	0.001***
Pasture	1412078	<<0.001***
Paved Roads	1448490	0.0006***

Tree canopy	3865834	0.003**
Water	3897122	0.002**

We also found differences on step lengths across land use (Kruskal-Wallis test, p-value $<< 0.005$), with significant variation (Dunn test, p-value < 0.05) between Forest and Grassland; Forest and Pasture; Forest and Tree; Forest and Water; Forest and Agriculture; Grassland and Pasture; Pasture and Tree; and, Pasture and Water (**Table 6**). The random steps were statistically different between all land uses (**Table 7**).

Table 6. Results of Dunn test with Bonferroni adjustment and p-values comparing Step length in land use pairs. P-values < 0.05 show statistical difference of Step lengths between land use classes.

	Agriculture	Forest	Grassland	Pasture	Roads	Tree
Forest	11.18978					
p-value	$<< 0.001^{***}$					
Grassland	13.37904	4.402911				
p-value	$<< 0.001^{***}$	$<< 0.001^{***}$				
Pasture	-0.442020	-11.87120	-13.96400			
p-value	0.999873	$<< 0.001^{***}$	$<< 0.005^{***}$			
Roads	-0.658173	-12.30640	-14.33429	-0.213457		

p-value	1.0000	<<0.001***	<<0.001***	1.0000		
Tree	14.35398	3.264327	-2.115641	15.13662	15.66721	
p-value	<<0.001***	0.015*	0.3609	<<0.001***	<<0.001***	
Water	13.86895	2.610172	-2.636430	14.64599	15.16980	-0.740817
p-value	<<0.001***	0.0950	0.088	<<0.001***	<<0.001***	0.9

Table 7. Mann-Whitney and p-values calculated comparing Random-steps and real steps of each land use.

Land use	W (Mann-Whitney)	p-value
Forest	292013	<0.001***
Grassland	291992	0.00158***
Pasture	358261	<<0.001***
Roads	325112	<0.001***
Tree canopy	258866	0.00935**
Agriculture	357689	<0.001**
Water	258841	<0.001***

4. DISCUSSION

4.1 - *Habitat suitability*

In this study we successfully used different approaches to assess habitat suitability of *Panthera onca* by Species Distribution Modeling (a climate model, with a resolution of 1km; a landscape model, with a resolution of 30 m; and a final map merging both previous approaches). The difference in the extent of habitat suitability portrayed in our models suggests that while climatic conditions may play a dominant role in defining *Panthera onca*'s distribution in the Pantanal, the landscape attributes further influence the finer-scale distribution patterns within the region. Thus, it is important to use both resolutions separately to obtain a first layer in the occurrence, that is the climate filter that influences species presence in a larger scale, then construct the landscape model, which influences species in a finer-scale. Merging both information, obtaining a proper and more complete habitat suitability prediction is equally important, once it allows a broader comprehension on jaguars needs and preferences.

Ferraz et al. (2012), performed a species distribution modeling (SDM) for *Panthera onca* in the entire Brazilian territory, as well as a specific one for the Atlantic forest. They highlight the importance of scale and resolution in SDM. The incorporation of both landscape and climatic variables, was suggested to improve model accuracy, especially in areas where human influence is significant. Our findings resonate with key principles discussed which is evident that selecting landscape and climate variables is essential. Although, in Ferraz et al. (2012) study climate and landscape are incorporated together and we propose to use it separately, because they are a two-scale process and then engender a more trustworthy model.

On a methodology similar to the one we used on this study, Oshima (2019) realized a SDM modeling for White-lipped-peccaries (*Tayassu pecari*) using climate and landscape variables separately, and obtained a habitat suitability map for the entire Brazilian territory by overlapping the ensemble frequency of both models. As well as on our results, they highlight the importance of a comprehensive approach that considers both climatic and landscape

variables for a more accurate understanding of species distribution dynamics, highlighting the importance of climate and landscape acting synergically determining habitat suitability of species.

The use of climatic and landscape information allowed us to have a more complete view on what impacts the presence and the habitat suitability for *Panthera onca*. Considering these two scale processes separately, as well as in an integrated way, is an important tool for effective conservation strategies and decision making.

4.2 - Influence of habitat suitability on Jaguar's movement

Using the final map, which merged the SDM climatic and landscape habitat suitability predictions, we could assess the influence of habitat suitability on jaguars' movement. Our findings show that the step length, indicative of individual stride and travel distances, was significantly greater within habitat zones, suggesting a strong association between jaguar movement and the habitats identified by the SDM. Moreover, this approach indicates the species' ecological preferences, once the most suitable areas will be the ones that contain the resources this species needs.

Tyre et al. (2020) emphasized the importance of habitat suitability in influencing the movement and spatial behavior of large felids, corroborating our results. Our findings that denser step lengths are within habitat areas, corroborates with the efficient habitat suitability predictions by SDM and highlight the importance of habitat in shaping jaguar movement emphasizing the role of habitat conservation for the species in the Pantanal region. The Pantanal is the world's largest wetland and is facing significant landscape changes due to agricultural expansion and the habitat suitability range for jaguars is expected to decrease. In 30 years, the biome faced a great change in the landscape features (Souza et al., 2020), water sources area, the variable that most contributed to SDM modeling, decreased by 29% since 1988. Thus, we highlight the relevance of incorporating habitat-based analyses in wildlife conservation efforts.

4.3 - Seasonal movement

In the context of seasonal rainfall variation, we observed differences in step lengths between the dry and wet seasons and between some land uses. The different step length density considering rainfall and land use during the dry season compared to the wet season suggests potential shifts in resource availability, prey distribution, or vegetation structure. Additionally, the flood period in Pantanal is a significant factor influencing animal movement, as observed in our results, where the density of jaguar step lengths are shorter during the wet season.

Across different land uses, such as forest, water, tree canopy, grassland, roads, pasture and agriculture we observed a significant difference between the dry and wet seasons such as in rainfall. Thus, these shifts in movement patterns could be also attributed to an adaptation on the jaguars' spatial behavior based on habitat attributes (Cullen Junior et al., 2013; Alegre et al., 2023). Variations in vegetation prey availability, and water sources associated with different land uses influence jaguars to exhibit distinct movement strategies, optimizing their resource utilization.

Jaguars are known to exhibit remarkable behavioral plasticity, adjusting their movements according to the prevailing environmental conditions (Alegre et al., 2023; Cavalcanti & Gese, 2009). Bischof et al. (2012) demonstrated how carnivore movement patterns can be influenced by habitat features. It was also evidenced by Alegre et al. (2023) with jaguars in Pantanal, in which the species exhibit differential selection patterns according to habitat, and it was influenced by tree cover, shrubland, and areas with water. We noted similar behavioral adaptations, in which jaguars modify their movements across different land uses, possibly driven by variations in vegetation structure, prey distribution, and water availability.

Our results indicate a synergistic influence of both climate and landscape on jaguar's movement, which provide important insights into jaguars adaptive strategies, that is essential

for constructing effective conservation efforts and ensuring the persistence of jaguars and other wildlife through changing environmental conditions.

4.4 Perspectives for conservation

The Pantanal, the world's largest wetland, is suffering with a significant landscape transformation due to the expansion of agriculture and livestock farming. Over the last 30 years, pasture areas have increased by more than 285%, comprising about one-sixth of the land use in the biome when combined with other agricultural activities such as farming and soybean cultivation. In 2021, approximately 16% of the Pantanal area was dedicated to agropecuary (with pasture representing 99% of this land use category), a substantial increase from the 4% registered in 1985 (Souza et al., 2020).

Human activity growth in the biome has had a negative impact, resulting in a reduction of natural areas from 95.58% to 83.01% between 1985 and 2021 (Souza et al. 2020). Furthermore, the Pantanal is experiencing increasing droughts, with 2018 being the last year with a significant flood. The area covered by water, flooded fields, and swampy areas during floods decreased by 29% since 1988. Climate change is contributing to this reduction, along with decreased water flow from external sources into the biome, due to deforestation and pesticide use in the water supply regions (Souza et al. 2020).

The reduction in flooding time and water supply cause great impact in the dynamics of the Pantanal, which relies on floods for its ecological cycles, affecting the wildlife, as we showed for jaguars. The water is the resource that most contributed for habitat suitability models for jaguars and the rainfall also affected seasonality movement patterns. If these changes in Pantanal continue, we expect a great impact in the ecosystem dynamics, since jaguars are a top chain predator and an umbrella species (Rabinowitz and Zeller, 2010), in which its conservation and protection indirectly benefits a wide range of other species. The impacts on wildlife are even higher when considering the effects of global climatic change, as well as the decreasing reliability on climate prediction due extreme weather events.

The climate change is intrinsically related to landscape change, forcing the wildlife to adapt their movement patterns and space use. Large carnivores, including jaguars, can be deeply affected by changing climate patterns, once their movements are intricately connected to habitat structure and prey dynamics. On the other hand, they are keystone species, playing an important role in shaping ecosystem dynamics. Thus, effective conservation, mitigation, and habitat restoration strategies are vital for maintaining the ecosystem balance in this unprecedented dynamic scenario.

Although, the growing global population has led to an increased demand for food and resources, intensifying pressures on habitats and ecosystems (Foley et al., 2005). Consequently, implementing regenerative conservation measures becomes vital for ecosystem conservation and the provision of resources for humans. Agroforestry and agro-silvopastoral systems, which integrate trees, crops, and livestock, are sustainable land-use approaches that not only enhance productivity but also contribute to biodiversity conservation (Nair et al., 2012; Torralba et al., 2016; Udawatta et al., 2019; Criado et al., 2021). These systems offer a multifaceted solution, providing habitats and food sources for wildlife while promoting sustainable agricultural practices and mitigating the impacts of climate change. By adopting such regenerative measures, we can reach a balance between meeting human needs and preserving ecosystems, ultimately securing a more sustainable and harmonious coexistence with the natural world.

5.CONCLUSIONS

Our results represent an important step in evaluating synergetic effects of climate and landscape on habitat suitability and animal movement, specifically jaguars. Our habitat suitability map, considering climate and landscape variables, presented complementary perceptions, acting as two scale processes. The final habitat suitability map, reinforced the association between jaguar movement and variables related to climate and landscape, highlighting the relevance of habitat-based analyses in wildlife conservation efforts.

Furthermore, we observed that the movement patterns of jaguars are influenced by seasonal variations of rainfall, habitat type, and anthropogenic features, indicating shifts in resource availability, prey distribution, vegetation structure or human features presence. Understanding these seasonal variations in step lengths is crucial for elucidating how jaguars adapt their movement strategies to cope with changing environmental conditions and resource availability throughout the seasons. The observed synergetic effects of climate and landscape on jaguar movement that offer vital insights into their adaptive strategies.

Effective conservation, mitigation, and regenerative strategies, such as agroforestry and agro-silvopastoral are crucial to balance ecosystem dynamics in the face of growing human demands and climate challenges. Climate change is not anymore a problem for future generations, but a current challenge not only for wildlife, but also for humans and their needs. Therefore, this study can be an important tool and source of information on planning and decision making related to jaguar conservation, affecting not only the wildlife, but also people.

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7. SUPPLEMENTARY MATERIAL

Table S1. PCA values of bioclimatics

	Dim.1	Dim.2	Dim.3	Dim.4	Dim.5
bio01	7.01	6.21	0.92	0.07	0.38
bio02	3.42	4.62	1.83	21.11	2.26
bio03	5.37	0.03	12.98	1.43	2.73
bio04	5.84	0	16.78	0.77	3.83
bio05	3.44	12.03	10.59	0.14	1.73
bio06	8.27	1.99	0.3	1.51	0.69
bio07	6.12	1.02	12.95	2	5.37

bio08	5.43	7.85	3.69	0.42	1.73
bio09	7.45	3.28	0.04	2.4	0
bio10	5.1	8.65	7.41	0.75	0.04
bio11	7.81	3.97	0.11	0.01	0.85
bio12	6.96	4.64	0.51	2.3	4.49
bio13	6.66	1.56	0.39	8.21	10.76
bio14	2.8	13.61	4.57	0.04	2.63
bio15	1.23	7.74	14.98	14.75	2.9
bio16	7.08	1.22	0.2	6.1	11.38
bio17	2.99	14.27	5.32	0	1.16
bio18	2.37	3.57	6.1	32.4	12.6
bio19	4.64	3.75	0.35	5.56	34.46

Table S2. Pearson correlation values of landscape variables. Bold values indicate a high correlation between variables (habitat diversity and paved roads; habitat diversity and human density; paved roads and human density).

	Agropecuary	Forest	Habitat diversity	Human Density	Paved roads	Slope	Tree canopy	Water
Agropecuary	1.000							
Forest	-0.3120	1.000						
Habitat diversity	0.0213	0.0584	1.000					

Human Density	-0.0210	-0.0032	0.8569	1.000				
Paved road	-0.0086	-0.0001	0.9803	0.9661	1.0000			
Slope	-0.0255	0.1728	-0.0434	-0.0227	-0.0181	1.000		
Tree canopy	-0.2270	0.6183	0.0386	0.0156	0.0029	0.1871	1.000	
Water	-0.0864	-0.1444	-0.3079	-0.1401	-0.0159	0.0359	-0.0899	1.000

Table S3. Mann-Whitney between Random Steps and real steps in different land use.

Variable	W	P-value
Mann-Whitney		
Agriculture	1406840	<<0.001
Forest	2607344	<<0.001
Grassland	140728	0.001
Pasture	1412078	<<0.001

Paved Roads	1448490	0.0006
Tree canopy	3865834	0.003
Water	3897122	0.002

Figure S1. Bioclimatic PCA vectors

