ECOLOGY AND CONSERVATION OF THE JAGUAR *(PANTHERA ONCA)* IN CENTRAL AMERICA

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Sometimes I am a jaguar
running through ravines,
leaping boulders,
climbing mountains.

I look beyond the sky,
beyond the water,
beyond the earth.

I chat with the sun,
play with the moon,
pluck stars
and stick them to my body.

My tail stirs,
as I stretch out on the grass
tongue panting.

[Humberto Ak’abal, K’iche’ Maya poet from Guatemala]

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Summary

Conservation of the jaguar relies on holistic and transdisciplinary conservation strategies that integratively safeguard essential, connected habitats, sustain viable populations and their genetic exchange, and foster peaceful human-jaguar coexistence. These strategies define four research priorities to advance jaguar conservation throughout the species' range. In this thesis I provide several relevant ecological and sociological insights into these research priorities, each addressed in a separate chapter. I focus on the effects of anthropogenic landscapes on jaguar habitat use and population gene flow, spatial patterns of jaguar habitat suitability and functional population connectivity, and on innovative governance approaches which can work synergistically to help achieve human-wildlife conviviality. Furthermore, I translate these insights into recommendations for conservation practice by providing tools and suggestions that conservation managers and stakeholders can use to implement local actions but also make broad scale conservation decisions in Central America. In *Chapter 2*, I model regional habitat use of jaguars, producing spatially-explicit maps for management of key areas of habitat suitability. Using an occupancy model of 13-year-camera-trap occurrence data, I show that human influence has the strongest impact on jaguar habitat use, and that Jaguar Conservation Units are the most important reservoirs of high quality habitat in this region. I build upon these results by zooming in to an area of high habitat suitability loss in *Chapter 3*, northern Central America. Here I study the drivers of jaguar gene flow and I produce spatially-explicit maps for management of key areas of functional population connectivity in this region. I use microsatellite data and pseudo-optimized multiscale, multivariate resistance surfaces of gene flow to show that jaguar gene flow is influenced by environmental, and even more strongly, by human influence variables; and that the areas of lowest gene flow resistance largely coincide with the location of the Jaguar Conservation Units. Given that human activities significantly impact jaguar habitat use and gene flow, securing viable jaguar populations in anthropogenic landscapes also requires fostering peaceful human-wildlife coexistence. This is a complex challenge that cannot be met without transdisciplinary academic research and cross-sectoral, collaborative governance structures that effectively respond to the multiple challenges of such coexistence. With this in mind, I focus in *Chapter 4* on carnivore conservation initiatives that apply transformative governance approaches to enact transformative change towards human-carnivore coexistence. Using the frameworks of transformative biodiversity governance and convivial conservation, I highlight in this chapter concrete pathways, supported by more inclusive, democratic forms of conservation decision-making and participation that promote truly transformative changes towards human-jaguar conviviality.

Zusammenfassung

Die Erhaltung des Jaguars beruht auf ganzheitlichen und transdisziplinären Erhaltungsstrategien, die wesentliche, zusammenhängende Lebensräume schützen, lebensfähige Populationen und deren genetischen Austausch erhalten und die friedliche Koexistenz von Mensch und Jaguar fördern. Diese Strategien werden durch die vier Forschungsprioritäten veranschaulicht, die den Schutz des Jaguars im gesamten Verbreitungsgebiet der Art vorantreiben sollen. In dieser Arbeit möchte ich die Forschung zum Schutz des Jaguars vorantreiben, indem ich mehrere relevante ökologische und soziologische Einblicke in diese Forschungsschwerpunkte gebe, die jeweils in einem eigenen Kapitel behandelt werden. Ich konzentriere mich auf die Auswirkungen anthropogener Landschaften auf die Lebensraumnutzung von Jaguaren und den Genfluss in der Population, auf räumliche Muster der Lebensraumeignung von Jaguaren und die funktionale Konnektivität von Populationen sowie auf innovative Governance-Ansätze, die synergetisch wirken können, um die Konvivenz zwischen Mensch und Wildtier zu fördern. Darüber hinaus setze ich diese Erkenntnisse in Empfehlungen für die Naturschutzpraxis um, indem ich konkrete Instrumente und Vorschläge für Maßnahmen anbiete, die Naturschutzmanager und Interessenvertreter nutzen können, um lokale Maßnahmen umzusetzen, aber auch um weitreichende Naturschutzentscheidungen in Zentralamerika zu treffen. In Kapitel 2 modelliere ich die regionale Lebensraumnutzung von Jaguaren und erstelle räumlich explizite Karten für das Management von Schlüsselgebieten mit geeigneter Lebensraumnutzung. Mithilfe eines Habitatmodells basierend auf 13-Jahres-Kamerfangdaten-Studien zeige ich, dass der menschliche Einfluss die stärkste Auswirkung auf die Lebensraumnutzung von Jaguaren hat und dass die Jaguar-Schutzgebiete die wichtigsten Reservoirs für hochwertige Lebensräume in dieser Region sind. Auf diesen Ergebnissen baue ich auf, indem ich in Kapitel 3 ein Gebiet mit einem hohen Verlust an Lebensraumeignung, das nördliche Mittelamerika, näher betrachte. Hier untersuche ich die Triebkräfte des Genflusses bei Jaguaren und erstelle räumlich explizite Karten für das Management von Schlüsselgebieten mit funktionaler Populationskonnektivität in dieser Region. Ich verwende Mikrosatellitendaten und pseudo-optimierte multiskalige, multivariate Widerstandsflächen des Genflusses, um zu zeigen, dass der Genfluss von Jaguaren durch Umweltvariablen und noch stärker durch menschliche Einflussfaktoren beeinflusst wird und dass die Gebiete mit dem geringsten Genflusswiderstand weitgehend mit den Standorten der Jaguar-Schutzgebiete übereinstimmen. Da sich menschliche Aktivitäten erheblich auf die Lebensraumnutzung der Jaguare und den Genfluss auswirken, ist für die Sicherung lebensfähiger Jaguarpopulationen in anthropogenen Landschaften auch die Förderung einer friedlichen Koexistenz von Mensch und Wildtieren erforderlich. Dies ist eine komplexe Herausforderung, die ohne transdisziplinäre akademische Forschung und

sektorübergreifende, kooperative Governance-Strukturen, die wirksam auf die vielfältigen Herausforderungen einer solchen Koexistenz reagieren, nicht zu bewältigen ist. Vor diesem Hintergrund konzentriere ich mich in Kapitel 4 auf Initiativen zum Schutz von Raubtieren, die transformative Governance-Ansätze anwenden, um einen Wandel hin zu einer Konvivenz zwischen Mensch und Raubtier zu bewirken. Unter Verwendung des Rahmens der transformativen Biodiversitäts-Governance und des konvivialen Naturschutzes zeige ich in diesem Kapitel konkrete Wege auf, die durch integrativere, demokratische Formen der Entscheidungsfindung im Naturschutz unterstützt werden und wirklich transformative Veränderungen in Richtung Konvivialität zwischen Mensch und Jaguar fördern.

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CHAPTER 1

General Introduction

1

Anthropogenic activities have significantly impacted life on Earth over the past 50 years. Changes in land and sea use, direct exploitation, and climate change have led to declines in the number and size of wildlife populations, the distinctiveness of ecological communities, and the integrity of ecosystems (Díaz et al. 2019), as well as increases in global species extinctions of up to 1000-fold (Pimm et al. 2014). These trends will unfortunately intensify if integrated actions are not taken to address both the direct and indirect causes of this biodiversity loss (Díaz et al. 2019). Across terrestrial ecosystems, one of the most affected vertebrate groups is that of large carnivores. Intact carnivore guilds have lost more than 64% of their historical range, 88% of carnivore species have experienced range contractions of 20% or more, and 50% of all large carnivore mammal species are at risk of extinction, primarily due to habitat loss and degradation, direct exploitation, prey removal, and direct persecution (Ripple et al. 2014; Ingeman et al. 2022).

Large carnivores are not only among the most threatened species, but also the most controversial and difficult to conserve, especially in anthropogenic landscapes. In such landscapes, the distribution and abundance of large carnivores are determined by a combination of ecological factors, such as habitat suitability and connectivity (Lamb et al. 2020), and social factors, such as human values and socio-political contexts, which ultimately determine people’s tolerance and behaviour toward large carnivores (Carter & Linnell 2016; Marino et al. 2021b). Large carnivore conservation therefore involves not only ecological challenges, but also social and political challenges (Hovardas et al. 2021), with many factors interacting at multiple levels (Rutherford & Clark 2014). Ecological challenges include the intrinsic biological characteristics of carnivores (e.g., energetic limitations, slow life histories, low population densities) that, in combination with environmental factors and human impacts (e.g., habitat loss and fragmentation, direct exploitation), not only make it difficult for species to meet their requirements for large, suitable, and connected habitats, but also increase their vulnerability to extinction (Cardillo et al. 2004, 2005; Burton et al. 2011). Social challenges include the different, sometimes conflicting values, emotions, and norms that different stakeholders have regarding carnivores (Dietsch et al. 2016); the direct conflicts that arise between people and carnivores due to competition for prey, predation of livestock, or public safety issues (Inskip & Zimmermann 2009; Klees van Bommel et al. 2020); and overall the negative impacts that carnivores can have on people’s livelihoods and well-being (Braczkowski et al. 2023). Political challenges relate to governance issues, which may include lack of trust, equal representation of stakeholders, legitimacy, and recognition of diverse knowledge and perspectives in decision-making processes (Sjölander-Lindqvist et al. 2015), as well as the instrumentalization of carnivores to further political goals (Darimont et al. 2018). All these challenges make conservation of carnivores a complex endeavour, especially for certain carnivore groups such as felids, which are among the three groups with worst conservation status worldwide (Fernández & Carlos 2022).

In this thesis, I study a near-threatened felid in a region of conservation concern: the jaguar *(Panthera onca)* in Central America. Jaguar conservation relies on holistic and transdisciplinary conservation strategies that integratively safeguard essential, connected habitats, sustain viable populations and their genetic exchange, and foster peaceful human-jaguar coexistence (Medellín et al. 2016). This conservation vision is supported by the four research priorities (RPs) designed to advance jaguar conservation throughout the species' range (de la Torre et al. 2016). These include studying the species' spatial requirements, the functional connectivity of its populations, relationships of human-jaguar coexistence, and monitoring population sizes and trends across ecosystems and human disturbance gradients. In this thesis I aim to advance jaguar conservation research by providing several relevant ecological and social insights into these research priorities, each addressed in a separate chapter, and by providing tools and actions that conservation managers and stakeholders can use to implement local actions but also to make broad scale conservation decisions.

I begin this introduction with a brief overview on the jaguar ecology and conservation and a description of the study region. I then address each of the jaguar conservation research priorities studied in this thesis, beginning with the importance of studying the spatial requirements of the species and the challenges of conservation planning in Central America (RP: Species' spatial requirements across ecosystems), moving to the importance of studying gene flow and the challenges of securing functional jaguar population connectivity in northern Central America (RP: functional population connectivity across human disturbance gradients), and then, with addressing the importance of transformative governance as well as the challenges of its implementation to enact transformative change towards human-carnivore conviviality (RP: human-jaguar coexistence). I conclude this introduction by summarizing the overall structure of this thesis, briefly describing the objectives and how each chapter of this thesis is meant to advance jaguar conservation research and practice in the study region.

Jaguar ecology and conservation status

The jaguar is the largest felid in the Neotropics. It regulates trophic dynamics and contributes to ecosystem's integrity and functionality (Terborgh et al. 2001). It also serves as an effective focal or umbrella species in environmental management (Thornton et al. 2016; Figel et al. 2018), e.g. as an indicator of functional ecosystems, and as a planning basis for reserve design and management (Rabinowitz & Zeller 2010). Jaguars were historically distributed from the United States to Argentina, but by the beginning of this century the species had lost 54% of its historic range (Sanderson et al. 2002b). Therefore a wide-range conservation strategy was planned. Ecologically distinct jaguar populations across the species' range were identified (Jaguar Conservation Units-JCUs; Sanderson et al. 2002b), and dispersal corridors to connect them were delineated to ensure gene flow and long term population viability (Rabinowitz & Zeller, 2010; Fig. 1). JCUs are defined as areas that have sufficient prey base and habitat quality to sustain a population of at least 50 breeding jaguars, or less if adequate conditions allow the populations to increase (e.g. enough habitat and controlled conservation threats; Sanderson et al. 2002b). Whereas both JCUs and corridors were delineated using exclusively expert opinion, subsequent efforts have been carried out to further validate such delineations (e.g. Petracca et al. 2018; De Angelo et al. 2013).

Since the first continental assessment of jaguar populations in 2002 (Sanderson et al. 2002b), much has been learned about the ecology, space use and conservation status of the species (Medellin et al. 2002, 2016). Across the species range, jaguars have been closely and positively related to prey abundance (Rabelo et al. 2019), extent of forest cover (Conde et al. 2010; Foster et al. 2010; Petracca et al. 2018) and wetlands (Figel et al. 2019), and primary productivity (Jędrzejewski et al. 2017b), as well as negatively related to human disturbance (Morato et al. 2018; McBride & Thompson 2019). Contrary to habitat use, jaguars' space use patterns have shown large variation across the species distribution range (Thompson & Morato 2021). Average home range sizes vary from 10-34 Km^2 (de la Torre & Rivero 2019) to as much as 2454Km^2, the latter typical for jaguars living in highly disturbed areas such as the Cerrado Biome in South America, where <50% of natural habitat remains (Morato et al. 2016; McBride & Thompson 2018; Thompson et al. 2021). Overall female home ranges are shaped by prey distribution and abundance (Sandel 1989; Sunquist & Sunquist 1989; Kanda et al. 2019), as well as safe refugees for offspring (Nuñez 2006). Males' home ranges instead are largely determined by the spatial distribution of females, encompassing enough females as to increase opportunities for mating, as well as by intraspecific competition with other males (Cavalcanti & Gese 2010; Kanda et al. 2019).

Currently, the jaguar is classified as a Near threatened species by the IUCN (Quigley et al. 2017), mainly due to habitat loss and human persecution (Jędrzejewski et al. 2017b; De Angelo et al. 2013), the latter being the main driver of the species' extinction (Villalva & Palomares 2022). Furthermore, 14.5% and 3.5% of the species' distribution range encompasses jaguar populations with high and extremely high risk of extinction, respectively (Villalva & Palomares 2022). Overall, 91% of all jaguar populations are at medium and high risk of extinction (de la Torre et al. 2017), with Central American populations, particularly those in Guatemala and Honduras, at a higher risk (Villalva & Palomares 2022).

Study region: Central America

Central America extends across the tropics and subtropics. It includes the countries of Guatemala, Belize, Honduras, El Salvador, Nicaragua, Costa Rica, and Panama; all of which – with the exception of El Salvador – are jaguar range countries (Fig. 1). This region has high biodiversity and is a hotspot for endemic plants and animals (Myers et al. 2000). However, it also holds one of the highest rates of deforestation and forest degradation in the world (Redo et al. 2012), being Guatemala and Nicaragua the countries with the highest loss of woody vegetation (Aide et al. 2013). The region is characterized by a highly diverse land use and a high population density of 94.27 ind./km^2 (World Bank 2020). Just over 60% of the region is covered by evergreen and deciduous broadleaf forests (61%) and mosaics of natural vegetation and cropland (21%). The remainder of the region consists of a diverse matrix of land uses, the main categories of which are cropland (6%), secondary forests (4%), grasslands (3%), wetlands (1%), and urban areas (0.5%, ESA, 2015).

Central America is the second largest stronghold for jaguars after the Amazon (Sanderson et al. 2002a), and most jaguar 'connectivity hubs' are concentrated here (Zeller et al. 2013). The region includes sixteen Jaguar Conservation Units (JCUs) and corridors to connect them, the latter distributed very similarly to a single chain along the Isthmus, thus any loss of connectivity in this region would disproportionately affect the overall connectivity of the entire jaguar corridor network (Zeller et al. 2013). Despite the importance of this region for jaguar conservation, jaguar habitat here is severely threatened by land use change (Powers & Jetz 2019) and forest loss (Olsoy et al. 2016), and jaguar populations have been extirpated from 67% of their former range, leaving remaining populations small, in severely degraded landscapes, and showing early signs of genetic isolation due to habitat loss and low structural connectivity (Wultsch et al. 2016). Currently the jaguar's extent of occurrence (EOO) in this region is almost entirely restricted to the Caribbean Slope, where much of the forest remains (Fig. 1), and within this area, the Guatemalan and Honduran jaguar populations at most conservation risk (Villalva & Palomares 2022).

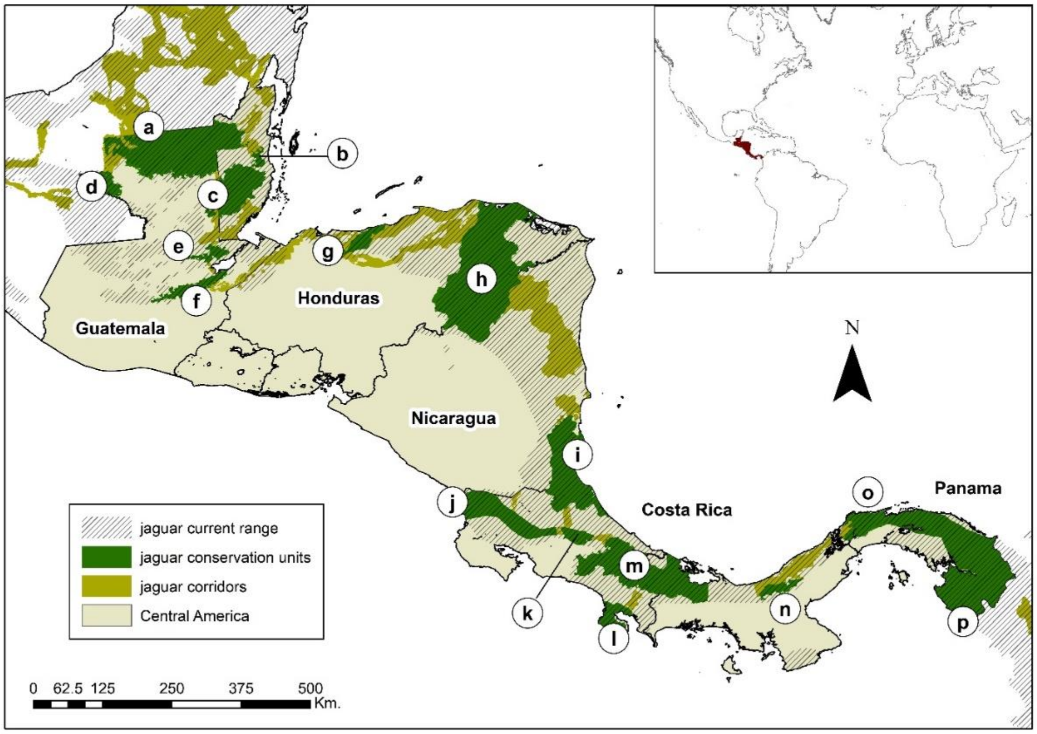

Fig. 1. Central American study region, showing the current distribution range of the species, jaguar conservation units and corridors. Insert in right upper corner: Global map with Central America shaded in dark red colour. Main map: Jaguar Conservation Units and potential corridors according to Rabinowitz & Zeller (2010). Jaguar Conservation Units are identified by letters as follows: a) Selva Maya; b) Central Belize; c) Maya Mountains; d) Montes Azules/Sierra del Lacandon; e) Sierra Santa Cruz; f) Sierra de las Minas; g) Cordillera Nombre de Dios; h) Reserva de Biosfera Transfronteriza; i) Cerro Silva Indio Maiz-Tortuguero, j) Cordillera de Guanacaste; k) Cordillera Volcanica Central; l) Peninsula de Osa, m) Talamanca-Cordillera Central; n) Santa Fe; o) Chagres; and p) Chagres-Darien.

Studying species' spatial requirements and the challenges of conservation planning

A central task in conservation planning is identifying and prioritizing key areas for protection of endangered species and the preservation of landscape connectivity. This endeavour requires a thorough understanding of the drivers of species presence, habitat associations, and avoidance mechanisms. For species living in degraded landscapes and at high risk of extinction, conservation strategies must be based on integrated assessments across political boundaries, spatial scales and species' entire ranges (Wikramanayake et al. 2004; Rabinowitz & Zeller 2010). This is particularly relevant for species like the jaguar, given that they are broadly distributed and encompass a wide range of habitat types and land uses.

Habitat suitability models can contribute to the prioritization of protected areas and support conservation planning for several species (Cabeza et al. 2004; Li et al. 2020; Mukherjee et al. 2020). These models relate species occurrence data to environmental conditions, using derived response curves that best reflect the set of ecological requirements of the species of concern (Guisan et al. 2017). However, regional and globally comprehensive species occurrence datasets are scarce and publicly available spatial data are often heterogeneous, discontinuous across species ranges, lack standardized study designs, and are strongly biased temporally and spatially (Boitani et al. 2011; Rondinini et al. 2011). These limitations make the prioritization of conservation areas at the appropriate scales challenging (Ferrier 2002).

New methods for studying distribution and habitat suitability of species have emerged over the last two decades. Occupancy modelling allows for the study of species-habitat relationships while accounting for imperfect detection of the species or 'false absences' (i.e. not always detected when present, MacKenzie et al., 2005). Not accounting for imperfect detection can underestimate the distribution of the target species (i.e. modelling only the apparent distribution, Kéry et al., 2010), estimate covariate relationships biased towards zero (Tyre et al. 2003), and confound detectability with occurrence covariates (Guillera-Arroita et al. 2014). Thus, site-occupancy models are particularly useful to study the habitat relationships of rare elusive species with low population densities, such as the jaguar in Central America.

The jaguar is a species for which much research on species-habitat relationships has been conducted. Throughout their range, jaguar distribution has been strongly and positively related to prey abundance (Rabelo et al. 2019), amount of forest cover (Conde et al. 2010; Foster et al. 2010; Petracca et al. 2018) and wetlands (Figel et al. 2019); and negatively related to human disturbance (Morato et al. 2018; McBride & Thompson 2019). Furthermore, ecosystem productivity has been positively related to jaguar presence, with populations surviving better in humid, productive environments (Jędrzejewski et al. 2017b). Despite the large research efforts on this subject, most studies of jaguar habitat use to date have been conducted at small, local scales (Foster et al. 2010; Zeller et al. 2011; Rabelo et al. 2019), with the exception of studies which rely heavily on either input from experts or interviews to local people (Rabinowitz & Zeller 2010; Jędrzejewski et al. 2018; Petracca et al. 2018), or which have very low representation of Central American data (Thompson et al. 2021).

Extrapolating local and expert-witness studies to larger areas may result in spurious inferences (e.g. generalizing patterns that may be true only locally, under unique conditions), due to a lack of standardized monitoring schemes and analysis, use of different environmental predictors, and most importantly, because patterns of jaguar resource selection vary across their geographic range (Morato et al., 2018).

Therefore this thesis advances jaguar research and conservation in two main ways. First, it advances the understanding of species' spatial requirements by representing the first broad-scale quantitative analysis of jaguar habitat use in Central America using a comprehensive dataset of direct jaguar observations (i.e. camera traps records) from multiple locations and surveys across the region. Second, it contributes to jaguar conservation by providing useful information for prioritizing key areas and actions for the persistence of the species, with quantified uncertainty, and providing the basis for future jaguar habitat connectivity studies in the region.

Studying gene flow and the challenges of securing functional population connectivity

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

The permeability of landscapes to the movement of animals is defined as connectivity (Taylor et al. 1993). Landscape connectivity is the result of the overall structure of the landscape as well as the individuals' response to this landscape structure in terms of movement and survival ability (Tischendorf & Fahrig 2000). This functional aspect of connectivity can be measured as successful gene flow across the landscape (Baguette & Van Dyck 2007; Pe'er et al. 2011). Functional connectivity allows populations to adapt to changing conditions, thus its estimation can help inform successful management of wildlife (Auffret et al. 2015; Schmidt et al. 2020).

Several models have been created and adapted to provide insights on the connectivity of populations of different species. These models have been derived either directly from movement data (Richard & Armstrong 2010; Elliot et al. 2014), or indirectly from genetic data and patterns (Kimmig et al. 2020; Lecis et al. 2022; Portanier et al. 2022). Whereas movement-based models provide fine-scale insights on individuals' movement decisions in real time, they require measuring animal dispersal at the relevant spatial and temporal scales (Tesson & Edelaar 2013). Measuring animal dispersal is a challenge, particularly for wide-ranging species of conservation concern, such as large carnivores. Alternatively, genetic data have been used to relate gene flow patterns to landscape structure (Holderegger & Wagner 2008). They provide insights into how landscapes affect individual's movement, dispersal, and breeding over generations (Lowe & Allendorf 2010). Thus, genetic data and associated analyses provide valuable and cost-effective ways to model gene flow and functional connectivity (Zeller et al. 2012; Tesson & Edelaar 2013), shedding light on population processes that are not possible to assess using exclusively movement data (e.g. effective population sizes, bottlenecks, inbreeding, population structure, contemporary versus historic genetic isolation; Willi et al., 2022).

Gene flow of several large carnivore populations are negatively impacted by human development, including that of pumas (*Puma concolor*; Ernest et al., 2014) and American black bears (*Ursus americanus*; Cushman & Lewis, 2010) in North America, tigers and leopards in India *(Panthera tigris* and *Panthera pardus*; Thatte et al., 2020), Eurasian lynx in Europe (*Lynx*; Bull et al., 2016), and jaguars in Mexico and Brazil (*Panthera onca*; Roques et al., 2016).

In this thesis, I employ the jaguar as a focal species to understand how gene flow is shaped in a heavily human-impacted landscape; mapping the expected functional connectivity of jaguar populations in northern Central America. The jaguar is a model species to study functional connectivity because of its large area requirements (Thompson et al. 2021), high level of conservation concern (91% of subpopulations show medium to high threat; de la Torre et al., 2017), and decreased genetic exchange in heavily human-influenced landscapes (Roques et al. 2016; Wultsch et al. 2016). Whereas JCUs and corridors were delineated to improve jaguar population connectivity at a continental scale (Rabinowitz & Zeller 2010; Petracca et al. 2018), they are not based on impartial quantitative data.

Jaguar populations have shown moderate to high levels of genetic diversity and no strong population structure across most of their range (Eizirik et al. 2001; Ruiz-Garcia et al. 2006; Roques et al. 2014). However, connectivity of jaguar populations is being lost at local and regional scales. In South America there are jaguar populations currently suffering from bottlenecks, genetic diversity loss, and high genetic differentiation due to strong signals of anthropogenic-driven drift (Haag et al. 2010; Lorenzana et al. 2020). In Central America, signals of gene flow restriction and high anthropogenic impact have been found, particularly in the region between Guatemala and Honduras (Wultsch et al. 2016).

The study of jaguar gene flow in this thesis aims at advancing jaguar conservation in two main ways. First, it is the first study to assess functional connectivity of jaguar populations using empirical data at a regional extent. Previous research in the region has been based solely on literature or local/expert input, either to assess structural connectivity at large regional scales (Rabinowitz & Zeller 2010; Petracca et al. 2018), or functional (de la Torre et al. 2017) and habitat connectivity (Menchaca et al. 2019) at small, local scales. Second, it responds to continental and regional jaguar conservation priorities by conducting 'genetic ground-truthing' (assess functional connectivity) of jaguar dispersal corridors to improve and maintain population connectivity, particularly in northern Central America (Wultsch et al. 2016; de la Torre et al. 2017). Previous findings suggested that whereas gene flow between jaguars from the Selva Maya (northern Guatemala and central Belize) is high, geographically close jaguar populations in the Selva Maya and Honduras exhibit differences in genetic structure (Wultsch et al. 2016). Therefore, it is likely that jaguar gene flow could be influenced not only by geographic distance, but also by dynamic landscape changes in the region.

Transformative governance and the challenge of enacting transformative change towards human-carnivore conviviality

Human activities have impacted ecological communities worldwide (Pimm et al. 2014), and half of the worlds' large carnivore mammal species are at risk of extinction (Ripple et al. 2014; Ingeman et al. 2022). These trends are expected to worsen unless integrated actions are taken to address the direct drivers of carnivore loss, however intervening on these drivers remains challenging (Díaz et al. 2019). Direct drivers, such as overexploitation or persecution are in turn caused by indirect drivers such as conflict, missing governance, and various demographic, economic, and political factors, all of which influence and affect the values, behaviours, and institutions of our society. Therefore, to be effective, conservation actions must go beyond the direct causes of carnivore loss and address the indirect drivers that are at the root of carnivore declines and extinctions (Ehrlich & Pringle 2008; Díaz et al. 2019).

Despite the above challenges, population recovery of and coexistence with large carnivores is seemingly possible, as illustrated by the following examples. Densities of jaguars *(Panthera onca)* in multi-used landscapes (e.g. cattle ranches) are sustained at levels comparable to those from parks in the Brazilian Pantanal, largely because of protection from hunting and human retaliation (Devlin et al. 2023). Pumas *(Puma concolor)* show high occupancy in highly modified landscapes in the Brazilian Cerrado despite high levels of anthropogenic fragmentation, largely because of effective management of protected areas and federal laws that enforce protection on private lands (Vynne et al. 2011; Ferreira et al. 2020). Large populations of hyenas *(Hyaena hyaena)* and leopards *(Panthera pardus)* survive in urbanized landscapes with high human densities in western Indian due to a combination of high social tolerance and conservation laws (Athreya et al. 2013). And lastly, populations of lynx *(Lynx lynx)*, wolves *(Canis lupus)*, bears *(Ursus arctos)* and wolverines *(Gulo gulo)* have increased or stabilized in areas of Europe where these populations were previously depleted or locally extirpated (Chapron et al. 2014); this is largely due to a combination of well-enforced, integrated legislation, effective use management plans, and improved habitat quality and connectivity resulting from rural abandonment (Knott et al. 2014; Bartoń et al. 2019; Cimatti et al. 2021).

Nevertheless, the increasing sharing of landscapes between large carnivores and humans also has negative consequences. It may increase the potential for human-carnivore (Klees van Bommel et al. 2020; Braczkowski et al. 2023) and social conflicts (Sjölander-Lindqvist et al. 2020; Jürgens et al. 2023), which can lead to unsustainable carnivore management and poor governances. For example, social conflicts can mislead decision-making processes (Fernández-Gil et al. 2016), bias carnivore management in favour of political interests (Darimont et al. 2018), and ultimately, impact the viability of carnivore populations (Immonen & Husby 2016; Quevedo et al. 2019; Laikre et al. 2022). Effective conservation of large predators in anthropogenic landscapes is therefore possible, but it requires fundamental changes in how we interact with and manage carnivores. Innovative governance strategies will be particularly useful in addressing this challenge, especially the implementation of governance approaches that promote adaptation of social systems through learning, critical thinking, leadership, and co-production (Termeer et al. 2017). In summary, it will demand *transformative change* in large carnivore conservation practice (Blythe et al. 2018; Massarella et al. 2021).

Transformative change involves a profound transformation of social systems that changes indirect drivers, particularly society's paradigms, values, and behaviours, as well as the corresponding socio-political, economic, and technological structures. It involves fundamental changes at the personal and social levels (Woiwode et al. 2021), including social behaviour and values (Palmer et al. 2014). Transformative changes are meant to produce axial change, i.e. radical changes that challenge current systems and disrupt the *status quo* (O'Brien et al. 2013). Such changes are also meant to address indirect drivers with sensitivity to the local context and ultimately lead to more just, equitable, and sustainable futures (Temper et al. 2018; Visseren-Hamakers et al. 2021).

A robust body of knowledge on transformative change has been developed in the sustainability (Westley et al. 2011; Olsson et al. 2014; Blythe et al. 2018; McPhearson et al. 2021) and climate change literature for over a decade (Pelling 2010; Burch et al. 2014), however a specific focus on biodiversity has only recently emerged (Massarella et al. 2021, 2022; Naito et al. 2022; Visseren-Hamakers & Kok 2022; de Koning et al. 2023; White et al. 2023). Moreover, knowledge of how to manage and implement this transformative change in biodiversity conservation, and particularly with respect to sustainable states between humans and carnivores, i.e. coexistence, is only recently gaining momentum. One such advance is the development of the conceptual framework for transformative biodiversity governance (TBG), which comprehensively links the need to address the root causes (i.e., indirect drivers) of species loss and extinction with the implementation of holistic, innovative governance approaches (Visseren-Hamakers et al. 2021).

TBG refers to the collection of formal and informal, public and private rules, regulatory systems, and local to global stakeholder networks which work synergistically to enable compassionate, just and sustainable social-ecological systems (Visseren-Hamakers et al. 2021). Because it is grounded on the transformative theory of change, it offers a guiding framework to steer and evaluate transformative change towards human-large carnivore coexistence in the conservation practice. TBG represents an innovative governance strategy that holds transformative power by addressing the root causes of species loss in ways that are simultaneously adaptive, inclusive, integrative, and transdisciplinary in the face of uncertainty (Díaz et al. 2019). It ensures that conservation interventions produce axial change by acting across-scales, sites and sectors (integrative); empowering underrepresented, marginalized groups with transformative change values (inclusive); building resilience in the face of environmental change, complexity, and social conflict (adaptive); recognizing different ways of knowing, valuing, and representing biodiversity (pluralistic); and exercising caution in the face of uncertainty (precautionary; Visseren-Hamakers et al., 2021).

In this thesis, I use the term 'conviviality' of humans and wildlife instead of coexistence. I do so because of the strong transformative potential of the term, which is rooted in the transformative theory of change of 'convivial conservation' (Büscher & Fletcher 2020). Convivial conservation is a radical alternative to mainstream conservation approaches which uses transformative methodologies and an innovative conceptual framework to address the global biodiversity loss and extinction crisis. It challenges the hegemonic capitalist order and the dichotomies embedded within it (e.g. human vs nature), while building on equity, environmental justice and structural change to facilitate coexistence between human and all non-human nature (Büscher & Fletcher 2020; Massarella et al. 2022).

Conviviality in the context of this thesis is thus conceptualized as a balanced state between human and large carnivores in which the former develop committed, long-term, ethical relationships with the latter, creating sustainable social-ecological systems which are based on the principles of social equity, structural change, environmental ethics and justice. I believe that such an approach expands the transformative potential of the term 'coexistence', both conceptually and practically, by explicitly linking efforts to address the root causes of large carnivore loss with governance approaches that promote societies' adaptation to the current challenges of the biodiversity crisis.

Structure of this thesis

In this thesis, I focus on the effects of anthropogenic landscapes on jaguar habitat use and population gene flow, spatial patterns of jaguar habitat suitability and functional population connectivity, and finally, innovative governance approaches that can act synergistically to achieve human-carnivore conviviality. Furthermore, I translate these findings into conservation practice by presenting concrete tools and actions that can be used by conservation managers and stakeholders to implement local and regional actions.

In *Chapter 2*, I examine the habitat suitability of Central America for jaguars using the most comprehensive compilation of jaguar camera trapping data from the region to date, spanning five of six jaguar-range Central American countries from 2005 to 2018 (Fig. 1). I used data from 1,457 camera-traps to develop a species distribution model based on an occupancy framework accounting for imperfect detection. I used the model to: i) test *a priori* hypotheses about influences of vegetation cover, primary productivity, rivers, protected areas and human disturbance on jaguar habitat use; ii) map habitat suitability for jaguars in Central America; iii) refine and target areas of conservation concern across political boundaries, using entirely empirical jaguar data for the first time in the region, and iv) prioritize international management efforts in Central America. This chapter contributes to the understanding of the species' spatial requirements by representing the first broad-scale quantitative analysis of jaguar habitat use in Central America; it usefully informs the prioritization of key areas and actions for the persistence of the species, with quantified uncertainty; and it provides the basis for future studies on connectivity between jaguar habitats.

In *Chapter 3*, I follow up on the findings of the previous chapter *(Chapter 2)* and other studies (Antonio De La Torre et al. 2018; Villalva & Palomares 2022) which point towards high extinction risk of and lack of connectivity between jaguar populations in Guatemala and Honduras. Here, I determine jaguar gene flow using microsatellite data to address four main objectives: i) identify landscape variables that facilitate or hinder gene flow between jaguar populations in northern-Central-America, ii) assess functional connectivity of jaguar populations in the study landscape, iii) compare spatial predictions of functional connectivity based on gene flow versus expert input (Rabinowitz & Zeller 2010; Petracca et al. 2018) and jaguar habitat suitability data (Calderón et al. 2022); and iv) identify priority areas for corridor planning that promote genetic exchange and secure the long-term viability of Central American jaguar populations. The study presented in this chapter is the first to model jaguar gene flow and connectivity across spatial scales, heterogeneous landscapes, and a large regional extent of conservation concern in Central America. It also explicitly accounts for spatial scale dependence in jaguar-landscape interactions and the species' dispersal ability. These are critical but often neglected steps for achieving robust conclusions and improving management inputs that support habitat and population connectivity efforts (Jackson & Fahrig 2015; Krishnamurthy et al. 2016).

In *Chapter 4*, I reviewed all carnivore conservation initiatives published between 1990 and 2023 and assessed their contribution to producing transformative change towards human-carnivore conviviality using the TBG framework. I sought to assess: i) the extent to which carnivore conservation initiatives address indirect causes of carnivore declines and extinction, ii) the extent to which these initiatives are embedded in a transdisciplinary framework that integratively considers ecological and social factors, iii) the governance approaches that are implemented in carnivore conservation practice, and iv) the challenges and lessons that can be drawn from the conservation initiatives in relation to implementing transformative change towards conviviality in social-ecological systems. This chapter helps to address the challenge of transdisciplinarity in conservation science and practice, particularly of incorporating social science into conservation (Niemiec et al. 2021), and learning from the interdisciplinary approaches of the climate change and sustainability literature (Kothari 2014; Steffen et al. 2018; Visseren-Hamakers et al. 2021). It contributes to a deeper understanding of the broader socio, political and economic contexts in which conviviality with large carnivores takes place, while shedding light on concrete pathways, to move beyond technocratic approaches of conflict mitigation towards restoring the social fabric that promotes truly transformative change towards human-jaguar conviviality.

Finally in *Chapter 5*, I provide a general discussion of my results and contextualize them within the current carnivore literature and contemporary jaguar conservation efforts. I highlight here the key findings in each chapter, their conservation implications, and concluding remarks. Finally, a Supplement contains supporting information for the *Chapters 2-4*.

CHAPTER 2

Occupancy models reveal potential of conservation prioritization for Central American jaguars‡

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Abstract

Understanding species-environment relationships at large spatial scales is required for the prioritization of conservation areas and the preservation of landscape connectivity for large carnivores. This endeavour is challenging for jaguars *(Panthera onca)*, given their elusiveness and the local nature of most jaguar studies, precluding extrapolation to larger areas. We developed an occupancy model using occurrence data of jaguars across five countries of Central America, collected from camera-trap studies of two to twelve months' duration, deployed over an area of 14,112 km^2 from 2005 to 2018. Our occupancy model showed that habitat use of jaguars increased with primary net productivity, distance to human settlements, and distance to rivers. Detection of the species was related to survey effort and research team identity. Within the jaguar extent of occurrence, 73% was deemed suitable for the species, with 47% of it lying within Jaguar Conservation Units (JCU), and 59% of JCU land being legally protected. Suitable areas were divided into four distinct clusters of continuous habitat shared across country borders. However, large areas of predicted low habitat suitability may constrict connectivity in the region. The reliability of these spatial predictions is indicated by the model validation using an independent dataset (AUC=0.82; sensitivity=0.766, specificity=0.761), and concordance of our results with other studies conducted in the region. Across Central America, we found that human influence has the strongest impact on jaguar habitat use and JCUs are the main reservoirs of habitat. Therefore, conservation actions must focus on preventing habitat loss and mitigating human pressure, particularly within the clusters of continuous areas of high suitability, and on restoring habitat to foster connectivity. The long term persistence of jaguars in the region will depend on strong international cooperation that secures jaguar populations and their habitat across Central American borders.

KEYWORDS: Large carnivores, habitat suitability, species distribution models, camera-traps, carnivore conservation, jaguar conservation units, human influence

Introduction

A central task in conservation planning is identifying and prioritizing key areas for protection of endangered species and preservation of landscape connectivity. This endeavour requires a thorough understanding of the drivers of species presence, habitat associations, and avoidance mechanisms. For species living in degraded landscapes and at high risk of extinction, conservation strategies must be based on integrated assessments across political boundaries, spatial scales and species' entire ranges (Wikramanayake et al. 2004; Rabinowitz & Zeller 2010). This is particularly relevant for broadly distributed species that encompass a wide range of habitat types and land uses, such as some charismatic large carnivores, like the jaguar (*Panthera onca*).

Habitat suitability models can contribute to the prioritization of protected areas and support conservation planning for several species (Cabeza et al. 2004; Li et al. 2020; Mukherjee et al. 2020). These models relate species occurrence data to environmental conditions, using derived response curves that best reflect the set of ecological requirements of the species of concern (Guisan et al. 2017). However, regional and globally comprehensive species occurrence datasets are scarce and publicly available spatial data are often heterogeneous, discontinuous across species ranges, lack standardized study designs, and are strongly biased temporally and spatially (Boitani et al. 2011; Rondinini et al. 2011). These limitations make the prioritization of conservation areas at the appropriate scales challenging (Ferrier 2002).

The jaguar is a near threatened apex predator in the tropical Americas (Quigley et al. 2017), whose populations are decreasing and which has been subjected to much research on their habitat relationships. The species relies mainly on habitats with forest cover, water and a sufficient prey base (Sanderson et al. 2002b), although it can tolerate a variety of conditions across their geographic range (Morato et al., 2018). Most studies of jaguar habitat use to date have been conducted at local scales (Foster et al. 2010; Zeller et al. 2011; Rabelo et al. 2019), except some relying heavily on either input from experts or interviews to local people (Rabinowitz & Zeller 2010; Jędrzejewski et al. 2018; Petracca et al. 2018), or with very low representation of Central American data (Thompson et al. 2021). Extrapolating local and expert-witness studies to larger areas may result in spurious inferences (e.g. generalizing patterns that may be true only locally, under unique conditions), due to a lack of standardized monitoring schemes and analysis, use of different environmental predictors, and most importantly, because patterns of jaguar resource selection vary across their geographic range (Morato et al., 2018).

New methods for studying distribution and habitat suitability of species have emerged over the last two decades. Occupancy modelling allows for the study of species-habitat relationships while accounting for imperfect detection of the species or 'false absences' (i.e. not always detected when present, MacKenzie et al., 2005). Not accounting for imperfect detection can underestimate the distribution of the target species (i.e. modelling only the apparent distribution, Kéry et al., 2010), estimate covariate relationships biased towards zero (Tyre et al. 2003), and confound detectability with occurrence covariates (Guillera-Arroita et al. 2014). Thus, site-occupancy models are particularly useful to study the habitat relationships of rare elusive species with low population densities, such as the jaguar in Central America.

Central America is the second largest stronghold for jaguars after the Amazon (Sanderson et al. 2002a), serving as a bridge to connect populations from the northern and southern ranges of the species' distribution (Fig. 1). It holds sixteen Jaguar Conservation Units (JCUs), priority areas for jaguar conservation delineated by expert opinion. JCUs are defined as areas with enough prey base and habitat quality to sustain resident jaguar populations of at least 50 breeding individuals, or less if habitat is adequate and threat reduction allows population increase (Sanderson et al. 2002b). Despite this, Central America holds one of the highest deforestation rates and proportional forest degradation worldwide (Redo et al. 2012). In this region, jaguar populations have been extirpated from 67% of their former range, leaving the remaining populations at small sizes, in highly degraded landscapes, and exhibiting early signs of genetic isolation due to habitat loss and decreased structural connectivity (Wultsch et al. 2016). Currently, the jaguar's extent of occurrence (EOO) in Central America is limited almost entirely to the Caribbean slope where much of the forest still remains (Fig. 1).

Here we study the habitat suitability of Central America for jaguars using the largest compilation to date of jaguar camera-trap data from the region, spanning five out of the six jaguar-range Central American countries from 2005 to 2018 (Fig. 1). We used data from 1,457 camera-traps to develop a species distribution model based on an occupancy framework accounting for imperfect detection. We used the model to: a) test *a priori* hypotheses about influences of vegetation cover, primary productivity, rivers, protected areas and human disturbance on jaguar habitat use; b) map habitat suitability for jaguars in Central America; c) refine and target areas of conservation concern across political boundaries, using entirely empirical jaguar data for the first time in the region, and d) prioritize international management efforts in Central America.

Methods

Study area

Central America encompasses Guatemala, Belize, Honduras, El Salvador, Nicaragua, Costa Rica, and Panama; all of which –with the exception of El Salvador– are jaguar range countries (Fig. 1). This region holds a high biological diversity and represents a hotspot of plant and animal endemism (Myers et al. 2000). It is characterized by a highly diverse pattern of land uses and a high human density of 94 ind./km^2 (World Bank, 2020). Central America is covered mainly by broadleaved evergreen and deciduous trees (61%) and mosaics of natural vegetation with croplands (21%). The rest of the region is represented by a diverse matrix of land uses, including croplands (6%), secondary growth forests (4%), grasslands (3%), wetlands (1%) and urban areas (0.5%, ESA, 2015). For further details of the study region see Appendix S1.

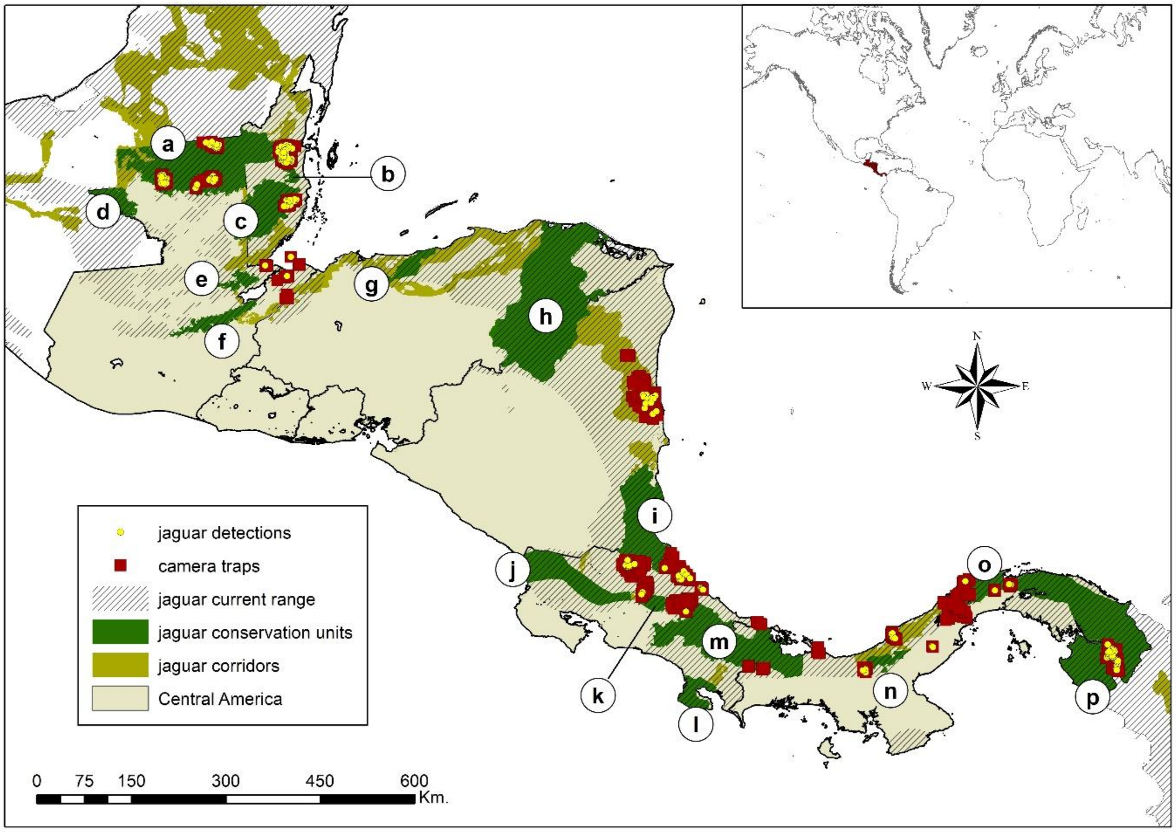

Fig. 1. Central American study region, showing the camera-trap locations and the current distribution range of the species. Insert in right upper corner: Global map with Central America shaded in dark red color. Main map: Jaguar Conservation Units and potential corridors according to Rabinowitz & Zeller (2010). Jaguar Conservation Units are identified by letters as follows: a) Selva Maya; b) Central Belize; c) Maya Mountains; d) Montes Azules/Sierra del Lacandon; e) Sierra Santa Cruz; f) Sierra de las Minas; g) Cordillera Nombre de Dios; h) Reserva de Biosfera Transfronteriza; i) Cerro Silva-Indio Maiz-Tortuguero, j) Cordillera de Guanacaste; k) Cordillera Volcanica Central; l) Peninsula de Osa, m) Talamanca-Cordillera Central; n) Santa Fe; o) Chagres; and p) Chagres-Darien.

Camera-trap data

We compiled records of jaguar detections and non-detections from camera-trap stations deployed in the study region from 2005 to 2018. The data were collected by eight well-established scientific teams working permanently with jaguars in each of these countries, as part of different research projects and jaguar conservation and monitoring activities in the region. Surveys' duration ranged from one to twelve months, and data recorded at each site also differed depending on project objectives (Appendix S2-S3).

We created a study grid with a cell size of 36 km^2, to create a balance between accuracy of environmental measures, minimum estimations of jaguar home-range size (Rabinowitz & Nottingham, 1986; Salom-Pérez et al., 2007), and comparability with previous studies in the region (Zeller et al. 2011; Petracca et al. 2018). Hence, we processed the camera-trap data by aggregating the detections-non detections of all camera-traps within 36km^2-cells. A detection was recorded whenever a jaguar was detected at a camera-trap *i* at grid-cell *j* and event *k* (sampling occasion: one month). Thus, grid-cell *j* obtained the value 1, regardless of how often a jaguar was detected there per event, otherwise a non-detection was noted 0.

Predictors of jaguar occupancy and detection

We compiled information on environmental and human disturbance covariates that could influence jaguar occurrence in the region. Variables for analysis were chosen based on previous research on jaguar ecology across the species range (Appendix S4) and after checking for collinearity ($|r| < 0.7$, $P > 0.05$; Appendix S5-S7). We obtained covariate values at the respective year of camera-trapping when possible, otherwise at the closest year available. For jaguar occurrence we selected the environmental variables of elevation (*elev*), tree cover percent (*treecov%*), distance to rivers (*dist_riv*), and primary net productivity (*npp*); and variables related to human disturbance such as agricultural area (*agriculture*), distance to settlements (*dist_sett*), distance to roads (*dist_roads*), distance to protected areas (*dist_pa*), interaction between tree cover percent and area of agriculture (*treecov*agriculture;* details on covariate calculations in Appendix S8).

For modelling jaguar detectability we selected two additional covariates, survey effort (*eff*) and the identity of the research team (*team*), which collected the data in each grid-cell *j* and event *k,* as a site-specific covariate. Survey effort was calculated by summing the days each camera-trap was active within each grid-cell over the year. All covariate values for occupancy and detection were standardized (mean=0; SD=1) for the occupancy analysis.

Occupancy analysis

We used site-occupancy models to estimate the occurrence probability of jaguars at grid-cells *j* using the package unmarked (Fiske & Chandler 2011) in R-4.0.4 (R Core Team, 2021). Detection histories were created using the package *camtrapR* (Niedballa et al. 2016), and aggregated into monthly sample intervals (*k*, 'events') to avoid overdispersion and aid in model convergence. We designed three general *a priori* sets of hypotheses explaining occupancy probability by a) natural habitat variables, b) human influence variables, or c) a mixture of both (as in Jordan et al., 2016). Within each of these, we developed a subset of several biologically plausible candidate models, representing different hypotheses of increasing complexity on the environmental characteristics associated with jaguar occurrence in the region.

We fitted single-state, single-season occupancy models treating each unique site-year combination sampled ('grid cell – year') as independent sites. We used a static approach because we were interested in the static occupancy patterns of jaguars across the region, rather than the turnover rates between years; and temporal replication was limited due to grid cells not being surveyed consistently on the same years (72% of the grid cells had data on one year only, 19% on two years, and the rest on three to six years). We expected 'year' to be more related to changes in the environment across time than on the jaguar habitat use per se, and that this variability would be accounted for by matching the covariate values to the respective year of camera-trapping or the closest year available. However, we also tested for any potential year effects by running a model version with year as random effect for each of the models in the candidate set, using the R package *ubms* (Kellner, 2021; Appendix S9).

We used the most parsimonious model (i.e. top ranked) for extrapolation and evaluated it using a goodness of fit test (GOF; MacKenzie & Bailey, 2004) and checking the Dunn–Smyth residuals for both its occupancy and detection components (Warton et al. 2017). We also used an independent dataset (Jędrzejewski et al., 2018) to evaluate the predictive accuracy of the top model using the area under the receiver operating characteristic (AUC, details in Appendix S10). This top model was then used to predict jaguar occupancy probability in the region based on predictor values for the year 2020 (Appendix S9). We assessed model's performance using the value that minimised the difference between sensitivity and specificity as threshold (Liu et al. 2005). For this we finally used a threshold value of probability of occupancy of $\Psi \geq 0.55$. We interpret here probability of occupancy as 'probability of habitat use'.

Results

Camera-trap data

We collected 409 independent jaguar detections from 1,457 camera-traps and 113,308 trapping-days. The surveyed grids (n = 392) covered an area of 14,112 km^2 across five countries (6% of the jaguar EOO in Central America). When aggregating the data at country level, the average number of surveyed years was 6.2 (range=2–8 years, for Nicaragua and Panama respectively) and the average effort per year per country was 3,657 camera-trap-days (range=1547–5174 camera-trap-days, for Guatemala and Panama respectively).

Predictors of jaguar habitat use and detection

Habitat use of jaguars in Central America was best explained by models combining both natural habitat and human disturbance covariates. Out of the competing models, those including both types of covariates accounted for 99% of the cumulative AIC-weight (Appendix S11). The top model for jaguar habitat use included net primary productivity, distance to settlement, and distance to river; all with 95% confidence intervals not overlapping zero. This top model was also consistent with the model selection results performed within the Bayesian framework, in which 'year' as a random effect was evaluated but did not appear in the top ranked model (Appendix S12-S13). Therefore, from here on we refer to the results of the analysis of this top model within the frequentist framework.

Jaguar habitat use increased with net primary productivity (npp: β=0.651, SE=0.214), distance to settlements (dist_sett: 3.910, SE=0.651), and distance to rivers (dist_riv: 0.981, SE=0.245). The greatest relative impact on predicted jaguar habitat use was given by distance to settlements, evidenced by the magnitude of its β-coefficient of 3.910. One standard deviation (SD) increase in distance to settlement had an effect size 3.98 times greater than a similar increase in distance to rivers, and an effect size 6.01 times greater than a 1SD increase in net primary productivity. Jaguar detection probability was strongly influenced by survey effort, with higher detection in grid-cells with higher survey effort (β=0.629, SE=0.082), and research team (Table 1). The top model had a good predictive performance (AUC= 0.821; sensitivity=0.766, specificity=0.761).

Spatial prediction of jaguar habitat suitability

The spatial prediction of our top model predicted habitat for jaguars in half of Central America surface ($\Psi \geq 0.55$; Fig. 2a), comprising a total area of 269,388Km^2, of which 33% is encompassed by JCUs. Within the EOO of the jaguar (i.e. boundary of its distribution; Quigley et al., 2017), more than two thirds (73%) are suitable for the species (192,306.539km^2), with 47% lying within JCUs and 59% of JCU land being legally protected (Fig. 3). Habitat was concentrated mainly in the Selva Maya in northern Guatemala and Belize, north-eastern Honduras, eastern Nicaragua, and eastern and western Panama (Fig. 2a). Overall mean jaguar habitat use probabilities were lowest for El Salvador (Ψ_{mean}=0.199, SD=0.219) and Costa Rica (Ψ_{mean}=0.458, SD=0.319) and the

Panamanian JCU Chagres (Ψ_{mean}=0.454, SD=0.340); whereas highest for Belize (Ψ_{mean}= 0.787, SD=0.282) and the Honduran-Nicaraguan JCU Reserva de Biosfera Transfronteriza (Ψ_{mean}=0.990, SD=0.045). The JCU's with the highest coverage of habitat were Selva Maya, Central Belize and Peninsula de Osa (>98%, Table 2), whereas the lowest coverage is reported for Chagres and Cordillera Volcanica Central (<28%).

Table 1. Parameter estimates of the top model of jaguar habitat use in Central America. The baseline team included in the intercept was CECON.

Covariate	β	SE	Lower 95%CI	Upper 95%CI	z	P(>|z|)
Occupancy						
Intercept[a]	2.130	0.415	1.316	2.943	5.128	< 0.001
npp[b]	0.651	0.214	0.232	1.071	3.042	0.002
dist_sett[a]	3.910	0.651	2.634	5.186	6.006	< 0.001
dist_river[a]	0.981	0.245	0.501	1.461	4.005	< 0.001
Detection						
Intercept[a]	-1.025	0.245	-1.506	-0.545	-4.181	< 0.001
Effort[a]	0.629	0.082	0.469	0.789	7.713	< 0.001
Site (Team) effects:						
Coastal-Jaguar-Conservation	0.772	0.280	0.223	1.321	2.758	0.006
Yaguará-Panamá	0.144	0.295	-0.434	0.723	0.489	0.625
Panthera-Costa Rica[a]	-1.081	0.497	-2.054	-0.107	-2.175	0.030
Panthera-Guatemala	-1.219	0.813	-2.813	0.375	-1.499	0.134
Panthera-Nicaragua	-0.729	0.368	-1.450	-0.008	-1.982	0.047
Panthera-Southampton-UB-ERI[a]	1.373	0.283	0.819	1.927	4.856	< 0.001
WCS-Washington	0.529	0.325	-0.108	1.166	1.627	0.104

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[b] Significance level of coefficients at $\alpha = 0.05$

Table 2. Mean jaguar habitat use probabilities (Ψ_{mean}), standard deviations (SD), and percentage covered by suitable areas per country and Jaguar Conservation Units in Central America.

Name	Ψ_{mean}	SD	% suitable areas
Country[c]			
Guatemala	0.51	0.34	43.78
Belize	0.78	0.28	76.82
Honduras	0.60	0.34	53.97
El Salvador	0.19	0.21	7.52
Nicaragua	0.64	0.37	58.84
Costa Rica	0.45	0.31	36.96
Panama	0.59	0.37	54.75
Jaguar Conservation Unit			
Selva Maya	0.95	0.11	98.52
Central Belize	0.94	0.04	100.00
Montes Azules/Sierra del Lacandon	0.90	0.11	92.79
Maya Mountains	0.86	0.2	89.89
Cordillera Nombre de Dios	0.64	0.26	70.30
Sierra Santa Cruz	0.81	0.16	87.78
Reserva de Biosfera Transfronteriza	0.99	0.04	99.66
Sierra de las Minas	0.71	0.19	77.22
Cerro Silva-Indio Maiz-Tortuguero	0.88	0.18	90.92
Cordillera de Guanacaste	0.59	0.31	53.81
Chagres	0.45	0.34	36.05
Cordillera Volcanica Central	0.49	0.18	27.65
Chagres-Darien	0.69	0.32	70.65
Talamanca-Cordillera Central	0.80	0.21	84.64
Santa Fe	0.95	0.08	81.21
Peninsula de Osa	0.82	0.22	99.99

The largest continuous habitat were predicted in four main clusters, all of which extend across political boundaries, a) Guatemala-Belize (62,172.861 Km^2), b) eastern Honduras-Nicaragua

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[c] Countries sorted by decreasing latitude.

(128,149.928 Km^2), c) South Costa Rica-Northern Panama (29,304.690 Km^2), and d) Panamanian Darien (17,346.392 Km^2, Fig. 3). In contrast, four large areas of predicted low habitat suitability within the EOO of the jaguar are located along eastern-Guatemala, western-Honduras, central-Costa Rica, and north-central- Panama (Fig. 2a). Habitat was also predicted by our model in non-surveyed areas. Within the jaguar EOO, these areas are the east of Honduras, a country for which we had no data on jaguar occurrence; most of the Nicaraguan Atlantic-coast, and areas across central Guatemala. Outside the jaguar EOO, small and fragmented areas of high suitability were predicted along the Pacific coast of Central America (Fig. 2a). Overall the uncertainty of our habitat suitability predictions was lowest for the areas with higher habitat suitability values (Fig. 2b), and for the countries of Belize and Nicaragua. Uncertainty was higher for areas such as central-Guatemala, eastern-Honduras and central Costa Rica (Fig. 2b).

Discussion

We conducted a broad-scale quantitative analysis of jaguar habitat use, using for the first time a comprehensive dataset of direct jaguar observation records from multiple locations and surveys across Central America, a region in which the current EOO of the species holds one of the highest deforestation rates within all Latin America and the Caribbean (Aide et al. 2013). Such a broad scale approach is required when addressing jaguar conservation (Sanderson et al. 2002b), and accordingly, we identified key areas for conservation and population connectivity across international borders using a jaguar database of camera-trap records across Central America.

We found evidence that jaguar suitability at broad-scale is related to both environmental and human influence variables, however the latter impacted the species more strongly. Jaguars were positively associated with primary productivity, supporting findings of previous studies (Jędrzejewski et al. 2017b; Jędrzejewski et al. 2018), and with distance to rivers. Primary productivity is associated with higher mammal diversity (Fritz et al. 2016) and herbivore densities (Jedrzejewski & Jedrzejewska 1996), thus could represent higher prey availability. Additionally, the persistence of jaguar populations is also associated with primary productivity, given that jaguar populations exhibit higher extirpation probabilities in drier areas with lower vegetation productivities than in more humid, productive areas (Jędrzejewski et al. 2017b). We did not find that habitat use of jaguars was positively related to water sources as previously found (Foster et al. 2010). This could be partly attributed to limitations of our water source layer, which lacked information on streams, intermittent rivers, wetlands, ponds, marshes, and rainwater ponds 'aguadas' –the latter important for jaguars in dry areas away from permanent/large water sources (Gaitán et al. 2020). Nonetheless, previous research has shown that jaguars with home-ranges

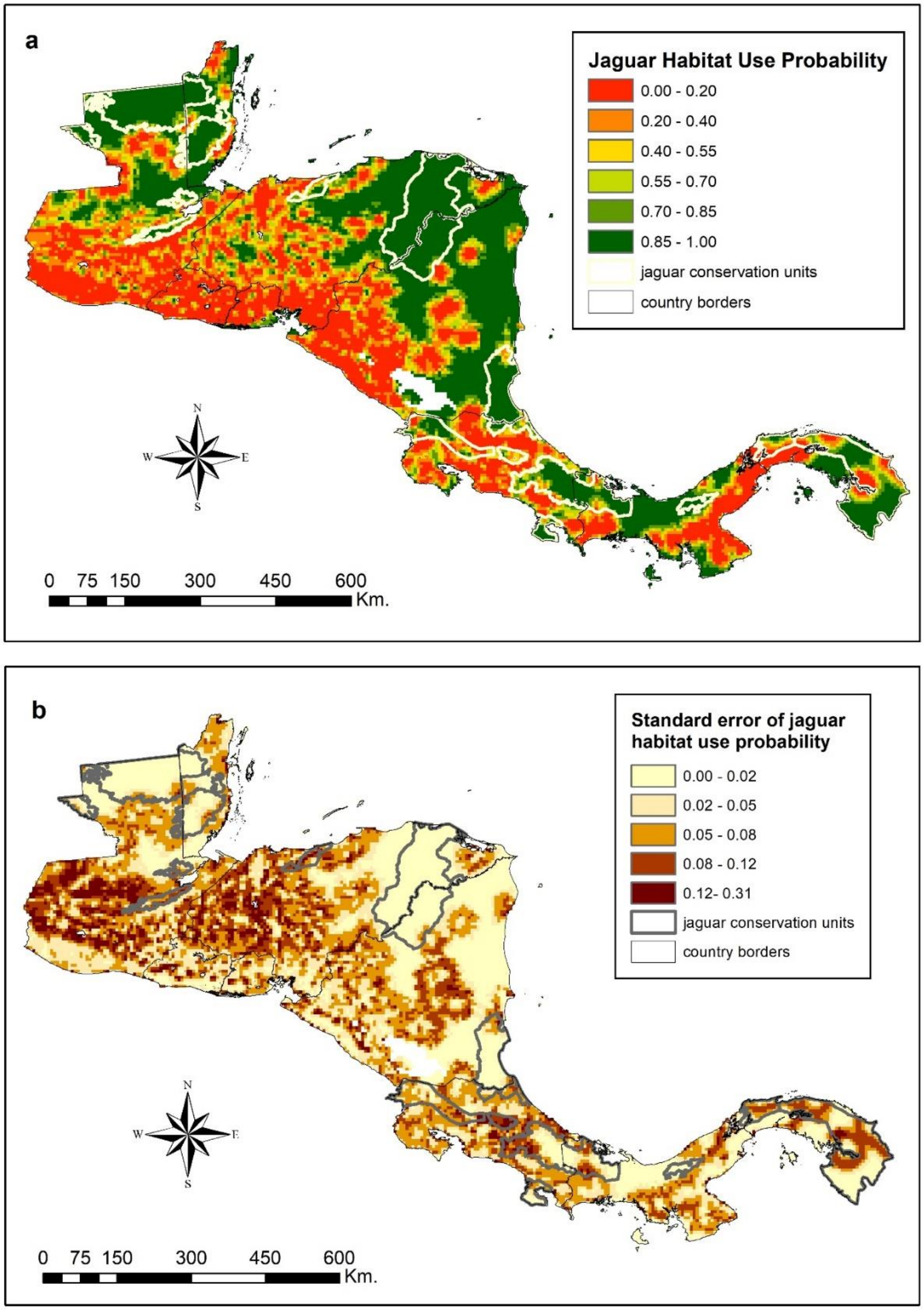

Fig. 2. Prediction of jaguar habitat use in Central America, a) Predicted probability of jaguar habitat use, b) Standard error of the predicted probabilities of jaguar habitat use.

distant from watercourses exhibit responses independent from water locations (Morato et al., 2018). The strong negative response of jaguars towards human settlements (dist_sett: β= 3.910, SE= 0.651) evidences an avoidance to human proximity (Petracca et al. 2018; Meyer et al. 2019) and compensatory mechanisms the species uses to adapt to human-dominated landscapes (Morato et al., 2018). However, the effect of human presence on jaguars likely depends not only on the presence of humans *per se* but on human activities. In our model however, we could not consider different human activities due to the scale of our study. At local scales, we expect some variability on jaguar response to human presence, based on how humans interact with jaguars and the environment. An illustration of this is Guna Yala in Panama, an area occupied exclusively by indigenous communities where habitat suitability was underestimated by our model (Meyer et al. 2019).

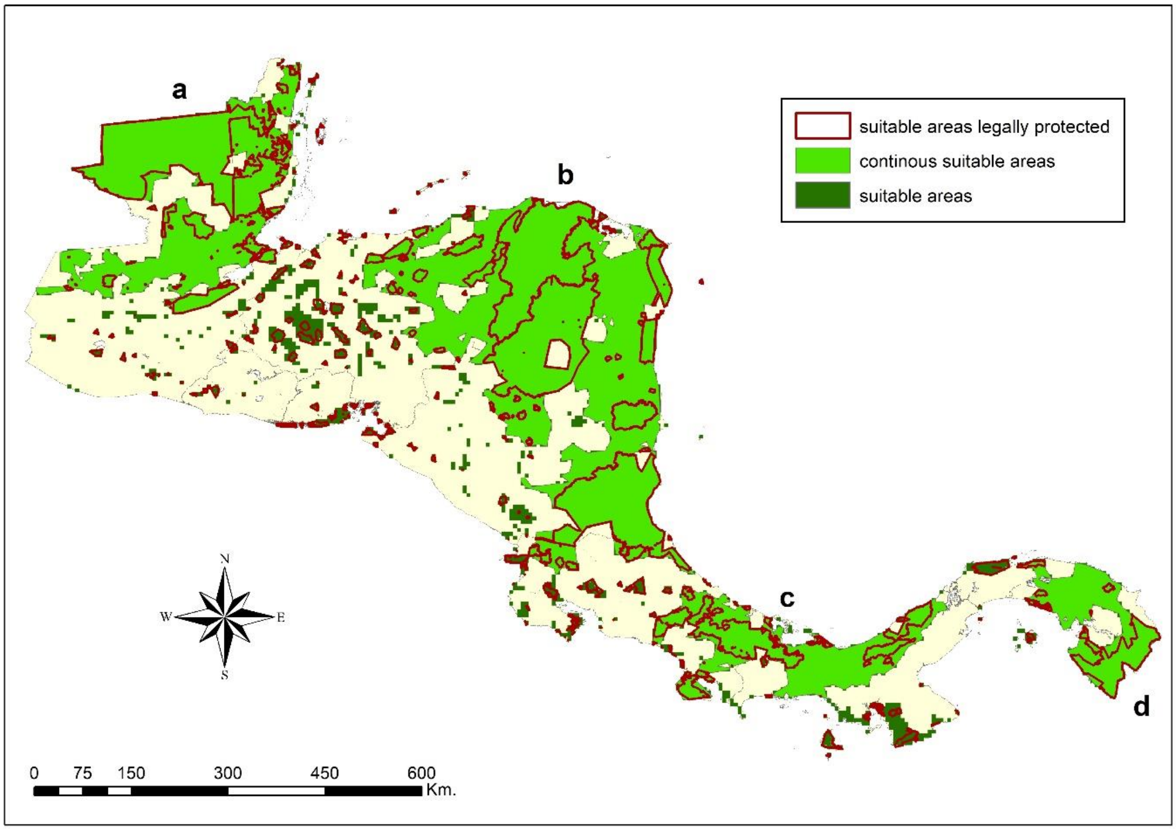

Fig. 3. Continuous areas (light green) of jaguar habitat suitability (Ψ ≥ 0.55) in Central America: a) Guatemala-Belize, b) eastern Honduras-Nicaragua, c) South Costa Rica-Northern Panama, and d) Panamanian Darien. Dark green: remaining suitable areas. Red outline: legally protected areas registered up to January 2021 (UNEP-WCMC & IUCN 2021).

Overall, our predictions of habitat use suggest that there are 192,306.539 km^2 of habitat available for jaguars across the species EOO in Central America, and that JCUs represent the most important reservoirs of it. JCUs encompass almost half of all available habitat within the jaguar EOO, with >50% being protected by law. They also contribute to structural connectivity across political boundaries, especially to the four largest continuous zones of habitat in Central America (Fig. 3), all of which share bi-national borders. Notwithstanding, there are two JCUs of special conservation concern that exhibit the lowest mean habitat suitability ($\Psi_{mean} < 0.50$) and habitat coverage (<35%), namely Chagres (Panama) and Volcanica Central (Costa Rica; Table 2). The latter JCU most likely does not act as a jaguar stronghold anymore (Salom-Pérez et al. 2021) and this status should be reflected in an updated list of current JCUs.

We identified four areas of low habitat suitability that could impair connectivity in the region, central-Costa Rica, central-Panama, and eastern-Guatemala and western-Honduras (Fig. 2a), with the first two acting as potential constriction points of population connectivity from South to Central America, which coincides with Salom-Pérez et al. (2021) and Meyer et al. (2020). Particularly concerning for the northern-Central American jaguar populations is the low habitat suitability in the Guatemala-Honduras connection, given that this area connects the Trinational-Selva Maya, the largest continuous neotropical forest north of the Amazon, and the Reserva de Biosfera Transfronteriza; two JCUs of great importance within the jaguar corridor (Rabinowitz & Zeller, 2010; Fig. 2a).

Our jaguar habitat use predictions seem robust despite the uncertainty of our estimates (Fig. 2b). They generally coincide with previous broad-scale jaguar space use studies encompassing Central America (Jędrzejewski et al. 2018; Petracca et al. 2018; Thompson et al. 2021), and match general gene flow patterns found by Wultsch et al. (2016). However, our model has the advantage of being the first jaguar habitat use model that can be extrapolated to a broad-scale by including local studies' uncertainties across several Central American ecoregions, providing more precise estimates than those extrapolated from small-scale studies, for which patterns cannot be generalized. Our camera-trap data also represents reliable presence-based evidence of jaguars for Central America, a region significantly underrepresented in recent range-wide studies (Thompson et al. 2021), and that in comparison to more widely available interview-derived data (Petracca et al. 2018), does not require to account for false positives that can severely bias occurrence estimates (Miller et al. 2011). Lastly, our occurrence estimates account for sampling biases explicitly by including jaguar detection probability, not considered in previous approaches (Jędrzejewski et al. 2018).

We believe our model is general and representative enough of the Central American jaguar populations to effectively identify the drivers of the species' habitat use in our study region, as supported by our model's external validation. However, there are four potential sources contributing to uncertainty. First, even with the extensive camera-trapping effort, we were unable to cover the full gradient range of environmental variables such as forest cover and agriculture across our study region. Our data is biased towards areas occupied by the species, given that in jaguar camera-trap studies, effort is commonly maximized by placing cameras in areas known *a priori* to have jaguars. While human factors can have disproportionate effects on jaguar occurrence (Thompson et al. 2020), it is possible that this spatial bias might be partially responsible for the low importance of environmental variables in our model. Using a more comprehensive dataset might show that, whereas human variables have a strong effect on jaguar-occupied areas, there is a range of environmental values that strongly limit the species' presence in jaguar-unoccupied areas. Second, there are areas predicted with a much higher habitat suitability than expected, such as the patches of high jaguar habitat use south of Selva Maya in Guatemala, central Honduras (*pers. comm.*, F. Castañeda, 12 May 2021), central and north-eastern Nicaragua (Hernández Potosme 2019), and areas of Ngäbe-Buglé and around Darien in Panama (Meyer et al. 2019); all from which jaguars have either been extirpated or remain in low numbers. This limitation would be improved, as for the first, by adding data to our model on jaguar-unoccupied areas. A third limitation is that information on sex of individuals (Foster et al. 2010), prey abundance (Rabelo et al. 2019), and poaching (Romero-Muñoz et al. 2019) were unavailable to us and are closely related to jaguar occupancy. Therefore, predicted areas of high suitability may show smaller populations than expected due to high poaching of jaguars or their prey (Redford 1992). And lastly, despite we aggregated occurrence accounts within sample units, given the variability of jaguar home range sizes across the region (Figueroa 2013; Salom-Pérez et al. 2021; Thompson et al. 2021), there may be spatial non-independence at this spatial scale potentially affecting our standard errors.

Notwithstanding, our jaguar model usefully informs the prioritization of key areas and actions for the persistence of the species, with quantified uncertainty, and it provides the basis for future studies on connectivity between jaguar habitats in this region. Two main conservation actions supported by our results are the following. Firstly, prevent habitat loss and mitigate human pressure within the continuous suitable areas that provide structural connectivity, as to prevent further population decrease and extirpation due to landscape fragmentation (Zanin et al. 2015). Securing habitat for jaguars should therefore be focused on the largest JCUs with highest habitat coverage within: Selva Maya and Belize, Reserva de Biosfera Transfronteriza, Cerro Silva-Indio Maiz-Tortuguero, Talamanca-Cordillera Central and Chagres-Darien. In contrast, human pressure mitigation should be targeted at smaller JCU's with less remaining habitat coverage: Sierras Santa

Cruz and Minas, Cordilleras Nombre de Dios and Guanacaste. Secondly, support habitat restoration to improve connectivity, particularly in central Costa Rica and central Panama, where most habitat suitability has been lost. These suggested conservation targets could be supported by the implementation of conservation schemes in the buffer zones of JCUs and protected areas, such as indigenous/community managed reserves (Mena et al. 2020) or forestry concessions (Tobler et al. 2018), to encourage sustainable land management regimes more compatible with jaguar conservation and integrate local actors and stakeholders better.

Lastly, providing spatial requirements about the species status is crucial to assess the conservation status of the species and its evolution through time (IUCN 2012). Some conservation works focus on population size estimates; however, they are costly, require more intense field work, and produce estimates that cannot be extended to a subcontinental scale. Here our study provides a tool that conservation managers and stakeholders may use to implement local actions but also broad scale decisions.

We are aware that camera-trapping may not be feasible in all areas of species' environmental gradients, however camera-trap data can be complemented with data derived from other methods in areas where the latter are more cost-effective (Petracca et al., 2018). We encourage further international collaboration and coordination to secure the long term persistence of jaguars in this region of rapid human-induced transformation, designing standardized data collection protocols, facilitating more comprehensive jaguar datasets, and securing jaguar populations and their habitat across country borders.

Authors' contributions

APC, JL, AP, SKS conceived the ideas and designed methodology; **APC**, DA, SA, LB, JC, DC, CPD, RF, MG, RG, BH, SH, RL, DM, RM, NM, RM, RS, AS, IT, DT, YU collected the data; **APC**, JL, AP analysed the data; **APC** led the manuscript writing supported by SKS, JL, AP, VG. All authors contributed critically to the drafts and gave final approval for publication.

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CHAPTER 3

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

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3

Abstract

Safeguarding functional connectivity is a conservation priority to secure the long-term viability of spatially scattered subpopulations, such as jaguar populations in Central America. However, managing connectivity in this region is limited by the scant, local assessments of connectivity between remaining populations, some of which exhibit low levels of gene flow and genetic admixture. We employed the jaguar *(Panthera onca)* as a focal species to understand how gene flow of large carnivores is shaped in a heavily human-impacted landscape. We assess the effect of landscape features and spatial scale on jaguar gene flow in northern-Central-America, predict synoptic, landscape-wide functional connectivity across the region; and compare model-based connectivity predictions based on gene flow, habitat suitability and expert knowledge measures. Using genetic data on 335 faecal samples from 72 individual jaguars, we parameterized surfaces of gene flow resistance with linear mixed effects models and the maximum likelihood population-effects method. We evaluated nine landscape variables at six spatial scales, selecting the optimal scale and transformation for each variable. We developed multivariate models for predicting jaguar gene flow, and used resistant kernels to predict functional connectivity across the study region. Low resistance to jaguar gene flow was associated with greater tree cover and vegetation, lower areas of built-up and intermediate distances from water bodies/wetlands. Tree cover affected jaguar gene flow on a smaller scale compared to the rest of variables. Lower resistance, thus higher connectivity, was found within and around the largest jaguar conservation units (JCU; i.e. Reserva-de-Biosfera-Transfronteriza and Selva-Maya) in comparison to the smallest (i.e. eastern-Guatemala: Sierra-Santa-Cruz and Sierra-de-las-Minas). Across the region, lower connectivity was found in the Caribbean connection between eastern-Guatemala and Midwest-Honduras, and the Honduran and Nicaraguan Miskito area. While areas of high predicted connectivity were roughly consistent across measure types, low connectivity was overestimated by models based on aggregated habitat suitability metrics and expert knowledge in respect to gene flow. Gene flow of jaguars is positively driven by availability of forest and water sources, and negatively by human influence (built-up and non-vegetation). Areas of lowest resistance largely coincide with the location of source jaguar populations (jaguar conservation units; JCUs), which constitute the main reservoirs of high-quality jaguar habitat in the region. Pathways of connectivity were predicted between all JCUs, however the lower connectivity predicted between the smallest JCUs (i.e. Sierra-Santa-Cruz, Sierra-de-las-Minas and Cordillera-Nombre-de-Dios) suggests the need for conservation attention in these areas. Management actions such as habitat loss-prevention/restoration and anthropogenic impact mitigation should be prioritized in the binational area of Guatemala-Honduras, where most connectivity has been lost, and further monitoring is suggested in the Honduran-Nicaraguan Miskito area, where uncertainty on model-based connectivity predictions remains.

KEYWORDS: Landscape resistance, resistant kernel, Central America, large carnivores, carnivore conservation, corridors

Introduction

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

The permeability of landscapes to the movement of animals is defined as connectivity (Taylor et al. 1993). Landscape connectivity is the result of the overall structure of the landscape as well as the individuals' response to this landscape structure in terms of movement and survival ability (Tischendorf & Fahrig 2000). This functional aspect of connectivity can be measured as successful gene flow across the landscape (Baguette & Van Dyck 2007; Pe'er et al. 2011). Functional connectivity allows populations to adapt to changing conditions, thus its estimation can help inform successful management of wildlife (Auffret et al. 2015; Schmidt et al. 2020).

Several models have been created and adapted to provide insights on the connectivity of populations of different species. These models have been derived either directly from movement data (Richard & Armstrong 2010; Elliot et al. 2014), or indirectly from genetic data and patterns (Kimmig et al. 2020; Lecis et al. 2022; Portanier et al. 2022). Whereas movement-based models provide fine-scale insights on individuals' movement decisions in real time, they require measuring animal dispersal at the relevant spatial and temporal scales (Tesson & Edelaar 2013). Measuring animal dispersal is a challenge, particularly for wide-ranging species of conservation concern, such as large carnivores. Alternatively, genetic data have been used to relate gene flow patterns to landscape structure (Holderegger & Wagner 2008). They provide insights into how landscapes affect individual's movement, dispersal, and breeding over generations (Lowe & Allendorf 2010). Thus, genetic data and associated analyses provide valuable and cost-effective ways to model gene flow and functional connectivity (Zeller et al. 2012; Tesson & Edelaar 2013), shedding light on population processes that are not possible to assess using exclusively movement data (e.g. effective population sizes (Ne), bottlenecks, inbreeding (FIS), population structure, contemporary versus historic genetic isolation; Willi et al., 2022).

Gene flow of several large carnivore populations are negatively impacted by human development, including that of pumas (*Puma concolor*; Ernest et al., 2014) and American black bears (*Ursus americanus*; Cushman & Lewis, 2010) in North America, tigers and leopards in India *(Panthera tigris* and *Panthera pardus*; Thatte et al., 2020), Eurasian lynx in Europe (*Lynx*; Bull et al., 2016), and jaguars in Mexico and Brazil (*Panthera onca*; Roques et al., 2016). In this study, we employ the jaguar as a focal species to understand how gene flow is shaped in a heavily human-impacted landscape; mapping the expected functional connectivity of jaguar populations in northern-Central-America. The jaguar is a model species to study functional connectivity because of its large area requirements (Thompson et al. 2021), high level of conservation concern (91% of subpopulations show medium to high threat; de la Torre et al., 2017), and decreased genetic exchange in heavily human-influenced landscapes (Roques et al. 2016; Wultsch et al. 2016). Source jaguar populations (Fig.1, jaguar conservation units –JCUs) and corridors to connect them have been delineated across the species' range using expert input (Rabinowitz & Zeller 2010; Petracca et al. 2018), aiming to improve jaguar population connectivity at a continental scale, however, are not based on impartial quantitative analyses.

Jaguar populations have shown moderate to high levels of genetic diversity and no strong population structure across most of their range (Eizirik et al. 2001; Ruiz-Garcia et al. 2006; Roques et al. 2014). However, there are small, isolated jaguar populations living in fragmented areas of the South American range which currently suffer from bottlenecks, genetic diversity loss, and high genetic differentiation due to strong signals of anthropogenic-driven drift (Haag et al. 2010; Lorenzana et al. 2020). Signals of gene flow restriction and high anthropogenic impact have already been found in northern-Central-America, particularly between Guatemala and Honduras (Wultsch et al. 2016).

We focus this study in northern-Central-America for three main reasons. It represents the largest stronghold of jaguars after the Amazon (Rabinowitz & Zeller 2010), prime jaguar habitat here is severely threatened by land use change (Powers & Jetz 2019) and forest loss (Olsoy et al. 2016), and some jaguar populations already exhibit low levels of gene flow and genetic admixture (Wultsch et al. 2016). Furthermore, this research has the overarching goal to respond to continental and regional jaguar conservation priorities, by "genetic ground-truthing" (assess functional connectivity) of dispersal corridors for jaguars to improve and maintain population interconnectedness, particularly in northern-Central-America (Wultsch et al. 2016; de la Torre et al. 2017).

To our knowledge, this study is the first to assess jaguar functional connectivity using empirical data at a regional extent. Previous research in the region has been based solely on literature or local/expert input, either to assess structural connectivity at a large regional scale (Rabinowitz & Zeller 2010; Petracca et al. 2018), or functional (de la Torre et al. 2017) and habitat connectivity (Menchaca et al. 2019) at small, local scales. Furthermore, previous findings suggest that whereas gene flow is high among jaguars from the Selva-Maya (northern Guatemala and central Belize), differences in genetic structure are exhibited by geographically close jaguar populations in the Selva-Maya and Honduras (Wultsch et al. 2016). Therefore, it is likely that jaguar gene flow could be influenced not only by geographic distance but also by the dynamic landscape changes experienced by the region. Here, we determine jaguar gene flow using microsatellite data and address four main objectives: i) identify landscape variables that facilitate or hinder gene flow between jaguar populations in northern-Central-America, ii) assess functional connectivity of jaguar populations in the study landscape, iii) compare spatial predictions of functional connectivity based on gene flow versus expert input (Rabinowitz & Zeller 2010; Petracca et al. 2018) and jaguar habitat suitability data (Calderón et al. 2022); and iv) identify priority areas for corridor planning that promote genetic exchange and secure the long-term viability of Central American jaguar populations.

We predicted that jaguar gene flow is positively influenced by availability of shelter habitat (i.e. sites for resting, nursing, protection from humans, and cover for ambush hunting), such as forest cover and water sources, as well as areas with high net primary productivity (as a proxy for prey biomass); but negatively influenced by high elevation areas, areas with a large human development, large areas of non-vegetation, and roads. While our findings can inform jaguar management in Central America, our gene flow and connectivity modelling framework has a broader ecological application for understanding how anthropogenic landscapes affect the connectivity of elusive large carnivore populations.

Methods

Study area

Central America is a biodiversity hotspot (Myers et al. 2000). It acts as the largest stronghold for jaguar populations after the Amazon (trinational 'Selva-Maya'), and connects the two largest jaguar populations in the region ('Selva-Maya' and 'Reserva-Biosfera-Transfronteriza'; Fig 1). This region is characterized by a highly diverse pattern of land uses and a high mean human density of 94 ind./km^2 (World Bank 2020). It is covered mainly by broadleaved evergreen and deciduous trees (61%) and mosaics of natural vegetation with croplands (21%), with the rest represented by a diverse matrix of land uses that includes croplands (6%), secondary growth forests (4%), grasslands (3%), wetlands (1%) and urban areas (0.5%, ESA, 2015). Central America holds the highest projected vertebrate's habitat suitability range loss in the continent due to land use change (Powers & Jetz 2019), and the highest deforestation rates and the highest proportional forest degradation worldwide (Redo et al. 2012). We focus our study in the northern part of this region, northern-Central-America, comprised of Belize, Guatemala and Honduras (Fig. 1).

Genetic data and measures

We worked with a dataset of 335 jaguar faecal samples previously collected across northern-Central-America (Wultsch et al. 2016). Sampling sites were primarily located in lowland regions with subtropical and tropical climates and a diversity of land cover types within Belize, Guatemala, and Honduras. Samples were collected opportunistically in the field (Fig. 1) and genotyped using 12 microsatellite loci (Menchaca et al., 2019; Wultsch et al., 2016; Appendix S1). Seventy-two individuals were identified, 59 males, 3 females, and 10 of unknown sex. Population genetic summary statistics (Appendix S2), gene flow and genetic structure assessments for these sites were published in Wultsch et al., (2016). Menchaca et al. (2019) conducted a fine-scale conservation genetics and habitat connectivity study using the jaguar genotypes collected in central Belize. To assess genetic differentiation between jaguar populations in northern-Central-America, we calculated pairwise genetic distances based on Factorial Correspondence Analysis (FCA) in two steps. First by performing FCA on a multiple contingency table of the microsatellite genotypes with the software GENETIX v. 4.05.2 (Belkhir et al. 2001). Second, by creating a distance matrix using Euclidean distances between the first two FCA axes (the only significant) with the R package 'ecodist' (Goslee & Urban 2007).

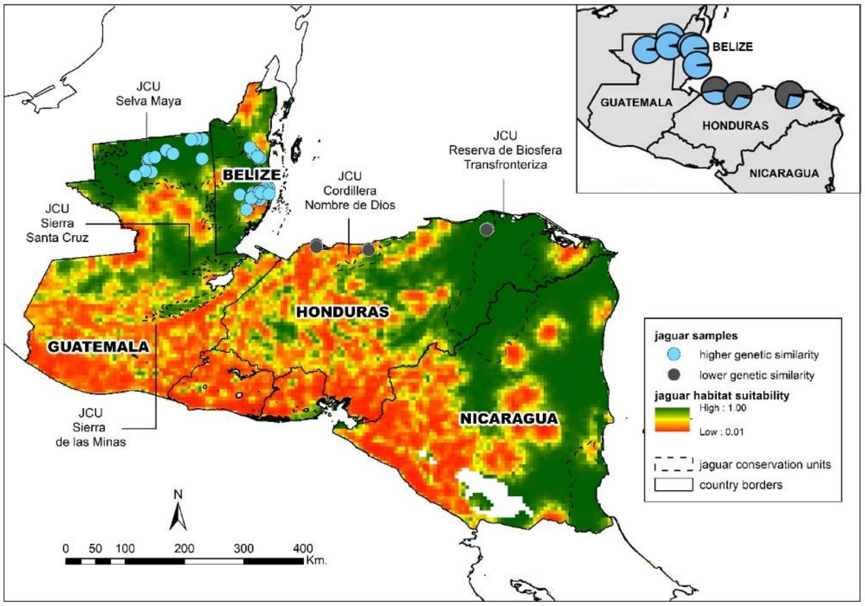

Fig. 1 Study region encompassed by Belize, Guatemala and Honduras in Central America, showing sampling locations and habitat suitability for jaguars. Main map: location of the collected scat samples (light blue and grey circles), Jaguar Conservation Units (black dashed borders), and jaguar habitat suitability (areas of high habitat suitability in green, and low suitability in red; Calderón et al., 2022). Insert in right upper corner: Genetic structure of jaguar populations in the study region; Wultsch et al., 2016)[e]

Landscape covariates, resistance surface generation and hypotheses

We selected nine environmental and anthropogenic covariates that influence jaguar habitat use, density, movement, and potentially gene flow (Jędrzejewski et al. 2018; Thompson et al. 2021; Calderón et al. 2022); specifically, distance from water, distance from rivers, distance from roads, elevation, ruggedness, net primary productivity, %built-up, %non-vegetation, and %tree cover (Appendix S3). We projected all datasets to the Universal Transverse Mercator coordinate system (EPSG: 32616) and resampled to a 1000m resolution.

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[e] The pie charts represent the genetic clusters identified for groups of jaguar individuals studied across sampling sites, with colors representing the fraction of membership for each of these sampled groups

The modelling procedure was as follows (Fig. 2, Appendix S4): We first assessed the scale of effect of each of our variables (Jackson & Fahrig 2015; Mcgarigal et al. 2016) on jaguar gene flow, given that gene flow processes and functional connectivity are spatial-scale dependent (Cushman & Landguth 2010; Cushman et al. 2016).

To identify the optimal scale for each variable, we smoothed each variable raster using a Gaussian kernel and varied its bandwidth across six scales: 1,000m; 3,000m; 6,000m; 8,000m; 16,000m; 32,000m. At every scale, each landscape variable was transformed into a gene flow resistance surface hypothesis, converting the raw variable's values into resistance values using seven transformational forms (Peterman 2018; Fig 2 A). To optimize landscape resistance values and evaluate how landscape features affect jaguar gene flow in our study region, we evaluated scenarios of isolation-by-distance (IBD; Wright, 1942) and isolation by resistance (IBR; McRae, 2006; Peterman et al., 2014). To this end, we identified the optimal scale and transformation for each covariate by running univariate models across all scales and transformational forms. We evaluated these models using Akaike's Information Criterion corrected for small sample sizes AIC_c (Burnham & Anderson 2002) and retained the model with the lowest AIC_c value for each covariate (Fig. 2 B). We then combined all non-correlated covariates at their optimal scale and transformation to create multi-variable, multi-scale models of resistance. We finally assessed functional connectivity of jaguar populations using cumulative resistant kernels, a synoptic modelling approach which predicts and maps expected functional connectivity as a continuous surface, accounting for species' dispersal abilities (Fig. 2 C). We applied this to the connectivity surfaces and for comparison to a recently developed habitat suitability model (Calderon et al., 2022). For details on the methods see Appendix S4.

Lastly, we compared the connectivity predictions obtained using our genetic model (this study) against the following two models: i) the habitat suitability model described above (Calderón et al. 2022), and ii) the expert input derived model (Rabinowitz & Zeller 2010; Petracca et al. 2018). For the first comparison we calculated the difference between the inverse habitat suitability-based and gene flow-based connectivity surfaces with the 'raster calculator' in ArcGIS 10.8.0 (ESRI 2022). For the second comparison, we evaluated the distribution of connectivity values within the expert-based corridors against that of the jaguar range across the study region, testing a random sample of 200 points for each extent using a two-sided Mann-Whitney U test with R package 'stats'.

Results

Landscape resistance and connectivity modelling

Resistance to jaguar gene flow decreased with higher tree cover and primary productivity, and increased with higher values of built-up, non-vegetation, elevation, ruggedness, and proximity to roads and rivers (Appendix S5). Gene flow resistance was lowest at intermediate distances from water, increasing with greater distances from these water sources, and being highest at their close proximity. Tree cover and ruggedness had the smallest scale of effect for jaguars (16,000m; Table 1), whereas the rest of the variables had a scale of effect of 32,000m. All univariate models outperformed the null model of isolation-by-distance (IBD; Euclidean distance).

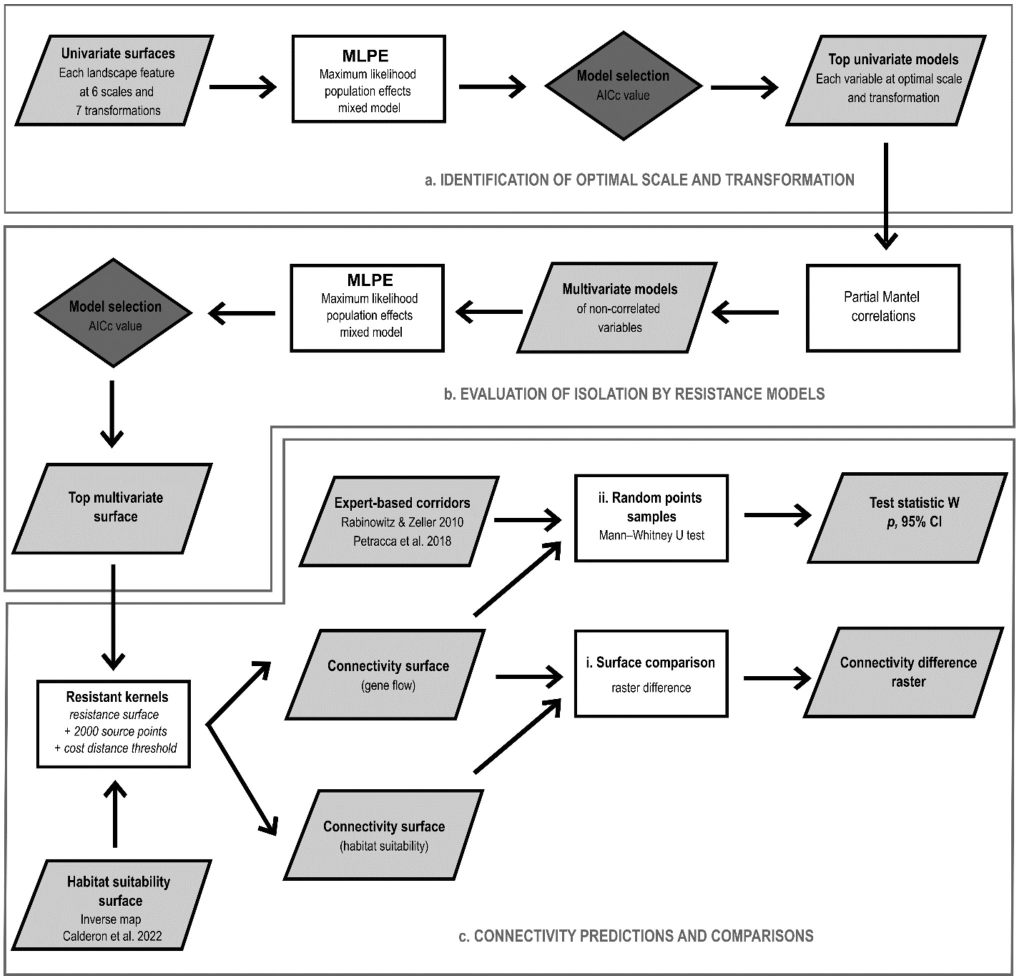


Fig 2 Conceptual flow diagram for analysis of jaguar gene flow and functional connectivity in northern-Central-America. For details on the methods cf. Appendix S4.

The top composite resistance surface included distance from water, tree cover, built-up and non-vegetation (AIC_c = -1084.168, BIC= -1054.961); explaining 83% of the variance observed in the genetic differences between individuals (mR^2 = 0.69, cR^2= 0.83; Table 2; complete model list in Appendix S6). Lower resistance, thus higher connectivity was found within and around the largest JCUs (i.e. Reserva-de-Biosfera-Transfronteriza and Selva-Maya), in comparison to the smallest JCUs (i.e. eastern-Guatemala: Sierra-Santa-Cruz and Sierra-de-las-Minas; Fig. 3). Lower connectivity in the region was found in the Caribbean connection between eastern-Guatemala and Midwest-Honduras and the Honduran-Nicaraguan Miskito area (north-eastern border of Honduras and Nicaragua).

The resistance and kernel connectivity surfaces obtained from the inverse of the jaguar habitat suitability map showed lowest resistance and higher connectivity in the north and east of the study region (Fig. 3). This latter kernel connectivity surface estimated very low connectivity for most areas in western-Honduras and eastern-Guatemala, with high connectivity mainly restricted to eastern-Honduras and north-eastern-Nicaragua, and to a lesser degree, to northern Guatemala, where the two largest JCUs in the region are located (Reserva-de-Biosfera-Transfronteriza and Selva-Maya respectively).

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

There was consistency between the overall connectivity pattern predicted by the models based on gene flow and jaguar habitat suitability (Fig. 3). Overall, both models predicted higher connectivity within and around the largest JCUs in the region (i.e. Selva-Maya and Reserva-de-Biosfera-Transfronteriza), and medium connectivity around the smallest JCUs located in eastern-Guatemala (i.e. Sierra-Santa-Cruz and Sierra-de-las-Minas) and midwest-Honduras (i.e. Cordillera-Nombre-de-Dios). Despite these concordances, habitat suitability-based connectivity was predicted much lower in comparison to that based on the gene flow model, particularly in eastern-Guatemala and western-Honduras, where no clear pathways were apparent between these two countries based solely on habitat suitability data. Conversely, the gene flow-model shows clearer movement pathways across the region, including those areas of lower predictive connectivity such as between Guatemala-Honduras.

Table 1 Best performing univariate resistance models of gene flow for jaguar populations in northern-Central-America. Values for the variables' scale of effect, AIC_c, BIC and marginal and conditional R^2 are reported for each model. Variables in bold were included in the best performing composite resistance surfaces

Variable	**Scale (m)**	**Transformation**	**AIC**	**BIC**	**mR^2**	**cR^2**
Tree cover	**16000**	**negative linear**	**-1013.09**	**-983.89**	**0.68**	**0.82**
Primary productivity	32000	negative monomolecular convex	-1000.48	-971.27	0.68	0.83
Distance from rivers	32000	negative linear	-856.34	-827.14	0.64	0.82
Non-vegetation	**32000**	**positive monomolecular concave**	**-832.08**	**-802.88**	**0.66**	**0.83**
Distance from roads	32000	negative monomolecular concave	-750.48	-721.27	0.62	0.81
Terrain ruggedness	16000	positive monomolecular convex	-736.98	-707.78	0.62	0.80
Elevation	32000	positive monomolecular convex	-734.00	-704.80	0.62	0.81
Distance from water	**32000**	**inverse Ricker**	**-593.97**	**-564.76**	**0.59**	**0.79**
Built-up area	**32000**	**positive linear**	**-558.88**	**-529.67**	**0.53**	**0.80**
Euclidean distance (null model)	NA	NA	-146.13	-122.76	0.26	0.63

Table 2 Top-ten multivariate resistance models of gene flow for jaguar populations in northern-Central-America including the isolation-by-distance model for reference (IBD). Values for AICc, BIC and marginal and conditional R^2 are reported for each model. The top model is shown in bold

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

The expert knowledge-based delineated corridors for jaguar movement (Rabinowitz & Zeller 2010; Petracca et al. 2018) were consistent with the areas of medium to high connectivity predicted by our genetic model (Fig. 4). Nonetheless, connectivity values within these corridors did not differ significantly from those across the jaguar range in the study region (W = 21940, *p* = 0.06, $CI_{95\%}$ = -0.0000220, 0.0000321). Our genetic model showed additional areas of connectivity not included in the expert-based corridor delineation. Specifically, the genetic model predicted high connectivity south of the Selva-Maya JCU (Guatemala) and south the Reserva-Transfronteriza (Nicaragua), and to a lesser degree, south-west-Honduras; all these not considered in the expert-based corridor delineation.

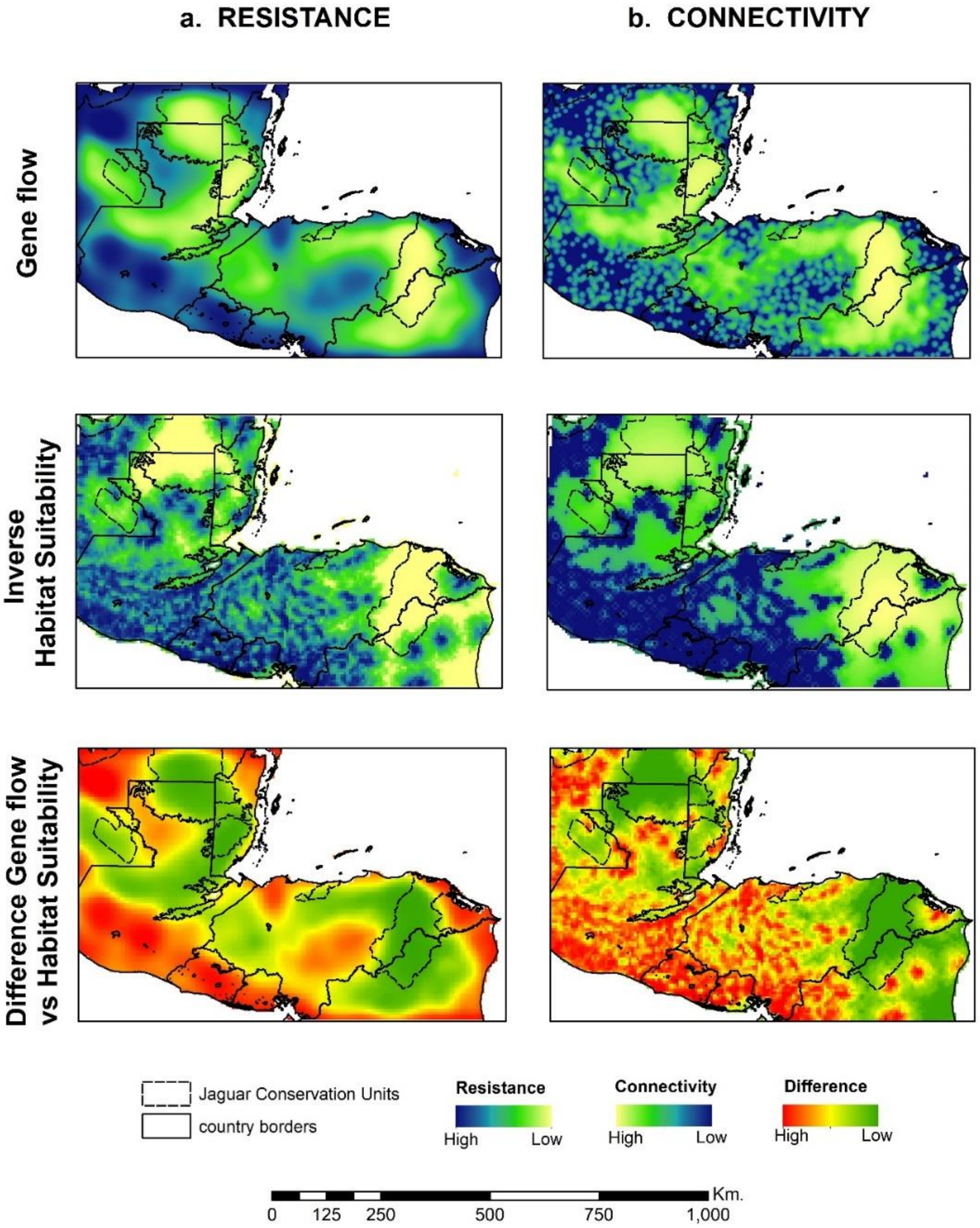
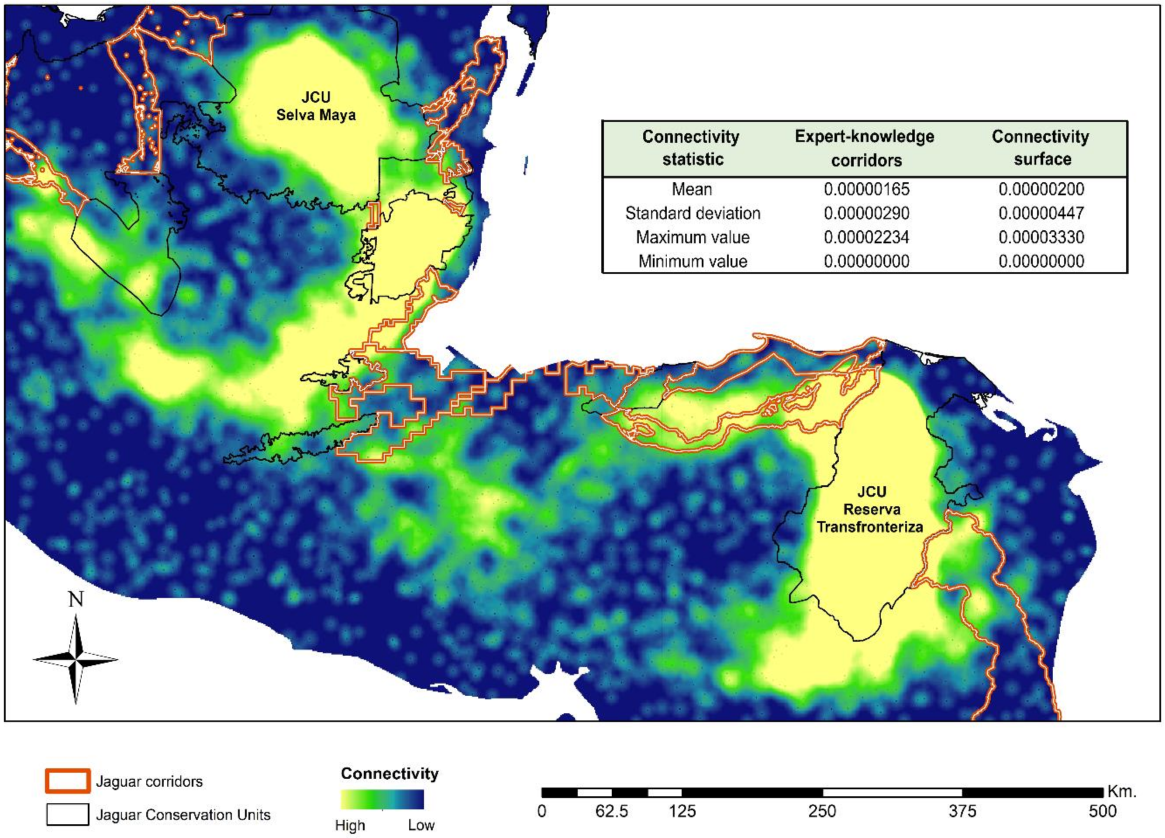


Fig 3 Resistance (a) and functional population connectivity surfaces (b) for jaguars in northern-Central-America obtained using genetic data (upper row), habitat use data (based on the habitat suitability map of Calderón et al., 2022; middle row), and the difference between the surfaces obtained with genetic data vs habitat use data (bottom row).



Connectivity statistic	Expert-knowledge corridors	Connectivity surface
Mean	0.00000165	0.00000200
Standard deviation	0.00000290	0.00000447
Maximum value	0.00002234	0.00003330
Minimum value	0.00000000	0.00000000

Fig. 4 Connectivity of jaguar populations in the study region predicted using the top gene flow resistance surface and resistant kernels, compared to the expert-based delineated corridors for jaguar movement (orange polygons) previously proposed by Petracca et al. (2018) and Rabinowitz & Zeller (2010). Top-right insert: summary table with raster statistics of the connectivity surface across the study region and the expert-based corridors.

Discussion

By taking advantage of recent methods for resistance surface estimation and conducting genetic sampling across international boundaries, our study is the first to model jaguar gene flow and connectivity across spatial scales, heterogeneous landscapes, and a large regional extent of conservation concern in Central America. Our top gene flow resistance model predicted lowest resistance in areas with higher tree cover and vegetation, lower built-up areas, and intermediate distances from water sources. These areas of lowest resistance largely coincide with the location of the JCUs, which constitute the main reservoirs of high-quality jaguar habitat in the region (Calderón et al. 2022). Tree cover showed a smaller scale of effect for jaguar gene flow compared to the rest of the variables. This could potentially reflect that tree cover may be mediating gene flow most strongly via local breeding or short-distance dispersal (as exhibited by philopatric female jaguars; Kantek et al., 2021), whereas built-up, non-vegetation and water sources via long-distance dispersal. Similar results have been found for cougars in North America (Zeller et al. 2023).

Jaguar gene flow seems to be mainly driven by availability of shelter habitat. However, the high resistance that built-up and non-vegetation provide to gene flow may also encompass the effects of direct human-jaguar interactions common in anthropogenic landscapes. In these landscapes, jaguar populations exhibit lower levels of gene flow (Roques et al. 2016) and increased human-caused mortality, via hunting (Jędrzejewski et al. 2017a; Arias et al. 2021), vehicle collisions (Srbek-Araujo et al. 2015), and retaliatory killing (Garcia-Alaniz et al. 2010; Moreno et al. 2015; Jędrzejewski et al. 2017a); the latter being the strongest driver of jaguar extirpation (Jędrzejewski et al. 2017b; Villalva & Palomares 2022). The impact of human-caused mortality on population viability can be significantly large, particularly when it disproportionally affects important demographic groups (i.e. juveniles), and when lack of connectivity restricts demographic rescue (Lamb et al. 2020). Therefore, securing connectivity between jaguar populations in anthropogenic landscapes is a current conservation priority for the populations' long-term viability (de la Torre et al. 2016).

Our model-based predictions show that functional connectivity for jaguar populations is concentrated within and around the JCUs in the region, decreasing further from these areas. Highest connectivity was observed along and around the biggest JCUs (i.e. Selva-Maya in Guatemala and Reserva-Transfronteriza in Nicaragua; Fig. 1); supporting previous findings of genetic diversity and population structure assessments of jaguar populations in the region (Wultsch et al. 2016). Areas of lower population connectivity were predicted in the south-west of the Selva-Maya, Caribbean area between Guatemala and Honduras, and the Honduran-Nicaraguan Miskito. The first and second areas are consistent with areas of high human development and forest loss (Aide et al. 2013; Olsoy et al. 2016), and also with highest jaguar habitat suitability loss (Calderón et al. 2022). However, the very low predicted connectivity in the Miskito area requires careful interpretation. Here, pine savannas which occur naturally (Parsons 1955) are characterized by our satellite data as areas with high percentage of non-vegetation and low tree cover. Therefore, it is likely that our model may underestimate connectivity in these areas. Nonetheless, the Miskito pine savannas are undergoing degradation (Mora et al. 2016), and here jaguar densities appear to be low (Gonthier & Castañeda 2013) and jaguar killings to resolve cattle predation common (Chinchilla et al. 2022); suggesting the need for further monitoring in this area.

Our study builds upon previous connectivity assessments in the region in two main ways. First, it employs a rigorous statistical modelling approach that explicitly accounts for spatial scale dependence in jaguar-landscape interactions. By doing this, we were able to identify the appropriate functional scale for each landscape predictor studied, a critical but often neglected step for achieving robust inference and improving management inputs that support habitat and population connectivity efforts (Jackson & Fahrig 2015; Krishnamurthy et al. 2016). Second, we predict spatially-explicit, synoptic connectivity maps for jaguar populations in the region while accounting for the species' dispersal ability.

We believe that our model results are robust enough to assist research and management actions for this species of conservation concern living in a hotspot of range loss for vertebrate species. However, there are three potential sources that contribute to uncertainty. Given our small sample size, internal validation with cross-validation folds (Row et al. 2017) was not possible. Furthermore, we were unable to externally validate our model given the lack of empirical data available for the study region. Whereas this prevented us from quantitatively assessing the uncertainty of our model predictions, we are confident that we addressed most of the main potential sources of this uncertainty by: i) using resistance surfaces that relate to ecological processes (Peterman et al. 2014) and are parameterized with empirical data (Clevenger et al. 2002; Shirk et al. 2010; Cushman et al. 2013), ii) using genetic data, which focuses only on movements relevant for populations' viability (i.e. successful breeding) and that represent the long-term average of effective dispersal, without the restrictions of limited observational periods (Spear et al. 2010); and iii) accounting for spatial-scale dependence and species' dispersal ability in the assessment of connectivity. We were also unable to explicitly account for human-caused mortality, a decisive factor in gene flow resistance with important implications for functional connectivity. There is scarce data on anthropogenic jaguar mortality across the species range (Altrichter et al. 2006; Jędrzejewski et al. 2017a; Romero-Muñoz et al. 2019), and even less in Central America (Moreno et al. 2015). We rely on built-up area and tree cover maps to encompass the effects of this anthropogenic-driven mortality in the absence of appropriate data, supported by the fact that jaguar extirpation is mostly an anthropogenic-driven mechanism, and that is led by deforestation, cattle breeding, and retaliatory killing (Jędrzejewski et al. 2017a).

We highlight two key findings from the connectivity patterns derived from gene flow, habitat suitability and expert-input data, which have important implications for guiding future work. We first highlight that gene flow connectivity is different than habitat connectivity and one may not be able to be used as a proxy for the other (Sartor et al. 2022), as habitat for permanent establishment not necessarily correspond to those facilitating dispersal (Mateo-Sánchez et al., 2015; Reding et al., 2013). Regarding expert input, we found correspondence between the proposed expert knowledge-based corridors and our gene flow-predicted high connectivity areas, however mostly within zones of good quality habitat. Accordingly, we agree that expert-input is useful for synthesizing knowledge about complex habitat relationships in resistance surfaces, particularly when there is limited empirical data (Rabinowitz & Zeller 2010; Zeller et al. 2012). Our gene flow data preceded the expert-based data, and while there might be an effect of time, these results support previous findings that empirical data provide more optimal parameterization of environmental variables (Clevenger et al. 2002; Shirk et al. 2010; Cushman et al. 2013). Therefore, when available, empirical data should be favoured.

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

Conservation implications

Our jaguar model usefully highlights key areas for population connectivity while supporting concrete conservation actions for securing the long-term persistence of the species in the region. Management actions should be prioritized in the binational area of Guatemala-Honduras, where most connectivity has been lost. This area holds the smallest JCU's in the region, represents a connectivity constriction point between the jaguar populations from North America to the rest of the continent, and it was highlighted to have a lack of connectivity by the habitat suitability and expert-based models. Further monitoring is also required in the Miskito pine savanna area, where uncertainty of our model-based connectivity predictions remains. In the short and medium terms, two concrete management actions to implement in priority areas are habitat loss-prevention/restoration and anthropogenic impact mitigation. The former goal could be achieved by implementing sustainable land management regimes compatible with jaguar conservation, such as community managed reserves (Mena et al. 2020) or forestry concessions (Tobler et al. 2018) in the buffer zones of the JCUs, particularly the smallest ones. Additionally, to reduce habitat loss between Honduras and Guatemala, there is a great opportunity for governments, projects, and organizations to support community base initiatives that are currently seeking to officially declare watersheds and corridors in this binational area. Furthermore, mitigation of anthropogenic pressure could be assisted via two actions: a) the implementation of integral wildlife-human coexistence approaches (e.g. König et al., 2020) that promote jaguar-human coexistence, and ensure low jaguar anthropogenic mortality; and b) better engaging local communities in conservation goals through community-based projects (e.g. community monitoring; Valsecchi et al., 2022) that promote the social acceptance of such goals (e.g. inclusive participation and decision-making in conservation solutions; Volski et al., 2021). In the long-term, however, achieving effective carnivore conservation in this region of increasing human development will require the implementation of holistic conservation approaches, grounded not only in wildlife-human coexistence principles and bottom-up participatory approaches, but also on democratic forms of governance and socio-environmental justice for the local communities inhabiting these landscapes (Büscher & Fletcher, 2020; Toncheva et al., 2022).

Authors' Contributions

APCQ, PLG, CW, RF, SKS and KZ conceived the ideas and designed the methodology. RF, BH, OF, RGA, FC, CW and GA contributed to the genetic sampling and analysis effort. Analyses were performed by **APCQ** and PLG, guided by KZ. **APCQ** led the manuscript writing supported by PLG, CW, RF, VG, SKS and KZ. All authors commented on manuscript drafts and gave final approval for publication.

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CHAPTER 4

Transformative change for carnivore conservation: a review and assessment of conservation initiatives for population recovery and human-wildlife conviviality

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Abstract

Large carnivores have been impacted heavily by human activity, with 50% of its species at risk of extinction due to habitat loss and degradation, direct exploitation, prey removal, and persecution. Reversing these declining trends is challenging, as it requires transformative change that targets the indirect causes of carnivore loss and implements innovative governance approaches that produce profound transformations across social, political and economic systems. An integrated framework that can guide efforts for enacting such change is that of transformative biodiversity governance. We conducted a scoping literature review to investigate the contribution of carnivore conservation initiatives for promoting transformative change towards conviviality in social-ecological systems. We selected conservation initiatives based on two criteria, whether they assessed any indirect driver of carnivore threat/loss, and whether they implemented any elements of the transformative biodiversity governance framework. Our analysis focused on i) indirect drivers of carnivore threat/loss, ii) the contributions to transformative governance, iii) lessons learnt and challenges for achieving transformative change in carnivore conservation and management. Our results evidence that very few initiatives within the carnivore conservation literature contribute to transformative change and that they focus heavily on resolving conflicts related to human-carnivore conviviality. We show that achieving transformative change towards conviviality with large carnivores requires expanding solutions beyond technocratic interventions while implementing governance repertoires that promote collective action, reflection, and dialogue in ways that are integrative, inclusive, empowering, and adaptive. Achieving conviviality is possible, however this will require new conservation practices that make science more democratic, participatory and adaptive by integrating diverse knowledge, treating local actors as equals partners, mainstreaming impact assessments, and above all, new ways of thinking about conservation that help discover alternatives for implementing truly transformative change.

KEYWORDS: transformative biodiversity governance, transformative change, human-wildlife conviviality, large carnivores, carnivore conservation

Introduction

Human activities have impacted ecological communities worldwide, accelerating global species extinctions by up to 1000-fold (Pimm et al. 2014). One of the most impacted vertebrate groups is that of large carnivores, with 50% of terrestrial mammal species at risk of extinction due to habitat loss and degradation, direct exploitation, prey removal, and persecution (Ripple et al. 2014; Ingeman et al. 2022). These trends are predicted to worsen unless integrated actions are taken to address the direct drivers of biodiversity loss, however intervening on these drivers remains challenging (Díaz et al. 2019). Direct drivers, like overexploitation or persecution, are in turn caused by indirect drivers such as conflict, missing governance, and various demographic, economic, and political factors, all of which are affected, and affect, our society's values, behaviours, and institutions. Therefore, in order to be effective, conservation actions must go beyond the direct drivers of carnivore loss and address the indirect drivers that are at the root of carnivore declines and extinction (Ehrlich & Pringle 2008; Díaz et al. 2019).

Despite the above challenges, population recovery of and coexistence with large carnivores is seemingly possible, as illustrated in the following examples. Densities of jaguars *(Panthera onca)* in multi-used landscapes (e.g. cattle ranches) are sustained at levels comparable to those from parks in the Brazilian Pantanal, mainly due to protection from hunting and human retaliation (Devlin et al. 2023). Pumas *(Puma concolor)* exhibit high occupancies in highly modified landscapes in the Brazilian Cerrado despite severe anthropogenic fragmentation, largely due to effective management of protected areas and federal laws that enforce conservation on private lands (Vynne et al. 2011; Ferreira et al. 2020). Large populations of hyenas *(Hyaena hyaena)* and leopards *(Panthera pardus)* persist within urbanized landscapes with high human densities in western India, due to a combination of high social tolerance and protective legislation (Athreya et al. 2013). And lastly, populations of lynx *(Lynx lynx)*, wolves *(Canis lupus)*, bears *(Ursus arctos)* and wolverines *(Gulo gulo)* have increased or stabilized in areas of Europe from which these populations were previously decimated or locally extirpated (Chapron et al. 2014); mainly due to a combination of well-enforced, integrated legislation, effective management plans for exploitation, as well as increased habitat quality and connectivity resulting from the abandonment of rural areas (Chapron et al. 2014; Knott et al. 2014; Bartoń et al. 2019; Cimatti et al. 2021).

Nevertheless, increased landscape sharing between large carnivores and humans has implications. It increases the potential for human-carnivore (Klees van Bommel et al. 2020; Braczkowski et al. 2023) and social conflicts (Sjölander-Lindqvist et al. 2020; Jürgens et al. 2023) which can lead to unsustainable carnivore management and poor governances. Social conflicts for example can mislead decision-making processes (Fernández-Gil et al. 2016), bias carnivore management as to favor political interests (Darimont et al. 2018), and ultimately, impact the viability of carnivore populations (Immonen & Husby 2016; Quevedo et al. 2019; Laikre et al. 2022). Therefore effective conservation of large carnivores is possible in anthropogenic landscapes, but it will require fundamental changes in the way we interact with and manage carnivores. Innovative governance strategies will be particularly useful for tackling this challenge, particularly the implementation of those governance approaches that promote the adaptation of social systems through learning, critical thinking, leadership, and co-production (Termeer et al. 2017). In summary, it will demand *transformative change* in the large carnivore conservation practice (Blythe et al. 2018; Massarella et al. 2021).

Transformative change involves a profound transformation of social systems that changes indirect drivers, in particular society's paradigms, values, and behaviors as well as the corresponding sociopolitical, economic, and technological structures. It involves fundamental changes at personal and social levels (Woiwode et al. 2021), including social behavior and values (Palmer et al. 2014). Transformative changes are meant to produce axial change, i.e. radical changes that challenge current systems and break the *status quo* (O'Brien et al. 2013). Such changes are also meant to address indirect drivers with sensitivity to the local context and ultimately lead to more just, equitable, and sustainable futures (Temper et al. 2018; Visseren-Hamakers et al. 2021). A robust body of knowledge on transformative change has been developed in the sustainability (Westley et al. 2011; Olsson et al. 2014; Blythe et al. 2018; McPhearson et al. 2021) and climate change literature for over a decade (Pelling 2010; Burch et al. 2014), however a specific focus on biodiversity has only recently emerged (Massarella et al. 2021, 2022; Naito et al. 2022; Visseren-Hamakers & Kok 2022; de Koning et al. 2023; White et al. 2023). Furthermore, knowledge on how to steer and operationalize this transformative change in biodiversity conservation, and more specifically towards sustainable states between humans and carnivores, i.e. coexistence, is just recently gaining traction. One of such advances is the development of the *Transformative biodiversity governance* conceptual framework (TBG; Visseren-Hamakers et al. 2021), which comprehensively integrates the need to address the root causes (i.e. indirect drivers) of species loss and extinction with the implementation of holistic, innovative governance approaches.

TBG refers to the collection of formal and informal, public and private rules, rule-making systems, and local to global stakeholder networks which work synergistically to enable compassionate, just and sustainable social-ecological systems (Visseren-Hamakers et al. 2021). As it is grounded in the transformative theory of change, it offers a guiding framework to steer and evaluate transformative change towards human-large carnivore coexistence in the conservation practice. TBG presents an innovative governance strategy that holds transformative power by addressing the root causes of species loss in ways that are simultaneously adaptive, inclusive, integrative, and transdisciplinary in the face of uncertainty (Díaz et al. 2019). It ensures that conservation interventions produce axial change by acting across-scales, sites and sectors (integrative); empower underrepresented, marginalized groups with transformative change values (inclusive); build resilience in the face of environmental change, complexity, and social conflict (adaptive); recognize different ways of knowing, valuing, and representing biodiversity (pluralistic); and exercise caution in the face of uncertainty (precautionary; Visseren-Hamakers et al., 2021).

In this paper we reviewed all carnivore conservation initiatives published between 1990 and 2023, evaluating their contributions for producing transformative change toward human-carnivore coexistence using the TBG framework. We sought to assess: 1) the extent to which carnivore conservation initiatives address indirect causes of carnivore declines and extinction, 2) the extent to which these initiatives are embedded in a transdisciplinary framework that integratively considers ecological and social factors, 3) the governance approaches that are implemented in carnivore conservation practice, and 4) the challenges and lessons that can be drawn from the conservation initiatives in relation to implementing transformative change towards conviviality in social-ecological systems. We focus on carnivores for two reasons: first, because the complex challenges of their conservation provide a rich arena for implementing the various types of transformative approaches advocated in the TBG framework for achieving global biodiversity and sustainability goals (Temper et al. 2018; Díaz et al. 2019; McPhearson et al. 2021), and second, because we want to evaluate the suitability of transformative approaches for addressing the multiple challenges posed by carnivore recovery and coexistence with humans.

From here on we adopt the term ‘conviviality’ instead of coexistence. We do so because of the strong transformative potential of the former, which is rooted in the transformative theory of change of ‘convivial conservation’ (Büscher & Fletcher 2020). Convivial conservation is a radical alternative to mainstream conservation approaches which uses transformative methodologies and an innovative conceptual framework to address the global biodiversity loss and extinction crisis. It challenges the hegemonic capitalist order and its embedded dichotomies (e.g. human vs nature), while building on equity, environmental justice and structural change to facilitate coexistence between human and all non-human nature (Büscher & Fletcher 2020; Massarella et al. 2022). Conviviality in the context of this chapter is thus conceptualized as a balanced state between human and large carnivores in which the former develop committed, long-term, ethical relationships with the latter, creating sustainable social-ecological systems which are based on the principles of social equity, structural change, environmental ethics and justice. We believe such concept expands, both conceptually and practically the transformative potential of coexistence, explicitly linking conservation efforts to the root causes of carnivore loss with governance approaches which promote societies’ adaptation to the current challenges posed by the biodiversity crisis.

Methods

Search strategy

We conducted a scoping literature review (Munn et al. 2018) to investigate the contribution of carnivore conservation initiatives for promoting transformative change towards conviviality in social-ecological systems. To achieve this we assessed the type of change these initiatives were trying to achieve and the means to do so (further details on how contribution of initiatives was conceptualized and evaluated in the 'Analysis' section). We used the Web of Science database to review carnivore articles on carnivore conservation published during the period from January 1990 to January 2023. We conducted our search based in three steps, an initial search and two selection phases. In the initial search, we developed a search string that included keywords related to carnivores, drivers of threat/loss and coexistence, and governance. This query was the following:

[ALL = ((carnivore) AND (threat OR conservation OR cohabitation OR coexistence OR convivial* OR coupled human-natural Systems OR social-ecological OR socio-ecological OR place-based OR "transformative change") AND (inclusiv* OR community OR local communities OR transdisciplinary OR governance OR collaboration OR power OR "transformative governance" OR "transformative biodiversity governance"))]*

This search resulted in a list of 1558 records, from which we made the first selection of articles by reading each abstract and title, and selecting potentially relevant articles based on two criteria. The first criterion was whether the article assessed any indirect driver of carnivore threat or loss (see below), and second, if it also addressed any elements of governance (see below). This first step resulted in the selection of 90 articles, all of which underwent a second selection phase in which we analyzed the full content of the article, assessing also the quality of the research based on the Critical Appraisal Skills Programme, an established approach to systematically assess the trustworthiness, relevance and results of published papers (Long et al. 2020). From this second selection step, we obtained 16 articles for final analysis (1% of the articles of our initial search, Appendix S1). The two main reasons for which articles were excluded in the second selection phase were that i) the keywords used resulted in articles that mentioned conservation or governance without addressing them directly (e.g. mentioning these terms as context in the introduction or as recommendations), and ii) the articles addressed either biological or governance issues but not both.

Analysis

Our analysis of the selected articles focused on i) indirect drivers of carnivore threat/loss, ii) the contributions to transformative governance, iii) lessons learnt and challenges for achieving transformative change in carnivore conservation and management. We deducted the contribution of the reviewed initiatives towards transformative change by assessing whether the implemented actions contributed to address the indirect drivers of carnivore threat/loss, and the extent to which they were consistent with the governance approaches delineated in the TBG framework. More specifically, we evaluated whether the conservation initiatives: i) achieved proposed conservation goals, ii) changed the indirect and direct drivers of carnivore threat/loss in ways such that indicators of the status of the intervened carnivore populations were improved, iii) implemented governance processes followed the transformative governance approach. The contributions of each article to TBG were assessed by explicitly evaluating each characteristic element within the inclusive, integrative, adaptive, transdisciplinary, and anticipatory governance approaches (Table 1; Visseren-Hamakers & Kok 2022). Each element within each approach was scored with either one, if that element was explicitly addressed in the article, or zero if it was not. These element scores were then summed within each governance approach as to obtain a subtotal score for each approach, and then each of these subtotal scores were summed to obtain a total transformative governance score (Table 1). Higher scores represent articles which applied more governance approaches and thus have a greater potential for supporting transformative change in carnivore conservation and management. It should be noted, though, that this scoring does not imply that articles with a low score had less or no value in general, as they might have explicitly chosen to align with specific governance approaches to address more specific questions and local contexts.

Results

Study Characteristics

The sixteen articles that matched our selection criteria focused on conviviality and studied six carnivore species using single-species or carnivore community approaches. The carnivore species represented were the wolf (26%), snow leopard (21%), brown bear (16%), lion (16%), Andean bear (5%), and jaguar (5%), and the remaining percentage represented carnivore communities in general (11%; Fig. 1). These studies were conducted across 17 countries within the continents of America (35%), Asia (29%), Africa (24%), and Europe (12%). Authors studied conviviality through several approaches, including social-ecological perspectives (29%), conflict management approaches (18%), conservation incentives and compensation programs (18%), prevention of livestock predation by carnivores (12%), policy development (12%), environmental education and carnivore killing prevention (each 6%). Two thirds of these studies (75%) included either quantitative or qualitative evaluations which directly or indirectly assessed the success of the initiatives in achieving conservation targets. Studies without impact evaluation did not report explicitly any causes for this absence (n= 4), and from these, evaluation was not relevant for one article, a theoretical model not yet implemented in practice (Boronyak et al. 2022).

Table 1: Reference for scoring the potential of the selected articles for supporting transformative change in biodiversity conservation. The criteria were taken from the Transformative Governance Approach (Visseren-Hamakers & Kok 2022). Each governance element that characterizes an approach (Characteristic element) is scored (Maximum element score) to obtain a governance approach score (Maximum approach score). Each governance approach score is summed to calculate the total transformative governance score (bottom row), which represents the potential of the selected articles for transformative change in biodiversity conservation. Highest scores mean higher transformative potential.

Governance Approach	**Characteristic element**	**Maximum element score**	**Maximum approach score**
Inclusive	addresses power asymmetries	1	2
	empowers underrepresented knowledge, rights or stakeholders	1	
Integrative	provides solutions across sectors	1	3
	provides solutions across sites	1	
	provides solutions across scales	1	
Adaptive	enables learning	1	3
	enables reflection	1	
	enables dialogue	1	
Transdisciplinary	builds capacity for transformative governance	1	4
	recognizes diverse values	1	
	recognizes diverse knowledge systems	1	
	recognizes diverse perspectives	1	
Anticipatory	applies the precautionary principle in the face of uncertainty	1	1
Transformative	**Inclusive + Integrative + Adaptive + Transdisciplinary + Anticipatory**	**13**	**13**

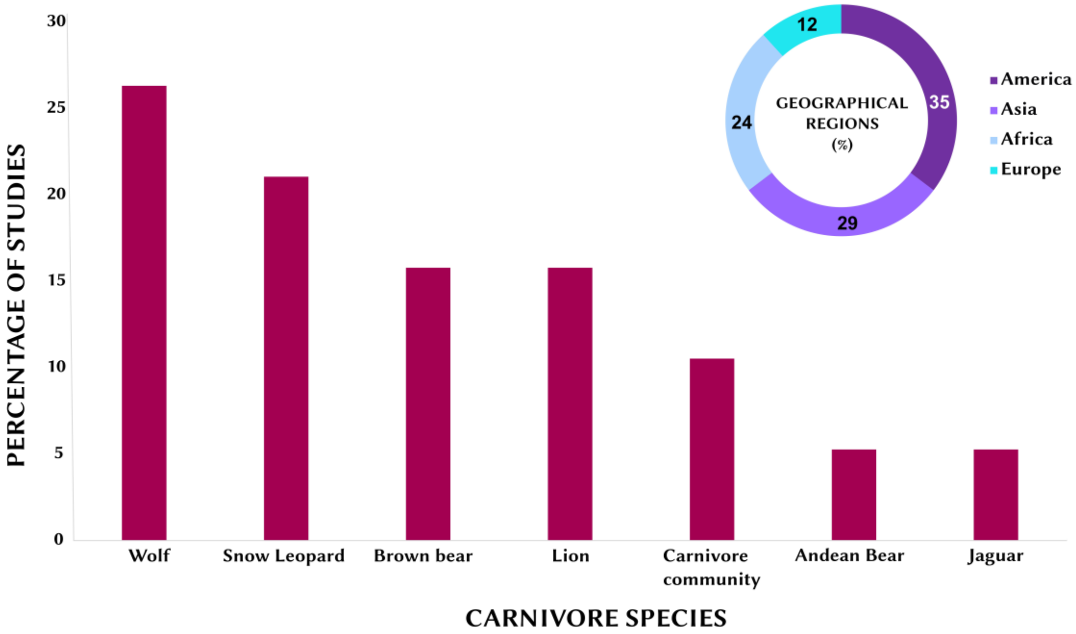

Fig. 1. Carnivore species and geographical regions represented in the selected studies.

Indirect drivers of carnivore loss

The studies focused on the same indirect driver of carnivore loss: conflicts. They addressed conflict from two different perspectives, either ecological, focusing on the human-carnivore interactions that caused conflict (e.g. livestock depredation), or social, studying the interactions between stakeholders regarding carnivore conservation (e.g. conflict over carnivore management policies). Additionally, 82% of these studies also explicitly addressed direct drivers of carnivore loss, specifically carnivore retaliation by humans, and just one article, land use change and the resulting carnivore prey loss (Mishra et al. 2003). Studies aimed to promote conviviality therefore mitigated declines in carnivore populations due to retaliatory killings and land-use change (direct factors) by addressing underlying conflicts with carnivores or other stakeholders (indirect factors). The causes of the conflicts examined in these studies were human values and behaviours, as well as sociocultural, economic, and governance factors. Conviviality was promoted in these studies by addressing the indirect causes of carnivore population decline through three main approaches: i) changing attitudes and behaviours, ii) building capacity for conservation, and iii) developing models for coexistence.

Firstly, studies that aimed at changing values and behaviours focused on social factors such as education (Espinosa & Jacobson 2012; Chausson et al. 2022), as well as economic and governance factors. Economic factors were addressed through compensating local communities for monetary losses due to predation, particularly through insurance programs (Mishra et al. 2003; Hazzah et al. 2014; Alexander et al. 2021), conservation incentives (Mishra et al. 2003; Alexander et al. 2022), and non-lethal predator management strategies (de la Torre et al. 2021; Martin 2021; Chausson et al. 2022). Governance factors were addressed via bylaws that banned the killing of carnivores and the resulting rewards (Mulder et al. 2019), but also through participation of local communities in the design, implementation and evaluation of conservation actions (Mishra et al. 2003; Alexander et al. 2021; de la Torre et al. 2021; Alexander et al. 2022; Sonam et al. 2022). An example of a successful initiative that changed human behaviour toward predators is the Lion Guardians Program (LG) and the Predator Compensation Fund (PCF), both implemented in the Amboseli ecosystem region in Kenya (Hazzah et al. 2014). The LG incorporated Maasai cultural values and beliefs into conservation objectives, while the PCF compensated pastoralists for depredated livestock. Through a combination of actions that provided conservation benefits to communities, reduced livestock depredation, and created a sense of community ownership of lions, the LG and PCF reduced the number of lions killed in the Amboseli Ecosystem by 99%.

Secondly, studies that aimed at building capacity for conservation did so by implementing participatory processes in decision making that fostered the ability to develop shared goals, build consensus, and co-create solutions (Richie et al. 2012; Wilson et al. 2017; Marino et al. 2021a; Salvatori et al. 2021); or by fostering reflection on conservation interventions based on community-based conservation principles (Young et al. 2021). An example of such successful approach was a project implemented in areas where centralized decision making for bear and wolf management had previously failed in Italy, Spain and Romania (Salvatori et al. 2021). Here, stakeholder platforms were established, and through a consensus-building approach, stakeholders with conflicting interests were able to agree on common goals and jointly implement management actions that improved conditions for stakeholders highly impacted by carnivores. The process itself also resulted in significant increased social capital, via increased empathy, knowledge, trust, social cohesion and social learning (Salvatori et al. 2021).

The last approach to promoting conviviality was the development of transformative change models presented by Boronyak et al. (2022). In this study, the authors articulated drivers of change and specific pathways for transitioning production systems based on lethal carnivore management to a state of human-carnivore coexistence. Qualitative models explicitly showed where and how to intervene to facilitate the creation of systems that foster compassionate relationships with animals, support thriving rural communities, and maintain biodiversity and ecosystem services.

Governance approaches

All studies promoted conviviality through the implementation of at least three of the five governance approaches proposed under the transformative biodiversity governance framework (Table 2). There were three approaches that were implemented most frequently across all studies: integrative, adaptive, and inclusive governance. Integrative governance was achieved by implementing actions at multiple scales: social (Espinosa & Jacobson 2012; Marino et al. 2021a), spatial (Young et al. 2021; Boronyak et al. 2022), and institutional (Wilson et al. 2017). Adaption was possible by addressing complexity and change through collaboration and co-management of carnivores. Examples include the Wood River Wolf and Blackfoot Challenge projects. In the first project, collaborative research and implementation of non-lethal carnivore control methods with local ranchers resulted in an adaptive carnivore program that successfully reduced livestock predation while preventing habituation of wolves (Martin 2021). In the second case, a program originally designed to resolve human-bear conflicts was expanded and refined to additionally prevent conflicts with wolves prior to their recolonization in the region, successfully maintaining low predation and retaliatory kill rates despite increasing wolf populations (Wilson et al. 2017).

Inclusivity was successfully implemented in studies by addressing power asymmetries either by empowering marginalized groups in conservation actions, such as women (Alexander et al. 2022) or impoverished rural communities (Mishra et al. 2003; Alexander et al. 2021; Sonam et al. 2022), or by decentralizing decision-making processes in carnivore management (Wilson et al. 2017; Martin 2021). An exemplary study of inclusive governance is the Shen project in the Spiti Valley, India (Alexander et al. 2022). This project succeeded in providing economic conservation incentives for women living in snow leopard conservation landscapes, as well as engaging program participants in various conservation activities. Engaging marginalized women in dialogue about snow leopard conservation led to women developing more positive attitudes about snow leopards, implementing self-driven conservation actions, and engaging other stakeholders in conservation compliance.

Transdisciplinary and anticipatory governance approaches were less common throughout the studies. The former included the incorporation of diverse values, perspectives and knowledge systems in building capacity for transformative governance. Examples of transdisciplinary studies included integrating Buddhist values of compassion toward living beings in deactivating

"Shandong" wolf pits in the Indian Trans-Himalayan region (Sonam et al. 2022)(Sonam et al. 2022)(Sonam et al. 2022)(Sonam et al. 2022); or integrating sociocultural values and traditions of the Samburu (Chausson et al. 2022) and Massai peoples (Hazzah et al. 2014) to promote human-lion coexistence in Africa. Anticipation was integrated in only a quarter of the studies, either through anticipatory measures to ensure the long-term sustainability of conservation incentive programs (Mishra et al. 2003) and participatory processes (Richie et al. 2012), or through preventive measures to avoid fomenting social conflict in participatory decision-making processes. Fomenting social conflict was prevented primarily by carefully maintaining trust among participants during participatory processes, either by setting realistic expectations for participants regarding the limits of these processes to influence policy (Salvatori et al. 2021), or by carefully selecting participants to allow for wide representation without jeopardizing the possibility of constructive dialogue (e.g. excluding participants with radical stands unable to engage in constructive dialogue, Marino et al., 2021).

Transformative Governance

Transformative governance requires that the five governance approaches described previously be simultaneously integrated into conservation efforts. Therefore, we present the evaluation scores for each of the governance approaches as a measure of how much potential each study has for transformative change in carnivore conservation. Scores for potential for transformative change ranged from the maximum score of 13 points, for the study that implemented all approaches and all elements within each approach (Wilson et al. 2017; first row Table 2), to four points for the study that implemented the fewest governance approaches and the fewest number of elements within each approach (Martin 2021; bottom row Table 2). Note however that low scores do not imply no or less potential in general, as these studies might have explicitly chosen to align with specific governance approaches to address more specific questions or fit local contexts better.

An example of how conviviality can be successfully promoted through the application of all transformative governance principles is the Blackfoot Community-based Conservation Program (BC) in Montana, USA (Wilson et al. 2017). BC is a nongovernmental organization of landowners that involves local, state, and federal land and environmental agencies. It addresses environmental issues in the Blackfoot watershed, focusing on information sharing and consensus-based decision making. A program to mitigate conflicts with bears was successfully implemented in this region when wolves began to re-establish themselves in Montana. To avoid conflicts with wolves when they arrived in the valley (anticipation), the bear program was modified and refined to manage future conflicts with wolves (adaptation). The program was based on an inclusive, multi-method approach to conflict mitigation (integration, transdisciplinarity) that included intensive local participation through workshops, group meetings, and collaboration on wolf research data collection (inclusiveness). The initiative kept the average number of livestock predations (2.2 individuals/year) and retaliatory kills by wolves (2.4 individuals/year) low, despite increases in the wolf population (from one to 12 packs).

The Grizzly Bear Dialogue Group (GBDG; Table 2) provides an opportunity for critical reflection on the challenges associated with attempting to achieve transformative governance (Richie et al. 2012). GBDG was a collaborative initiative for bear management in the Banff National Park (BNP) in Alberta, Canada. The bear population in BNP was threatened by high human-caused mortality and deep social conflict resulting from years of centralized management. The GBDG was introduced by BNP authorities to reduce this conflict and improve conservation outcomes by shifting management focus to shared interests and decentralized decision-making (inclusivity). The GBDG was successful in promoting shared decision-making and action, and in building relationships and respect among different stakeholders and sectors (inclusivity). However, this social process was not sustainable in the long term because precautions were not taken to make the initiative resilient to change (anticipation), in this case to a change in administrative authorities that shifted the focus of collaboration to eco-centric, centralized decision making. This change led to frustration, burnout, and high turnover among GBDG participants, which affected group participants' problem-solving skills and the respect, trust, and distribution of power among participants; this ultimately fuelled social conflict and prevented the incorporation of learning into future participatory processes in the region (adaptation).

Evaluation of success

Seventy five percent of the studies measured whether actions implemented achieved the proposed goals. Experimental and quasi experimental designs were used in 50% of these studies, measuring and comparing indicators of success (e.g retaliatory killings, livestock predation rates, attitudes change) between intervened vs not intervened sites (Alexander et al. 2021, 2022; Chausson et al. 2022) and before vs after interventions (Hazzah et al. 2009; Espinosa & Jacobson 2012; Wilson et al. 2017; Mulder et al. 2019; de la Torre et al. 2021). Furthermore, 50% of the studies which implemented quantitative evaluations also underpinned intervention outcomes with explicit theories of change (Mulder et al. 2019; Alexander et al. 2021, 2022; Chausson et al. 2022). The remaining studies, all related to social conflicts between stakeholders about carnivore management used either interviews (Marino et al. 2021a; Martin 2021; Salvatori et al. 2021) to assess indicators of success, such as whether original expectations had been met and levels of satisfaction on different characteristics of the participatory processes; or policy analysis to evaluate qualitatively the participatory process and its outcomes (Richie et al. 2012).

Table 2. Scores for the potential contribution of studies to transformative change in carnivore conservation. Highest scores mean highest potential for transformative change (in bold, the top three studies with the highest scores). Note that low scores do not imply no or less potential in general, as these studies might have explicitly chosen to align with specific governance approaches to address more specific questions and fit local contexts better.

		GOVERNANCE APPROACH					
No.	**Article**	**Inclusive**	**Integrative**	**Adaptive**	**Trans-disciplinary**	**Anticipatory**	**Total score**
1	**Wilson et al. 2017**	**2**	**3**	**3**	**4**	**1**	**13**
2	**Salvatori et al. 2021**	**2**	**2**	**3**	**4**	**1**	**12**
3	**Young et al. 2022**	**2**	**3**	**3**	**4**	**0**	**12**
4	Boronyak et al. 2022	1	3	3	4	0	11
5	Richie et al. 2012	2	2	3	4	0	11
6	Mishra et al. 2003	2	2	2	3	1	10
7	Alexander et al. 2022	2	1	3	2	1	9
8	Alexander et al. 2021	2	1	3	1	1	8
9	Chausson et al. 2022	2	1	3	2	0	8
10	Marino et al. 2021	2	1	1	4	0	8
11	Sonam et al. 2022	2	2	3	1	0	8
12	Espinosa et al. 2012	1	1	2	3	0	7
13	Hazza et al. 2014	2	1	2	2	0	7
14	de la Torre et al. 2021	2	1	2	1	0	6
15	Mulder et al. 2019	1	1	1	1	0	4
16	Martin 2021	1	1	1	0	0	3

Discussion

Transformative change in biodiversity conservation requires expanding solutions beyond technocratic interventions while enabling societies to adapt to change and uncertainty. To achieve transformative change, socio-political processes and economic relations must be considered (Kei Otsuki 2015), and governance repertoires that promote collective action, reflection, and dialogue in ways that are pluralistic, inclusive, empowering, and adaptive must be implemented (Termeer et al. 2017; Visseren-Hamakers & Kok 2022). The above conditions are addressed integratively within the Transformative Biodiversity Governance framework (Visseren-Hamakers & Kok 2022), making it a useful approach for evaluating the contributions of carnivore initiatives to promoting transformative change in carnivore conservation.

Our literature review (n=1558 articles) shows that very few initiatives within the carnivore conservation and management literature contribute to transformative change (1%, n=16 articles) and that this research focuses heavily on resolving conflicts related to human-carnivore coexistence. Given these findings, we frame transformative change in this paper in the context of 'conviviality', which we define here as balanced state between human and large carnivores in which the former develop committed, long-term, ethical relationships with the latter, creating sustainable social-ecological systems which are based on the principles of social equity, structural change, and social-environmental justice. This concept comes from the 'convivial conservation' theory of change, a post capitalist approach to conservation that promotes environmental ethic, social equity, structural change, and environmental justice (Büscher & Fletcher 2020).

Transforming landscapes toward conviviality requires restoring ecological processes and the social fabric that supports this change (Clark & Wallace 1999; Wilson et al. 2017; Ingeman et al. 2022). Therefore, creating landscapes of conviviality is a relevant area for implementing the types of transformative solutions advocated to achieve global biodiversity and sustainability Goals (Temper et al. 2018; Díaz et al. 2019; McPhearson et al. 2021). In the selected studies we found several strategies to restore human social processes that promote conviviality. These included working collaboratively with local communities in ways that empowered them and helped develop appropriate, legitimate conservation solutions. These conservation initiatives relied on time, presence, respect, and recognition of equal partnerships with local stakeholders to ultimately build trust, empathy, and aptitude (Mishra et al. 2017). Solid, equal partnerships with local actors were weaved through knowledge co-production and transparent data sharing (Wilson et al. 2017; Salvatori et al. 2020), fostering ownership of conservation decisions and actions (Young et al. 2021), and co-sharing conservation costs, benefits and risks (Mishra et al. 2003; Alexander et al. 2021).

The studies in our review reflect two important challenges in implementing conviviality in conservation landscapes: conducting impact evaluations and implementing transdisciplinary conservation actions. Impact evaluations in conservation are important for designing cost-effective interventions and supporting adaptive management (Cook et al. 2010), yet only two-thirds of the studies from our literature review addressed evaluation, supporting previous findings in the conservation literature including research on conviviality (Lozano et al. 2019). Several barriers contributing to this challenge have been identified, including limited resources, difficulties in selecting appropriate spatial scales, dealing with spill over and confounding effects, and various methodological limitations in developing experimental designs suitable for evaluation (Baylis et al. 2016). In the reviewed studies the challenges were related to potential confounding factors (Mulder et al. 2019; de la Torre et al. 2021), lack of baseline data (Mulder et al. 2019; Marino et al. 2021; Alexander et al. 2022), limited human and financial resources (Mulder et al. 2019), and difficulties to measure direct indicators of impact (e.g. number of carnivores killed illegally; Mulder et al. 2019; Alexander et al. 2021), particularly intangible indicators and outcomes (Marino et al. 2021; Young et al. 2021; Salvatori et al. 2021). Despite these obstacles, evaluations were tailored to fit contexts with small local capacity and limited resources, still providing robust results that supported adaptive management (Chausson et al. 2022).

The second challenge is that of transdisciplinary conservation. Most of the studies we found in our literature review failed to integrate the different disciplines into conservation solutions and impact assessments. Most studies addressed conservation issues from either an ecological or social perspective (n=1542 articles which did not met our selection criteria for this reason), and impact assessments in our selected studies, which when available, remained purely quantitative or qualitative. These findings highlight ongoing challenges in overcoming artificial boundaries between disciplines (Kothari 2014; Steffen et al. 2018), and especially in incorporating social science into conservation initiatives (Niemiec et al. 2021). In light of these findings, we echo the call for the integration of relevant social theories (e.g., power dynamics, governance, ethics, justice) and methods (e.g., social mapping, discourse and policy analysis, participatory action) into conservation studies, supporting similar suggestions for such integration in biodiversity conservation (Lozano et al. 2019; Castillo et al. 2020; Massarella et al. 2021). Incorporating social science theories and methods into carnivore conservation can therefore contribute to a deeper understanding of the broader socio, political and economic contexts in which coexistence with carnivores takes place and challenge the structures that prevent conviviality. A concrete example on this from our review is the appraisal of the grizzly bear management process in the BANF Park, Canada (Richie et al. 2012). Here, mapping the social process of the participatory process highlighted that effective governance of large carnivores cannot take place in contexts of asymmetric power relations, where there is resistance from powerful actors, in this case from park management authorities, to shifting power dynamics in decision making. In contrast, the explicit recognition and need to balance power relations between actors successfully promoted conviviality between large carnivores and humans in the Blackfoot conservation initiative in USA (Wilson et al. 2017), and throughout many other initiatives implemented throughout the Asian mountains (Young et al. 2021). These findings support previous research that shows that, not only power is understudied, understated and poorly understood on research related to human-environment relations (Fabinyi et al. 2014), but that shifts in power (e.g. power in decision making) underpin the political processes that drive transformative change (Blythe et al. 2018).

GUIDING PRINCIPLES FOR YOUNG CONSERVATION PRACTITIONERS FOR FACILITATING CONVIVIALITY

There are no silver bullets nor universal approaches for achieving conviviality. Nevertheless, our results show that the pursuit of conviviality requires more than technocratic interventions (Martin 2021), and that the success and sustainability of conservation outcomes depends on the capacity and resilience of societies to adapt and overcome challenges, particularly in contradictory or highly polarized contexts (Marino et al. 2021a). Governance strategies that allow actors to learn, think critically, lead, and co-produce knowledge have been argued to promote such adaptation (Termeer et al. 2017), a perspective supported by our review findings. In light of our review and the above insights, we provide three recommendations for young conservation scientists who seek to enact transformative change and work in ways that contribute to creating more just, equitable, resilient and sustainable futures. We base these recommendations on the lessons learned, challenges reported, and insights deducted from our selected articles, contextualizing these findings with pertinent literature on transformative change and collaborative governance.

Integrate multiple knowledge

Collaboration between different scientific disciplines is particularly important when promoting conviviality. While carnivore conservation depends on the ecological factors that support animals' reproduction and survival, social factors such as values, narratives, and the institutions through which they are expressed can also be critical factors in their survival (Clark & Slocombe 2011). Social science can specifically contribute in this integration by providing insights on the political and social processes that prevent (Richie et al. 2012) or favor conviviality (Wilson et al. 2017; Young et al. 2021), as well as for supporting the discovery and implementation of legitimate conservation actions that promote conviviality while avoiding social conflict (Marino et al. 2021a). A research gap in our review is the study of the social and economic factors that allow humans to bare tolerable risks for co-occurring with carnivores (*sensu* Carter & Linnell 2016). These socio-economic factors are important barriers to conviviality, particularly in contexts where the high costs of co-occurring with carnivores help perpetuate poverty and marginalization of rural communities (Inskip et al. 2013) and reproduce social inequality patterns (Braczkowski et al. 2023).

In the light of our review and the insights highlighted above, we suggest that a first step towards the integration of multiple knowledge, as to promote transformative change towards conviviality, is the integration of critical social theory (CST) into conservation science and practice (Massarella et al. 2021). The relevance of CST for transformative change is that it can help address the indirect drivers of conservation problems while preventing the exacerbation of injustices in conservation practice (Martin et al. 2016). More specifically, it can provide a structural approach to understand and address more effectively the political and economic actors and systems that underlie conservation problems (i.e. upper class elites and global processes; Büscher & Robert Fletcher 2019; Massarella et al. 2021), instead of only focusing on individual behaviors, which are too often targeted at poor marginalized groups (e.g., rural lower classes) and that don't resolve the root causes of the conservation problems. CST is also consistent with the transformative governance framework, given that it helps highlight alternatives that challenge the *status quo* of current sociopolitical systems, and it also promotes inclusivity and transdisciplinarity by creating space for diverse knowledge and perspectives, including those of underrepresented or marginalized groups that have great transformative potential (Temper et al. 2018; Khothari et al. 2019; Barkin & Sánchez 2020; Adloff & Caillé 2022).

There are two important caveats that we would like to highlight regarding the integration of multiple knowledge: i) integration of social sciences does not mean co-optation (*sensu* Chua et al. 2020), and ii) the types of knowledge we suggest to integrate are not limited to Western science knowledge. First, the integration of the social sciences that we call for here does not refer to a selective appropriation of its methods and concepts to fit the current conservation agenda (i.e., co-optation). Rather, we echo the need to collaborate transdisciplinarily and create new shared spaces in which we can challenge power structures, ethics, assumptions, methods, and social impacts of conservation in order to contribute to deep transformational change (see Chua et al. 2020). The nature of and the possibilities for creating such shared spaces will depend on what specific contexts allow, and most importantly, on the openness and commitment of scientists and conservation practitioners to collaboratively imagine and develop the conditions necessary to achieve this in their particular contexts.

Second, traditional indigenous and local knowledge (ILK) are legitimate and are valuable sources of information for conservation action. There are significant gaps in the implementation of ILK in conservation, a finding also reflected in our review given that only 12% of the studies included such knowledge (Mulder et al. 2019; Sonam et al. 2022). the reasons in the literature for this are the economic development pressures, the dominance of Western practices, and colonial perspectives on ILK (Ens et al. 2021). ILK integration to conservation is a fundamental step in achieving the principles of transdisciplinarity and inclusivity advocated by the TBG. It helps advancing in the conservation knowledge implementation gap (Tengö et al. 2017; Klütsch & Ferreira 2021), democratizes science (Turrini et al. 2018), contributes to environmental democracy and justice, enriches our understanding of species' status, trends and human-wildlife relations (Torrents-Ticó et al. 2021), and improves conservation outcomes (Camino et al. 2020). Linking ILK and scientific knowledge in synergistic ways to achieve conviviality and follow the TBG principles requires that scientists respect the integrity of each knowledge system and use scientific and ILK knowledge systems as complementary, mutually enriching frameworks (Whyte et al. 2016; Tengö et al. 2017; Torrents-Ticó et al. 2021).

Build equal partnerships with local actors

Carnivores co-occur with people in multifunctional landscapes (Wolf & Ripple 2017), therefore achieving conviviality requires large-scale, just, and inclusive engagement with local actors (Redpath et al. 2017; Chan et al. 2020). Local engagement can lead to stronger, improved and more sustainable conservation outcomes and impacts if scientific knowledge is enriched with community experience in ways that foster mutual trust and respect (Mishra et al. 2017), social learning (Hovardas 2020), and psychological ownership of conservation initiatives (Redpath et al. 2017; Greving et al. 2020). Genuine relations with local communities, built in a context that fosters trust, reliability, self-respect and social learning, provide the foundation for local communities to adapt to change and achieve sustainable conservation outcomes (Heimlich & Ardoin 2008; Termeer et al. 2017).

Our studies highlighted that success of conservation initiatives demand genuine and reciprocal relations that foster equal relationships with local actors. Conservation interventions that allowed co-development and shared responsibility of conservation programs successfully reduced retaliatory killings and behavioural intent to kill carnivores such as snow leopards (Alexander et al. 2021, 2022), African lions (Mulder et al. 2019) and wolves (Alexander et al. 2021). Such strategies also helped shift negative attitudes towards species such as snow leopards (Alexander et al. 2022). In the case of social conflicts between actors over carnivore management, similar governance strategies helped mitigate conflict successfully. Social conflicts that were addressed allowing dialogue, reflection, and opportunities for leadership, lead actors previously in conflict to reach consensus over carnivore management actions (Richie et al. 2012; Marino et al. 2021a), allowing them to also work together in the implementation of conservation actions (Salvatori et al. 2021).

Furthermore, some of these successful outcomes were achieved despite polarized contexts (Marino et al. 2021a; Salvatori et al. 2021) and contradictory environmental policy (Martin 2021). Some outcomes even remained after the conservation interventions ended (Wilson et al. 2017; Young et al. 2021). The sustainability of conservation actions and solutions relies on how adaptable local communities are to changing circumstances, which requires that conservation interventions engage local actors in ways that allow them to learn and experiment through action, engage in respectful and trusting dialogue, and improve their situational awareness through continuous evaluation and feedback. Studies focused on purely technocratic solutions that do not promote social learning run the risk of local actors feeling resistance to deep change or falling back into old patterns in the face of conflicting or highly polarized contexts (Termeer et al. 2017). An illustration of this is highlighted in the Wood River Wolf Project, a program that focused on technical solutions that effectively mitigated human-carnivore conflict (non-lethal tools for carnivore management), but did not restore the human social processes that could have supported adaptive governance in the face of an unfavourable political context (Martin 2021).

An important lesson from the reviewed articles, supported by Mishra et al. (2017), is that developing partnerships with communities is understanding that local people are autonomous partners with agency and dignity, not just recipients of aid. Our findings thus support three fundamental actions that help enact this understanding and forge solid, equal partnerships with local actors (Mishra et al. 2017; Lemos et al. 2018): knowledge co-production (Mulder et al. 2019; Alexander et al. 2021, 2022; de la Torre et al. 2021), transparent sharing of knowledge and data (Wilson et al. 2017; Marino et al. 2021a), and co-sharing of responsibilities, risks and financial burdens (Wilson et al. 2017; Alexander et al. 2021, 2022). An important consideration is that transparency in knowledge and data sharing should involve not only the actual sharing of scientific knowledge and its uncertainties, but also that we, as researchers and practitioners be explicit about our personal roles and values in the conservation initiatives we participate in, as highlighted by Clark & Wallace (1999), and implemented here by Richie et al. (2012) and Marino et al. (2021).

Don't forget to evaluate your impact

Our findings highlighted that while there are barriers to impact evaluation, there are also opportunities to tailor such evaluations to support adaptive management in conservation even when local capacities are low (Chausson et al. 2022). Approaches used in the selected studies that can help address confounding effects may include paired (i.e. intervened vs not intervened sites; Alexander et al. 2021, 2022) and longitudinal quasi-experimental designs (Hazzah et al. 2009; Espinosa & Jacobson 2012; Wilson et al. 2017; Mulder et al. 2019; de la Torre et al. 2021), along with explicit theories of change to underpin intervention outcomes (Mulder et al. 2019; Alexander et al. 2021, 2022; Chausson et al. 2022). Methodological constrains, such as lack of baseline data for comparison and constrained financial resources can be addressed by using participatory evaluation processes such as implemented in Mulder et al. (2019), Marino et al. (2021) and Alexander et al. (2022); or by using public records that do not require additional funding for data collection (Wilson et al. 2017).

Assessing impact can also be challenging when context-specific and intangible indicators are required (e.g., trust, transparency, leadership, power). In these cases, however, qualitative methods provided helpful insights into social processes and outcomes by using problem orientation and social process mapping (Richie et al. 2012), political ecology analysis (Martin 2021), or surveys to participants to evaluate the decision making processes (Marino et al. 2021a; Salvatori et al. 2021). In participatory processes targeted to address social conflict, evaluating outcomes, processes, and preconditions can be hampered by multiple limitations, however recent proposals have shed light on how to make these evaluations systematic and robust (Butler et al. 2015; Cox et al. 2020), including how to tailor approaches to be pluralistic and environmentally just (Massarella et al. 2020).

We believe that it is possible to achieve conviviality, even in the face of current carnivore declines and pervasive anthropogenic activity. This will require new conservation practices that make science more democratic and participatory by integrating diverse knowledge, collaborating with local actors in a manner consistent with the ideals of equal partnership, incorporating impact assessments into all conservation initiatives regardless of scale, and above all, new ways of thinking about conservation that promote the creation of safe transdisciplinary spaces where dominant conservation discourses, paradigms, practices, and trade-offs (including unintended consequences of conservation) can be critically analysed and challenged as to discover new alternatives that implement truly transformative approaches to change.

Authors' Contributions

APC conceived the idea and designed the methodology with the guidance of SKS and VK. APC conducted the literature review, collected and analysed the data. APC led the manuscript writing supported by SKS and VK. All authors contributed critically to the drafts and gave final approval for publication.

CHAPTER 5

General Discussion

5

Jaguar conservation relies on the implementation of holistic and transdisciplinary strategies that protect essential, connected habitats, maintain viable populations and their gene flow, and promote human-jaguar conviviality. In this thesis I aimed to support this endeavour, providing ecological and social insights into jaguars' habitat use, population gene flow, and human-wildlife conviviality, as well as offering management tools to guide local and regional conservation actions in Central America. I used three main research methodologies throughout this thesis: ecological modelling, scoping literature review, and theory-based evaluation. In *Chapter 2*, I used occupancy models to conduct a broad-scale quantitative analysis of jaguar habitat use based on the first comprehensive dataset of direct jaguar observations across Central America. In *Chapter 3*, I used resistance surface models and resistant kernels to predict jaguar gene flow and functional connectivity among populations in northern Central America. And finally, in *Chapter 4*, I used a scoping literature review and a theory-based evaluation framework to guide conservation efforts towards achieving conviviality between human and large carnivores, and more specifically, jaguars. In the following sections of this discussion I interpret my findings, starting with the main results of each chapter, following up with their conservation implications, and finalizing with conclusions.

Jaguar habitat use and spatial patterns of habitat suitability in Central America

I highlight two main findings from *Chapter 2*. Firstly that jaguar habitat use in Central America is related to both environmental and human influence variables, but the latter have a greater impact on the species. Secondly, that JCUs are the most important reservoirs of jaguar high quality habitat in this region. Jaguars were positively associated with primary productivity, supported by previous findings (Jędrzejewski et al. 2017b; Jędrzejewski et al. 2018), as well as with distance to rivers. The observed association between habitat use and primary productivity most likely reflects the higher prey availability (Jedrzejewski & Jedrzejewska 1996; Fritz et al. 2016) and higher persistence of jaguar populations which is generally found in more humid and productive areas (Jędrzejewski et al. 2017b). Previously documented associations between jaguars and proximity to water (Foster et al. 2010; Duarte et al. 2023) however, were not supported by my findings. This may result from either methodological constraints (e.g. missing spatial information on important intermittent water sources for jaguars such as rainwater ponds 'aguadas', Gaitán et al., 2020), or/and flexible responses of jaguars towards water in areas without strong seasonal patterns (Morato et al. 2018; Montalvo & Sáenz-Bolaños 2023).

Jaguars showed a strong negative response towards human settlements, suggesting an avoidance to human proximity (Petracca et al. 2018; Meyer et al. 2019) and compensatory mechanisms the species uses to adapt to human-dominated landscapes (Morato et al., 2018). A caveat from this result is that the effect of human presence on jaguars most likely depends not only on the presence of humans *per se*, but also on human activities. Due to the scale of this study, I was unable to consider different human activities in my analysis. However, I would expect some variability on jaguars responses to human presence at local scales based on how humans interact with jaguars and the environment. An example of this is that the estimates of jaguar habitat suitability for some areas occupied exclusively by indigenous communities were lower in this study, in comparison to others produced at finer spatial scales (e.g. Guna Yala in Panama; Meyer et al. 2019).

Across the region, I evidenced two main spatial patterns of jaguar habitat suitability. One is that high quality habitat was strongly associated with JCUs, the main reservoirs of jaguar habitat in the region. JCUs accounted for nearly half of all available habitat within the jaguar extent of occurrence, and >50% of this JCU land is protected by law. The other finding is that JCUs contributed to structural connectivity across political boundaries, as the four largest continuous zones of habitat in the region share bi-national borders. Nevertheless, one JCU in Panama (JCU Chagres) and one in Costa Rica (JCU Volcanica Central) showed low habitat suitability ($\Psi_{mean} < 0.50$) and habitat coverage (<35%). These findings suggest that both of these JCUs may act as potential constriction points of population connectivity and that, as previously cautioned by Salom-Pérez et al. (2021), 'JCU Volcanica Central' no longer functions as a jaguar stronghold. I also identified three areas of general concern due to low habitat suitability: central-Costa Rica, central-Panama, and eastern Guatemala-western Honduras; supporting the findings of Salom-Pérez et al. (2021) and Meyer et al. (2020). The latter area, eastern Guatemala-western Honduras is of particular importance, given that the jaguar populations here are predicted to have a high extinction risk (Antonio De La Torre et al. 2018; Villalva & Palomares 2022) and previous studies have identified the area as a potential constriction point for jaguar population connectivity (Sanderson et al. 2002b; Wultsch et al. 2016).

Four potential sources may contribute to uncertainty in my findings. First, even with the extensive camera-trapping effort, I was unable to cover the full gradient range of environmental variables across the study region, such as forest cover and agriculture. My data is biased towards areas occupied by the species, given that in jaguar camera trap studies, effort is commonly maximized by placing cameras in areas known *a priori* to have jaguars. While human factors can have disproportionate effects on jaguar occurrence (Thompson et al. 2020), it is possible that this spatial bias might be partially responsible for the low importance of environmental variables in my model.

Using a more comprehensive dataset might show that, whereas human variables have a strong effect on jaguar-occupied areas, there is a range of environmental values that strongly limit the species' presence in jaguar unoccupied areas. Second, there are areas predicted with a much higher habitat suitability than expected, such as the patches of high jaguar habitat use south of Selva Maya in Guatemala, central Honduras (*pers. comm.,* F. Castañeda, 12 May 2021), central and north-eastern Nicaragua (Hernández Potosme 2019), and areas of Ngäbe-Buglé and around Darien in Panama (Meyer et al. 2019); all from which jaguars either remain in low numbers or have been extirpated. This limitation would again be improved by adding data to my model from jaguar unoccupied areas. Third, information closely related to jaguar occupancy such as sex of individuals (Foster et al. 2010), prey abundance (Rabelo et al. 2019), and poaching (Romero-Muñoz et al. 2019) were unavailable for the region of study. Therefore, predicted areas of high habitat suitability may show smaller populations than expected due to high poaching of jaguars or their prey (Redford 1992). And lastly, despite I aggregated occurrence accounts within sample units, given the variability of jaguar home range sizes across the region (Figueroa 2013; Salom-Pérez et al. 2021; Thompson et al. 2021), it is possible that there may be spatial non-independence at the spatial scale used in this study, potentially affecting my standard errors.

Still, I believe the occupancy model presented here is general and representative enough of the Central American jaguar populations to effectively identify the drivers of the species' habitat use in the study region, as supported by my model's external validation.

Jaguar population gene flow in northern Central America

In *Chapter 3*, I built upon previous findings from this thesis *(Chapter 2)* and elsewhere (Antonio De La Torre et al. 2018; Villalva & Palomares 2022) which point towards high extinction risk of and lack of connectivity between jaguar populations in Guatemala and Honduras. I focussed on the study of functional population connectivity in northern Central America using various data sources, namely gene flow, aggregated habitat suitability, and expert-based input. Three main findings arose from this third chapter. First, that lowest resistance to jaguar gene flow is associated with vegetation and water sources. Second, that areas of lowest gene flow resistance largely coincide with the location of the JCUs, the main reservoirs of high quality jaguar habitat in the region (Calderón et al. 2022). And third, that my results have two important methodological implications for guiding future work on functional population connectivity, namely that the effects of landscape covariates on gene flow are scale dependent, and that jaguar data based on gene flow offers advantages over aggregated habitat suitability and expert input when studying functional connectivity.

Jaguar gene flow in northern Central America was driven by higher tree cover and vegetation, lower built-up areas, and intermediate distances from water sources. Whereas gene flow seemed mostly driven by availability of shelter habitat (i.e. sites for resting, nursing, protection from humans, and cover for ambush hunting), the high resistance that built-up and non-vegetation provided to gene flow may also encompass the effects of direct human-jaguar interactions common in anthropogenic landscapes. In these landscapes, jaguar populations exhibit lower levels of gene flow (Roques et al. 2016) and increased human-caused mortality via hunting (Jędrzejewski et al. 2017a; Arias et al. 2021), vehicle collisions (Srbek-Araujo et al. 2015), and retaliatory killing (Garcia-Alaniz et al. 2010; Moreno et al. 2015; Jędrzejewski et al. 2017a); the latter being the strongest driver of jaguar extirpation (Jędrzejewski et al. 2017; Villalva & Palomares 2022). Human-caused mortality on carnivore population viability can be significantly large, particularly when it disproportionally affects important demographic groups (i.e. juveniles), and when lack of connectivity restricts demographic rescue (Lamb et al. 2020). Therefore, securing connectivity between jaguar populations in anthropogenic landscapes is a current conservation priority for the long term viability of jaguar populations (de la Torre et al. 2016). Additionally, spatial patterns of functional population connectivity showed that pathways between all JCUs exist but lower connectivity exists between the smallest JCUs (i.e. Sierra Santa Cruz, Sierra de las Minas and Cordillera Nombre de Dios), suggesting conservation attention in the latter areas. Furthermore, patterns of low connectivity were also found in the Caribbean connection between eastern Guatemala and western Honduras, as well as in the Miskito area along Honduras and Nicaragua.

My findings also provide methodological insights for future studies of connectivity. Firstly, gene flow connectivity is different than habitat connectivity and one may not be able to be used as a proxy for the other (Sartor et al. 2022). This is because habitat for permanent establishment does not necessarily correspond to that facilitating dispersal (Mateo-Sánchez et al., 2015; Reding et al., 2013). Secondly, expert-input can be useful for synthesizing ecological knowledge about complex habitat relationships in resistance surface models, however empirical data should be favoured when available, as they provide more optimal estimates of environmental variables (Clevenger et al. 2002; Shirk et al. 2010; Cushman et al. 2013). And lastly, that the effects of landscape covariates on gene flow should be assessed across a wide range of multiple spatial scales (Jackson & Fahrig 2015; Moraga et al. 2019), as I found greatest support for overall broader scale effects and these varied depending on the type of landscape feature. In hindsight, this result is not surprising, given that the spatial scales at which gene flow operates are typically much larger than those for abundance or occurrence (Jackson & Fahrig 2014), the latter two typical inputs for habitat suitability models.

I believe that the model results presented in this chapter are robust enough to assist research and conservation for jaguars, however there are three potential sources that contribute to uncertainty. First, given my small sample size and the lack of empirical data available for the study region, internal validation with cross-validation folds (Row et al. 2017) and external validation of this model were not possible. Whereas this prevented me from quantitatively assessing the uncertainty of my model predictions, I am confident that I addressed most of the main potential sources of this uncertainty by: i) using resistance surfaces that relate to ecological processes (Peterman et al. 2014) and are parameterized with empirical data (Clevenger et al. 2002; Shirk et al. 2010; Cushman et al. 2013), ii) using genetic data, which focuses only on movements relevant for populations' viability (i.e. successful breeding) and that represent the long-term average of effective dispersal, without the restrictions of limited observational periods (Spear et al. 2010); and iii) accounting for spatial-scale dependence and species' dispersal ability in the assessment of connectivity. Second, I was unable to explicitly account for human-caused mortality, a decisive factor in gene flow resistance with important implications for functional connectivity. There is scarce data on anthropogenic jaguar mortality across the species range (Altrichter et al. 2006; Jędrzejewski et al. 2017a; Romero-Muñoz et al. 2019), and even less in Central America (Moreno et al. 2015). Therefore I relied on built-up area and tree cover maps to encompass the effects of this anthropogenic-driven mortality in the absence of appropriate data. I supported this decision on the fact that jaguar extirpation is mostly an anthropogenic-driven mechanism led by deforestation, cattle breeding, and retaliatory killing (Jędrzejewski et al. 2017a; Villalva & Palomares 2022).

The results described above illustrate that anthropogenic landscapes can pose strong barriers for jaguar gene flow and that safeguarding jaguar population connectivity in such landscapes is an important conservation challenge. Overcoming such challenge is essential for securing the long-term viability of jaguar populations in anthropogenic landscapes (de la Torre et al. 2016), as the latter can become lethal for large carnivores when human-carnivore conflict drives high rates of human-caused carnivore mortality (Lamb et al. 2020). This evidence thus suggests that securing viable populations of jaguars across the anthropogenic Central American landscapes also requires fostering human-jaguar conviviality, a subject that I address more thoroughly in the following chapter.

Transformative change for carnivore conservation, insights for human-carnivore conviviality

Ensuring that human and large carnivores coexist peacefully in anthropogenic landscapes is a complex challenge, one that cannot be met without transdisciplinary academic research and cross-sectoral, collaborative governance structures that effectively respond to the multiple challenges of such coexistence (Hartel et al. 2019). With this in mind, I focussed in *Chapter 4* on carnivore conservation initiatives that apply transformative governance approaches to enact transformative change towards human-carnivore conviviality. I reviewed and assessed the large carnivore conservation initiatives published in the last three decades to discuss insights gained for human-carnivore conviviality, and addressing how these insights can guide efforts to promote human-jaguar conviviality in Central America.

Two main results are highlighted in this chapter. One is that few initiatives within the large carnivore conservation and management literature contribute to transformative change by applying transformative governance approaches (1%). The second one is that achieving transformative change towards conviviality requires expanding solutions beyond technocratic interventions which mitigate human-carnivore conflict (e.g. non-lethal tools for carnivore management) towards restoring the human social fabric that supports conviviality. My results evidence that restoring such social fabric is possible via several strategies, and that these include working collaboratively with local actors in ways that empower and help them develop appropriate, legitimate conservation solutions. Such strategies include building solid, equal partnerships with local actors through knowledge co-production and transparent data sharing (Wilson et al. 2017; Salvatori et al. 2020), fostering ownership of conservation decisions and actions (Young et al. 2021), and co-sharing conservation costs, benefits and risks (Mishra et al. 2003; Alexander et al. 2021). Conservation interventions that allowed co-development and shared responsibility of programs were successful in shifting negative attitudes towards carnivore species (Alexander et al. 2022) as well as effectively reducing retaliatory killings and behavioural intent to kill carnivores across diverse landscapes and conditions (Mulder et al. 2019; Alexander et al. 2021, 2022).

Similarly, social conflicts about carnivore management were successfully addressed via governance strategies that promoted collective action, reflection, and dialogue. Actors who were previously in conflict reached consensus over carnivore management actions (Richie et al. 2012; Marino et al. 2021a), working together towards their implementation (Salvatori et al. 2021) when collective action, reflection, and dialogue were promoted in ways that were integrative, inclusive, empowering, and adaptive. Such successful outcomes were achieved even in situations where polarized contexts (Marino et al. 2021a; Salvatori et al. 2021) or contradictory environmental policy existed (Martin 2021), and some of these outcomes were even sustained after conservation interventions ended (Wilson et al. 2017; Young et al. 2021).

My review also identified challenges in implementing conviviality in conservation landscapes, mainly mainstreaming impact evaluation and implementing transdisciplinary conservation actions. Two-thirds of the studies from my literature review evaluated the impacts of their implemented actions, supporting previous findings in coexistence research (Lozano et al. 2019). The limitations that contributed to this challenge were the existence of potential confounding factors (Mulder et al. 2019; de la Torre et al. 2021), lack of baseline data (Mulder et al. 2019; Marino et al. 2021; Alexander et al. 2022), limited human and financial resources (Mulder et al. 2019), and difficulties to measure direct indicators of impact (e.g. number of carnivores killed illegally; Mulder et al. 2019; Alexander et al. 2021), particularly for intangible indicators and outcomes (Marino et al. 2021; Young et al. 2021; Salvatori et al. 2021). Despite these obstacles, evaluations were successfully tailored in most of the conservation initiatives reviewed, providing robust results that supported adaptive management even in contexts with small local capacity and limited resources were available for evaluation (Chausson et al. 2022).

The second challenge, transdisciplinary conservation was reflected in the fact that most of the studies reviewed failed to integrate different disciplines into conservation solutions and impact assessments. Most studies addressed conservation issues from either an ecological or social perspective (99% of the published articles did not met our selection criteria for this reason), and the impact assessments in the selected studies (1% of the studies which met my criteria), when available, remained either exclusively quantitative or qualitative. These results evidence the ongoing challenges in overcoming artificial boundaries between disciplines (Kothari 2014; Steffen et al. 2018), and especially in incorporating social science into conservation initiatives (Niemiec et al. 2021). Nonetheless, the value of social science theories and methods in carnivore conservation was evidenced in the reviewed studies, as they helped identify the political and social processes that prevented (Richie et al. 2012) or favoured human-carnivore conviviality (Wilson et al. 2017; Young et al. 2021), as well as the legitimate conservation actions that promoted conviviality without promoting social conflict (Marino et al. 2021a).

Examples of human-jaguar conviviality driven by transformative governance approaches, similar to those highlighted above, exist across the species' range. In the Amazon, cattle ranchers coexist peacefully with jaguars through a combination of mechanisms implemented to i) prevent carnivore and native prey hunting, ii) offset the financial losses due to livestock predation by jaguars via active involvement of ranchers in jaguar-based ecotourism. This combination of a technocratic approach with a co-sharing of conservation costs, benefits and risks made possible that cattle ranch landscapes could sustain similar or higher jaguar densities than those sustained in unmodified forest landscapes (Devlin et al. 2023).

In Guyana, human-jaguar conviviality is supported through a community-based research program grounded on transparency, local knowledge, co-creation of conservation goals and co-production of knowledge. This participatory research program, similarly to the successful conservation initiatives found in my review, fostered equal partnerships with local communities and built mutual trust by encouraging dialogue, feedback and learning, which ultimately led to adaptive management. Furthermore, following a convivial conservation approach which advocates social and environmental justice, this conservation initiative respected the cultural identity of the local people and empowered them to claim and exercise their rights while also improving peoples' food security and overall living conditions (FAO & IUCN SSC HWCTF 2022).

Also in Costa Rica, a conservation initiative for coexisting with jaguars was developed using a bottom-up approach based on the needs and concerns of local people. This initiative involved the development of a diverse incentive program which was co-developed with local actors and based on the principles of inclusivity, equity and transdisciplinarity. Whereas such program was not yet implemented, the transformative governance approach used for its design promoted social learning and helped develop mutual trust, a collaborative environment which prevented conflict and facilitated decision-making (Amit & Jacobson 2018).

Other valuable cases of local engagement in jaguar research and conservation exist. Examples of these are conflict mitigation programs co-designed and co-implemented with cattle ranchers in Mexico (de la Torre et al. 2021), or community-based jaguar research and monitoring in Mexico (Lavariega et al. 2020) and Brazil (Valsecchi et al. 2022). These efforts have successfully decreased cattle predation by jaguars in the local communities intervened, and they have also engaged local actors in research allowing valuable data collection on the conservation status of jaguars and on sensitive subjects such as jaguar hunting. Whereas such initiatives haven't been embedded in a broader context of human-jaguar conviviality, with further steps they could be implemented in diverse ways to effectively promote such goal. Such further steps are discussed in more detail in the section of conservation implications below.

Conservation implications of thesis

This thesis provides several key insights into how to improve conservation of jaguars in Central America. It provides tools that conservation managers and stakeholders may use to implement local actions but also make broad scale conservation decisions for securing habitat *(Chapter 2)* and population connectivity *(Chapter 3)*, but also for enacting transformative changes towards human-jaguar conviviality that lead to more just, equitable, and sustainable futures *(Chapter 4)*. Securing habitat for jaguars could be achieved by habitat loss prevention actions focused on the largest JCUs with highest habitat coverage: Selva Maya (Mexico-Guatemala-Belize), Reserva de Biosfera Transfronteriza (Honduras-Nicaragua), Cerro Silva-Indio Maiz-Tortuguero (Nicaragua-Costa Rica), Talamanca-Cordillera Central (Costa Rica), and Chagres-Darien (Panama).

In parallel, human pressure mitigation efforts should be targeted at the smaller JCUs with less remaining habitat coverage: Sierra Santa Cruz and Sierra Minas (Guatemala), Cordillera Nombre de Dios (Honduras), and Guanacaste (Costa Rica). Habitat restoration efforts can also be implemented to improve connectivity, and such efforts should be prioritized in two general areas i) central Costa Rica and central Panama, where most habitat suitability has been lost; and ii) eastern-Guatemala and western-Honduras. This latter area is of great importance for the wide-range connectivity of jaguar populations due to two reasons. First, it connects the two largest JCUs in Central America, including the largest continuous Neotropical forest north of the Amazon (i.e. Reserva de Biosfera Transfronteriza and the Trinational Selva Maya); and second, it connects the northern and southern ranges of the species (Rabinowitz & Zeller, 2010).

Useful conservation strategies that could support the aims listed above, encourage sustainable land management regimes more compatible with jaguar conservation, and integrate local actors and stakeholders better are: i) implementing conservation schemes such as indigenous/community managed reserves (Mena et al. 2020; Figel et al. 2022) and forestry concessions (Tobler et al. 2018) in the buffer zones of the JCUs and protected areas; ii) implement incentive programs to foster human-jaguar conviviality in anthropogenic landscapes critical for population connectivity, implementing proposals already existing (Amit & Jacobson 2018), or others which can be further developed and implemented within already existing international schemes (Hyde et al. 2022).

Furthermore, implementing 'convivial conservation' approaches (Büscher & Fletcher 2020) grounded in transformative governance principles that lead to more just, equitable, and sustainable futures (Temper et al. 2018; Visseren-Hamakers et al. 2021) in Central America would be of great benefit for jaguar conservation in the region. The spatially-explicit maps for management of key areas of habitat suitability *(Chapter 2)* and gene flow *(Chapter 3)* offer the foundations for such spatial prioritization. A concrete venue for advancing this goal would be the establishment of solid partnerships with indigenous communities, as suggested by Figel et al. (2022), leveraging jaguar conservation using the transformational values and stewardship capabilities of such communities (see Figel et al. 2011), specifically targeting the areas in which loss of habitat *(Chapter 2)* and/or population connectivity *(Chapter 3)* threaten the long term viability of jaguar populations. Indigenous groups have largely maintained the jaguar habitat and connectivity across the Americas, with up to 39% of the species range and the JCU lands overlapping with indigenous territories (IT), which at least in South America also exhibit significant lower rates of deforestation in comparison to private lands (Figel et al. 2022).

Examples of specific conservation initiatives that could be implemented in such partnerships are i) co-development and implementation of incentive programs to coexist with jaguars (Amit & Jacobson 2018), and ii) co-production of knowledge to fill research conservation gaps (de la Torre et al. 2016), such as the study of jaguar anthropogenic mortality (see Valsecchi et al. 2022) and the monitoring of jaguar population sizes and trends within JCUs and corridor areas. This suggested approach would be ideal for enacting transformative change towards human-jaguar conviviality via transformative governance as it would allow: i) inclusivity, by allowing the empowerment of indigenous groups who are underrepresented in conservation and who usually relate in asymmetric power relationships with conservationists (Saif et al. 2022); ii) transdisciplinarity, by recognizing indigenous values and knowledge which are currently underrepresented in conservation but hold transformative values of conviviality (e.g. ‘Buen Vivir’, ‘Communitarian feminism’; Khothari et al. 2019); iii) adaptation, if conservation initiatives were co-developed with local communities while fostering dialogue, reflection and learning to allow adaptation of actions to changes in local contexts (see FAO & IUCN SSC HWCTF 2022); and iv) integration, by implementing initiatives across sites and scales in Central America.

Conclusions

My thesis advances jaguar conservation research in different but complementary ways. *Chapter 2* provides the first broad-scale quantitative analysis of jaguar habitat use in Central America which uses a comprehensive camera-trap dataset that represents reliable presence-based evidence of jaguars for the region− a region which has been significantly underrepresented in recent range-wide studies (Thompson et al. 2021). It also offers advantages over previous regional studies because the latter either did not explicitly account for sampling bias (i.e. jaguar detection probability; Jędrzejewski et al. 2018), or relied on more widely available interview-derived data (Petracca et al. 2018). *Chapter 3* presents the first study of jaguar gene flow and functional connectivity across spatial scales, heterogeneous landscapes, and a large regional extent of conservation concern in Central America. It also provides spatially explicit, synoptic connectivity maps for jaguar populations in the region, accounting for the dispersal ability of the species and spatial scale dependence in jaguar-landscape interactions, both steps neglected in previous studies but critical for drawing robust conclusions and improving management inputs that support habitat and population connectivity management efforts (Jackson & Fahrig 2015; Krishnamurthy et al.

2016). Lastly, *Chapter 4* contributes to a deeper understanding of the broader social, political, and economic contexts in which conviviality with large carnivores occurs, while identifying concrete pathways to promote this conviviality by supporting more inclusive, collaborative forms of conservation participation and decision making.

The future of large carnivore research and conservation shall be transdisciplinary and it will require a ‘cross fertilization’ between the natural and social sciences (Hovardas et al. 2021). With this thesis I hope I can contribute both practically and conceptually to advancing this vision for jaguar conservation in Central America.

REFERENCES

Adloff F, Caillé A. 2022. Convivial Futures. Views from a Post-Growth Tomorrow. Transcript, Verlag, Bielefeld.

Aide TM, Clark ML, Grau HR, López-Carr D, Levy MA, Redo D, Bonilla-Moheno M, Riner G, Andrade-Núñez MJ, Muñiz M. 2013. Deforestation and Reforestation of Latin America and the Caribbean (2001-2010). Biotropica 45:262–271.

Alexander JS, Agvaantseren B, Gongor E, Mijiddorj TN, Piaopiao T, Redpath S, Young J, Mishra C. 2021. Assessing the Effectiveness of a Community-based Livestock Insurance Program. Environmental Management 68:87–99.

Alexander JS, Bijoor A, Gurmet K, Murali R, Mishra C, Suryawanshi KR. 2022. Engaging women brings conservation benefits to snow leopard landscapes. Environmental Conservation 49:180–186.

Altrichter M, Boaglio G, Perovic P. 2006. The decline of jaguars Panthera onca in the Argentine Chaco. Oryx 40:302–309.

Amit R, Jacobson SK. 2018. Participatory development of incentives to coexist with jaguars and pumas. Conservation Biology 32:938–948.

Antonio De La Torre J, González-Maya JF, Zarza H, Ceballos G, Medellín RA. 2018. The jaguar's spots are darker than they appear: Assessing the global conservation status of the jaguar Panthera onca. Oryx 52:300–315.

Arias M, Hinsley A, Nogales-Ascarrunz P, Carvajal-Bacarreza PJ, Negroes N, Glikman JA, Milner-Gulland EJ. 2021. Complex interactions between commercial and noncommercial drivers of illegal trade for a threatened felid. Animal Conservation 24:810–819.

Athreya V, Odden M, Linnell JDC, Krishnaswamy J, Karanth U. 2013. Big Cats in Our Backyards: Persistence of large carnivores in a human dominated landscape in India. PLoS ONE 8:e57872.

Auffret AG, Plue J, Cousins SAO. 2015. The spatial and temporal components of functional connectivity in fragmented landscapes. Ambio 44:51–59.

Baguette M, Van Dyck H. 2007. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. Landscape Ecology 22:1117–1129.

Barkin D, Sánchez A. 2020. The communitarian revolutionary subject: new forms of social transformation. Third World Quarterly 41:1421–1441.

Bartoń KA, Zwijacz-Kozica T, Zięba F, Sergiel A, Selva N. 2019. Bears without borders: Long-distance movement in human-dominated landscapes. Global Ecology and Conservation 17:1–8.

Baylis K, Honey-Rosés J, Börner J, Corbera E, Ezzine-de-Blas D, Ferraro PJ, Lapeyre R, Persson UM, Pfaff A, Wunder S. 2016. Mainstreaming impact evaluation in nature conservation. Conservation Letters 9:58–64.

Belkhir K, Borsa P, Chikhi L, Raufaste N, Bonhomme F. 2001. GENETIX 4.05, logiciel sous Windows TM pour la genetique des populations. nome, populations, interactions, CNRS UMR 5000, Université de Montpellier II, Montpellier, France. Available from https://kimura.univ-montp2.fr/genetix/.

Blythe J, Silver J, Evans L, Armitage D, Bennett NJ, Moore M, Morrison TH, Brown K. 2018. The dark side of transformation: latent risks in contemporary sustainability discourse. Antipode 50:1206–1223.

Boitani L, Maiorano L, Baisero D, Falcucci A, Visconti P, Rondinini C. 2011. What spatial data do we need to develop global mammal conservation strategies? Philosophical Transactions of the Royal Society B: Biological Sciences 366:2623.

Bonte D et al. 2012. Costs of dispersal. Biological Reviews 87:290–312.

Boronyak L, Jacobs B, Wallach A, McManus J, Stone S, Stevenson S, Smuts B, Zaranek H. 2022. Pathways towards coexistence with large carnivores in production systems. Agriculture and Human Values 39:47–64.

Braczkowski AR, Bryan CJO, Lessmann C, Rondinini C. 2023. The unequal burden of human-wildlife conflict. Communications Biology 6:1–9.

Bull JK, Heurich M, Saveljev AP, Schmidt K, Fickel J, Förster DW. 2016. The effect of reintroductions on the genetic variability in Eurasian lynx populations: the cases of Bohemian–Bavarian and Vosges–Palatinian populations. Conservation Genetics 17:1229–1234.

Burch S, Shaw A, Dale A, Robinson J, Burch S, Shaw A, Dale A, Triggering JR. 2014. Triggering transformative change : a development path approach to climate change response in communities Triggering transformative change : a development path approach to climate change response in communities. Climate Policy 0:1–21.

Burnham KP, Anderson DR. 2002. Model Selection and Multimodel Inference - A Practical Information-Theoretic Approach. Second. Springer-Verlag New York, New York, USA. Available from http://www.springer.com/us/book/9780387953649 (accessed May 30, 2015).

Burton AC, Sam MK, Kpelle DG, Balangtaa C, Buedi EB, Brashares JS. 2011. Evaluating persistence and its predictors in a West African carnivore community. Biological Conservation 144:2344–2353.

Büscher B, Fletcher R. 2020. The conservation revolution: radical ideas for saving nature beyond the Anthropocene. Verso Trade, London, UK.

Büscher B, Robert Fletcher. 2019. Towards Convivial Conservation. Conservation & Society 17:283–296.

Butler JRA, Young JC, McMyn IAG, Leyshon B, Graham IM, Walker I, Baxter JM, Dodd J, Warburton C. 2015. Evaluating adaptive co-management as conservation conflict resolution: Learning from seals and salmon. Journal of Environmental Management 160:212–225.

Cabeza M, Araujo MB, Wilson RJ, Thomas CD, Cowley MJR, Moilanen A. 2004. Combining probabilities of occurrence with spatial reserve design. Journal of Applied Ecology 41:252–262.

Calderón AP et al. 2022. Occupancy models reveal potential of conservation prioritization for Central American jaguars. Animal Conservation 25:680–691.

Camino M, Thompson J, Andrade L, Cortez S, Matteucci SD, Altrichter M. 2020. Using local ecological knowledge to improve large terrestrial mammal surveys, build local capacity and increase conservation opportunities. Biological Conservation 244:108450.

Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-emonds ORP, Sechrest W, Orme CDL, Purvis A. 2005. Multiple causes of high extinction risk in large mammal species. Science 309:1239–1242.

Cardillo M, Purvis A, Sechrest W, Gittleman JL, Bielby J, Mace GM. 2004. Human population density and extinction risk in the world's carnivores. PLoS Biology 2: 909-914.

Carter NH, Linnell JDC. 2016. Co-adaptation is key to coexisting with large carnivores. Trends in Ecology and Evolution 31:575–578.

Castillo A, Bullen-Aguiar AA, Peña-Mondragón JL, Gutiérrez-Serrano NG. 2020. The social component of social-ecological research: Moving from the periphery to the center. Ecology and Society 25:6.

Cavalcanti SMC, Gese EM. 2010. Kill rates and predation patterns of jaguars (Panthera onca) in the southern Pantanal, Brazil. Journal of Mammalogy 91:722–736.

Chan KMA et al. 2020. Levers and leverage points for pathways to sustainability. People and Nature 2:693–717.

Chapron G et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346:1517–1519.

Chausson A, Gurd H, Foley J, Bhalla S, Lekilelei J, Otieno T, Lejale B, Lenasalia P, Milner-Gulland EJ. 2022. Evaluating the impact of Warrior Watch: Behaviour change to promote human-lion coexistence. Biological Conservation 271: 109571.

Chinchilla S, van der Berghe E, Polisar J, Arevalo C, Bonacic C. 2022. Livestock – Carnivore Coexistence: Moving beyond. Animals 12:1–15.

Chua L et al. 2020. Conservation and the social sciences: Beyond critique and co-optation. A case study from orangutan conservation. People and Nature 2:42–60.

Cimatti M et al. 2021. Large carnivore expansion in Europe is associated with human population density and land cover changes. Diversity and Distributions 27:602–617.

Clark DA, Slocombe DS. 2011. Grizzly Bear conservation in the Foothills Model Forest: appraisal of a collaborative ecosystem management effort. Policy Sciences 44:1–11.

Clark TW, Wallace R. 1999. The professional in endangered species conservation: an introduction to standpoint clarification. Endangered Species Update 16:9–13.

Clevenger AP, Wierzchowski J, Chruszcz B, Gunson K. 2002. GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. Conservation Biology 16:503–514.

Conde DA, Colchero F, Zarza H, Christensen NL, Sexton JO, Manterola C, Chávez C, Rivera A, Azuara D, Ceballos G. 2010. Sex matters: Modeling male and female habitat differences for jaguar conservation. Biological Conservation 143:1980–1988.

Cook CN, Hockings M, Carter RW. 2010. Conservation in the dark? The information used to support management decisions. Frontiers in Ecology and the Environment 8:181–188.

Cox TR, Butler JRA, Webber AD, Young JC. 2020. The ebb and flow of adaptive co-management: A longitudinal evaluation of a conservation conflict. Environmental Science and Policy 114:453–460.

Cushman SA, Elliot NB, Macdonald DW, Loveridge AJ. 2016. A multi-scale assessment of population connectivity in African lions (Panthera leo) in response to landscape change. Landscape Ecology 31:1337–1353.

Cushman SA, Landguth EL. 2010. Scale dependent inference in landscape genetics. Landscape Ecology 25:967–979.

Cushman SA, Lewis JS. 2010. Movement behavior explains genetic differentiation in American black bears. Landscape Ecology 25:1613–1625.

Cushman SA, Mcrae B, Adriaensen F, Beier P, Shirley M, Zeller K. 2013. Biological corridors and connectivity. Key Topics in Conservation Biology 2:384–404.

Darimont CT, Paquet PC, Treves A, Artelle KA, Chapron G. 2018. Political populations of large carnivores. Conservation Biology 32:747–749.

De Angelo C, Paviolo A, Wiegand T, Kanagaraj R, Di Bitetti MS. 2013. Understanding species persistence for defining conservation actions: A management landscape for jaguars in the Atlantic Forest. Biological Conservation 159:422–433.

de Koning S, Boezeman D, Kaufmann M, Visseren-Hamakers IJ. 2023. Transformative change for biodiversity: A review on the contribution of landscape-oriented partnerships. Biological Conservation 277: 109858.

de la Torre JA, Camacho G, Arroyo-Gerala P, Cassaigne I, Rivero M, Campos-Arceiz A. 2021. A cost-effective approach to mitigate conflict between ranchers and large predators: A case study with jaguars in the Mayan Forest. Biological Conservation 256: 109066.

de la Torre JA, Ceballos G, Chávez C, Zarza H, Medellín RA. 2016. Prioridades y recomendaciones ¿Cuáles son las necesidades para el jaguar en los próximos años? Pages 495–505 in Medellín R, de la Torre A, Zarza H, Chávez C, Ceballos G, editors. El jaguar en el siglo XXI. La perspectiva continental. Ediciones Científicas Universitarias. México D.F., México.

de la Torre JA, Núñez JM, Medellín RA. 2017. Habitat availability and connectivity for jaguars (Panthera onca) in the Southern Mayan Forest: Conservation priorities for a fragmented landscape. Biological Conservation 206:270–282.

de la Torre JA, Rivero M. 2019. Insights of the Movements of the Jaguar in the Tropical Forests of Southern Mexico. Pages 217–241 Movement Ecology of Neotropical Forest Mammals. Springer International Publishing, Cham. Available from http://link.springer.com/10.1007/978-3-030-03463-4_13 (accessed February 11, 2019).

Devlin AL, Frair JL, Hoogesteijn R, Quigley HB, Tortato FR, Hunter LTB, Robinson N, Robinson HS. 2023. Drivers of large carnivore density in non-hunted, multi-use landscapes. Conservation Science and Practice 5:1–13.

Díaz S et al. 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. Science 366:1–10.

Dietsch AM, Teel TL, Manfredo MJ. 2016. Social values and biodiversity conservation in a dynamic world. Conservation Biology 30:1212–1221.

Dixon JD, Oli MK, Wooten MC, Eason TH, McCown JW, Cunningham MW. 2007. Genetic consequences of habitat fragmentation and loss: The case of the Florida black bear (Ursus americanus floridanus). Conservation Genetics 8:455–464.

Doherty TS, Driscoll DA. 2018. Coupling movement and landscape ecology for animal conservation in production landscapes. Proceedings. Biological sciences 285:20172272.

Duarte HOB, Carvalho WD, de Toledo JJ, Rosalino LM. 2023. Big cats like water: occupancy patterns of jaguar in a unique and insular Brazilian Amazon ecosystem. Mammal Research. Available from https://doi.org/10.1007/s13364-023-00681-7.

Ehrlich PR, Pringle RM. 2008. Where does biodiversity go from here? A grim business-as-usual forecast and a hopeful portfolio of partial solutions. Proceedings of the National Academy of Sciences of the United States of America 105:11579–11586.

Eizirik E, Kim JH, Menotti-Raymond M, Crawshaw PG, O'Brien SJ, Johnson WE. 2001. Phylogeography, population history and conservation genetics of jaguars (Panthera onca, Mammalia, Felidae). Molecular ecology 10:65–79.

Elliot NB, Cushman SA, Macdonald DW, Loveridge AJ. 2014. The devil is in the dispersers: predictions of landscape connectivity change with demography. Journal of Applied Ecology 51:1169–1178.

Ens E, Victoria Reyes-García HA, Hsu M, Reimerson E, Reihana K, Sithole B, Shen X, Cavanagh V, Adams M. 2021. Recognition of Indigenous ecological knowledge systems in conservation and their role to narrow the knowledge-implementation gap. Pages 109–139 in Ferreira CC, Klütsch CFC, editors. Closing the knowledge-implementation gap in conservation science. Interdisciplinary evidence transfer across sectors and spatiotemporal scales wildlife R. Springer, Svanvik, Norway.

Ernest HB, Vickers TW, Morrison SA, Buchalski MR, Boyce WM. 2014. Fractured genetic connectivity threatens a Southern California puma (Puma concolor) population. PLoS ONE 9: e107985.

ESA. 2015. ESA CCI Global Land cover. Available from https://www.esa-landcover-cci.org/?q=node/164 (accessed June 26, 2019).

Espinosa S, Jacobson SK. 2012. Human-wildlife conflict and environmental education: evaluating a community program to protect the Andean Bear in Ecuador. Journal of Environmental Education 43:55–65.

ESRI. 2022. ArcGIS Desktop. Environmental Systems Research Institute, Redlands, CA.

Fabinyi M, Evans L, Foale SJ. 2014. Social-ecological systems, social diversity, and power: Insights from anthropology and political ecology. Ecology and Society 19:28.

FAO, IUCN SSC HWCTF. 2022. Reducing human-carnivore conflict through participatory research. Roma, Italy. Available from https://www.hwctf.org/_files/ugd/7acc16_eb36aec416fc497296beab914ea0af87.pdf.

Fernández-Gil A, Naves J, Ordiz A, Quevedo M, Revilla E. 2016. Conflict misleads large carnivore management and Conservation: Brown bears and wolves in Spain. PloS one 11:1–13.

Fernández J, Carlos S. 2022. Conservation status of the world's carnivorous mammals (order Carnivora). Mammalian Biology 102:1911–1925.

Ferreira GB, Collen B, Newbold T, Oliveira MJR, Pinheiro MS, de Pinho FF, Rowcliffe M, Carbone C. 2020. Strict protected areas are essential for the conservation of larger and threatened mammals in a priority region of the Brazilian Cerrado. Biological Conservation 251:108762.

Ferrier S. 2002. Mapping Spatial Pattern in Biodiversity for Regional Conservation Planning: Where to from Here? Systematic Biology 51:331–363.

Figel JJ, Botero-Cañola S, Forero-Medina G, Sánchez-Londoño JD, Valenzuela L, Noss RF. 2019. Wetlands are keystone habitats for jaguars in an intercontinental biodiversity hotspot. PLOS ONE 14:e0221705.

Figel JJ, Botero-Cañola S, Lavariega MC, Luna-Krauletz MD. 2022. Overlooked jaguar guardians: Indigenous territories and range-wide conservation of a cultural icon. Ambio 51:2532–2543.

Figel JJ, Castañeda F, Patricia Calderón A, Antonio de la Torre J, García-Padilla E, Noss RF, la Torre de. 2018. Threatened amphibians sheltered under the big cat's umbrella: conservation of jaguars Panthera onca (Carnivora: Felidae) and endemic herpetofauna in Central America. Revista de Biologia Tropical 66: 1741-1753

Figel JJ, Durán E, Bray DB. 2011. Conservation of the jaguar Panthera onca in a community-dominated landscape in montane forests in Oaxaca, Mexico. Oryx 45:554–560.

Figueroa OA. 2013. The ecology and conservation of jaguars (Panthera onca) in Central Belize: conservation status, diet, movement patterns and habitat use. University of Florida. Available from https://ufdc.ufl.edu/UFE0045191/00001.

Fiske I, Chandler R. 2011. unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. Journal of Statistical Software 43. Available from http://www.jstatsoft.org/v43/i10/ (accessed February 19, 2018).

Foster RJ, Harmsen BJ, Doncaster CP. 2010. Habitat Use by sympatric jaguars and pumas across a gradient of human disturbance in Belize. Biotropica 42:724–731.

Fritz SA, Eronen JT, Schnitzler J, Hof C, Janis CM, Mulch A, Böhning-Gaese K, Graham CH. 2016. Twenty-million-year relationship between mammalian diversity and primary productivity. Proceedings of the National Academy of Sciences of the United States of America 113:10908–10913.

Gaitán CA, González-Castillo VR, Guzmán-Flores GD, Aguilera AL, García MJ. 2020. Visitation patterns of jaguars Panthera onca (Carnivora: Felidae) to isolated water ponds in a tropical forest landscape. THERYA 12:45–55.

Garcia-Alaniz N, Naranjo EJ, Mallory FF. 2010. Human-felid interactions in three mestizo communities of the Selva Lacandona, Chiapas, Mexico: Benefits, conflicts and traditional uses of species. Human Ecology 38:451–457.

Gonthier DJ, Castañeda FE. 2013. Large- and medium-sized mammal survey using camera traps in the Sikre River in the Río Plátano biosphere reserve, Honduras. Tropical Conservation Science 6:584–591.

Goslee SC, Urban DL. 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software 22:1–19.

Greving H, Bruckermann T, Kimmerle J. 2020. This is my project! The influence of involvement on psychological ownership and wildlife conservation. Current Research in Ecological and Social Psychology 1:100001.

Guillera-Arroita G, Lahoz-Monfort JJ, MacKenzie DI, Wintle BA, McCarthy MA. 2014. Ignoring imperfect detection in biological surveys is dangerous: a response to "fitting and interpreting occupancy models". PloS one 9:e99571.

Guisan A, Thuiller W, Zimmermann NE. 2017. Habitat Suitability and Distribution Models. Cambridge University Press, Cambridge. Available from http://ebooks.cambridge.org/ref/id/CBO9781139028271 (accessed April 17, 2020).

Haag T, Santos AS, Sana DA, Morato RG, Cullen L, Crawshaw PG, De Angelo C, Di Bitetti MS, Salzano FM, Eizirik E. 2010. The effect of habitat fragmentation on the genetic structure of a top predator: Loss of diversity and high differentiation among remnant populations of Atlantic Forest jaguars (Panthera onca). Molecular Ecology 19:4906–4921.

Haddad NM et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:1–10.

Hartel T, Scheele BC, Vanak AT, Rozylowicz L, Linnell JDC, Ritchie EG. 2019. Mainstreaming human and large carnivore coexistence through institutional collaboration. Conservation Biology 33:1256–1265.

Hazzah L, Dolrenry S, Naughton L, Edwards CTT, Mwebi O, Kearney F, Frank L. 2014. Efficacy of two lion conservation programs in Maasailand, Kenya. Conservation Biology 28:851–860.

Heimlich JE, Ardoin NM. 2008. Understanding behavior to understand behavior change: a literature review. Environmental Education Research 14:215–237.

Hernández Potosme SM. 2019. Factores del paisaje que influyen en la distribución de jaguares: Contribución de línea base para proponer una Unidad de Conservación del Jaguar, Nicaragua. Centro Agronómico Tropical de Investigación y Enseñanza.

Holderegger R, Wagner HH. 2008. Landscape Genetics. BioScience 58:199–207.

Hovardas T. 2020. A Social Learning Approach for stakeholder engagement in large carnivore conservation and management. Frontiers in Ecology and Evolution 8:1–19.

Hovardas T, Penteriani V, Trouwborst A, López-Bao JV. 2021. Editorial: Conservation and management of large carnivores—local insights for global challenges. Frontiers in Ecology and Evolution 9:1–3.

Hyde M, Boron V, Rincón S, Viana DFP, Larcher L, Reginato GA, Payán E. 2022. Refining carbon credits to contribute to large carnivore conservation: The jaguar as a case study. Conservation Letters 15:1–7.

Immonen E, Husby A. 2016. Norway wolf cull will hit genetic diversity. Nature 539:31.

Ingeman KE et al. 2022. Glimmers of hope in large carnivore recoveries. Scientific Reports 12:1–13.

Inskip C, Ridout M, Fahad Z, Tully R, Barlow A, Barlow CG, Islam MA, Roberts T, MacMillan D. 2013. Human-Tiger Conflict in Context: Risks to Lives and Livelihoods in the Bangladesh Sundarbans. Human Ecology 41:169–186.

Inskip C, Zimmermann A. 2009. Human-felid conflict: a review of patterns and priorities worldwide. Oryx 43:18.

IUCN. 2012. IUCN red list categories and criteria: version 3.1. Gland, Switzerland and Cambridge, United Kingdom. Available from https://portals.iucn.org/library/sites/library/files/documents/RL-2001-001-2nd.pdf (accessed October 20, 2021).

Jackson HB, Fahrig L. 2015. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24:52–63.

Jackson ND, Fahrig L. 2014. Landscape context affects genetic diversity at a much larger spatial extent than population abundance. Ecology 95:871–881.

Jędrzejewski W et al. 2018. Estimating large carnivore populations at global scale based on spatial predictions of density and distribution - Application to the jaguar (Panthera onca). PLoS ONE 13:1–25.

Jędrzejewski W et al. 2017a. Human-jaguar conflicts and the relative importance of retaliatory killing and hunting for jaguar (Panthera onca) populations in Venezuela. Biological Conservation 209:524–532.

Jędrzejewski W et al. 2017b. Predicting carnivore distribution and extirpation rate based on human impacts and productivity factors; assessment of the state of jaguar (Panthera onca) in Venezuela. Biological Conservation 206:132–142.

Jedrzejewski W, Jedrzejewska B. 1996. Rodent cycles in relation to biomass and productivity of ground vegetation and predation in the Palearctic. Acta Theriologica 41:1–34.

Jordan CA, Schank CJ, Urquhart GR, Dans AJ. 2016. Terrestrial Mammal Occupancy in the Context of Widespread Forest Loss and a Proposed Interoceanic Canal in Nicaragua's Decreasingly Remote South Caribbean Region. PloS one 11:e0151372.

Jürgens UM, Grinko M, Szameitat A, Hieber L, Fischbach R, Hunziker M. 2023. Managing wolves is managing narratives: views of wolves and nature shape people's proposals for navigating human-wolf relations. Human Ecology 51:35–57.

Kanda CZ, Oliveira-Santos LGR, Morato RG, de Paula RC, Rampim LE, Sartorello L, Haberfeld M, Galetti M, Cezar Ribeiro M. 2019. Spatiotemporal dynamics of conspecific movement explain a solitary carnivore's space use. Journal of Zoology 308:66–74.

Kantek DLZ et al. 2021. Jaguars from the Brazilian Pantanal: Low genetic structure, male-biased dispersal, and implications for long-term conservation. Biological Conservation 259:109153.

Kei Otsuki. 2015. Transformative Sustainable Development. Participation, reflection and change. Routledge Home. Taylor and Francis Group, NY, USA.

Kellner K. 2021. Package ubms: Bayesian Models for Data from Unmarked Animals using "Stan." Available from https://kenkellner.com/ubms/.

Kéry M, Gardner B, Monnerat C. 2010. Predicting species distributions from checklist data using site-occupancy models. Journal of Biogeography 37:1851–1862.

Khothari A, Salleh A, Escobar A, Demaria F, Acosta A, editors. 2019. Pluriverse. A post-Development Dictionary. Tulika Books and Authorsupfront, New Delhi, India.

Kimmig SE et al. 2020. Beyond the landscape: Resistance modelling infers physical and behavioural gene flow barriers to a mobile carnivore across a metropolitan area. Molecular Ecology 29:466–484.

Klees van Bommel J, Badry M, Ford AT, Golumbia T, Burton AC. 2020. Predicting human-carnivore conflict at the urban-wildland interface. Global Ecology and Conservation 24:e01322.

Klütsch CFC, Ferreira CC. 2021. Closing the gap between knowledge and implementation in conservation science:Cconcluding remarks. Pages 457–473 in Ferreira CC, Klütsch CFC, editors. Closing the Knowledge-Implementation Gap in Conservation ScienceWildlife R. Springer, Svanvik, Norway.

Knott EJ, Bunnefeld N, Huber D, Reljić S, Kereži V, Milner-Gulland EJ. 2014. The potential impacts of changes in bear hunting policy for hunting organisations in Croatia. European Journal of Wildlife Research 60:85–97.

König HJ, Kiffner C, Kramer-Schadt S, Fürst C, Keuling O, Ford AT. 2020. Human–wildlife coexistence in a changing world. Conservation Biology 34:786–794.

Kothari A. 2014. Radical Ecological Democracy: A path forward for India and beyond. Development (Basingstoke) 57:36–45.

Kramer-Schadt S, Revilla E, Wiegand T. 2005. Lynx reintroductions in fragmented landscapes of Germany: Projects with a future or misunderstood wildlife conservation? Biological Conservation 125:169–182.

Kramer-Schadt S, Revilla E, Wiegand T, Breitenmoser U. 2004. Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. Journal of Applied Ecology 41:711–723.

Krishnamurthy R, Cushman SA, Sarkar MS, Malviya M, Naveen M, Johnson JA, Sen S. 2016. Multi-scale prediction of landscape resistance for tiger dispersal in central India. Landscape Ecology 31:1355–1368.

Laikre L et al. 2022. Planned cull endangers Swedish wolf population. Science 377:162–163.

Lamb CT, Ford AT, McLellan BN, Proctor MF, Mowat G, Ciarniello L, Nielsen SE, Boutin S. 2020. The ecology of human–carnivore coexistence. Proceedings of the National Academy of Sciences of the United States of America 117:17876–17883.

Lavariega MC, Ríos-Solís JA, Flores-Martínez JJ, Galindo-Aguilar RE, Sánchez-Cordero V, Juan-Albino S, Soriano-Martínez I. 2020. Community-Based Monitoring of Jaguar (Panthera onca) in the Chinantla Region, Mexico. Tropical Conservation Science 13:1-16.

Lecis R et al. 2022. Main roads and land cover shaped the genetic structure of a Mediterranean island wild boar population. Ecology and Evolution 12:1–13.

Lehner B, Döll P. 2004. Development and validation of a global database of lakes, reservoirs and wetlands. Journal of Hydrology 296:1–22.

Lemos MC et al. 2018. To co-produce or not to co-produce. Nature Sustainability 1:722–724.

Li J et al. 2020. Defining priorities for global snow leopard conservation landscapes. Biological Conservation 241:108387.

Liu C, Berry PM, Dawson TP, Pearson RG. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393.

Long HA, French DP, Brooks JM. 2020. Optimising the value of the critical appraisal skills programme (CASP) tool for quality appraisal in qualitative evidence synthesis. Research Methods in Medicine & Health Sciences 1:31–42.

Lorenzana G, Heidtmann L, Haag T, Ramalho E, Dias G, Hrbek T, Farias I, Eizirik E. 2020. Large-scale assessment of genetic diversity and population connectivity of Amazonian jaguars (Panthera onca) provides a baseline for their conservation and monitoring in fragmented landscapes. Biological Conservation 242:108417.

Lowe WH, Allendorf FW. 2010. What can genetics tell us about population connectivity ? Molecular Ecology 19:3038–3051.

Lozano J, Olsza A, Morales-reyes Z, Antonio A, Malo AF, Moleón M, Sánchez-zapata JA. 2019. Human-carnivore relations: A systematic review. Biological Conservation 237 (2019) 480–492.

MacKenzie D, Nichols J, Royle J, Pollock K, Bailey L, Hines J. 2005. Occupancy estimation and modeling. Academic Press, Burlington, M.A. Available from http://www.elsevier.com/books/occupancy-estimation-and-modeling/mackenzie/978-0-12-088766-8 (accessed May 30, 2015).

MacKenzie DI, Bailey LL. 2004. Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics 9:300–318.

Marino A, Ciucci P, Redpath SM, Ricci S, Young J, Salvatori V. 2021a. Broadening the toolset for stakeholder engagement to explore consensus over wolf management. Journal of Environmental Management 296:113125.

Marino F, Ciucci P, Kansky R, Knight AT, Shivji I, Croce A Di. 2021b. Understanding drivers of human tolerance to gray wolves and brown bears as a strategy to improve landholder – carnivore coexistence:1–14.

Martin A, Coolsaet B, Corbera E, Dawson NM, Fraser JA, Lehman I, Rodriguez I. 2016. Justice and conservation: The need to incorporate recognition. Biological Conservation 197:254–261.

Martin JV. 2021. Peace in the valley? Qualitative insights on collaborative coexistence from the Wood River Wolf Project. Conservation Science and Practice 3:1–16.

Massarella K et al. 2021. Transformation beyond conservation: how critical social science can contribute to a radical new agenda in biodiversity conservation. Current Opinion in Environmental Sustainability 49:79–87.

Massarella K, Krauss JE, Kiwango W, Fletcher R. 2022. Exploring Convivial Conservation in theory and practice: Possibilities and challenges for a transformative approach to biodiversity conservation. Conservation and Society 20:59–68.

Massarella K, Sallu SM, Ensor JE. 2020. Reproducing injustice: Why recognition matters in conservation project evaluation. Global Environmental Change 65:102181.

Mateo-Sánchez MC, Balkenhol N, Cushman S, Pérez T, Domínguez A, Saura S. 2015. A comparative framework to infer landscape effects on population genetic structure: are habitat suitability models effective in explaining gene flow? Landscape Ecology 30:1405–1420.

McBride RT, Thompson JJ. 2019. Spatial ecology of Paraguay's last remaining Atlantic forest Jaguars (Panthera onca): Implications for their long-term survival. Biodiversity 20:20–26.

Mcgarigal K, Yi H, Zeller KA, Timm BC, Cushman SA. 2016. Multi-scale habitat selection modeling : a review and outlook. Landscape Ecology 31:1161–1175.

McPhearson T, M. Raymond C, Gulsrud N, Albert C, Coles N, Fagerholm N, Nagatsu M, Olafsson AS, Soininen N, Vierikko K. 2021. Radical changes are needed for transformations to a good Anthropocene. npj Urban Sustainability 5:1-13.

McRae BH. 2006. Isolation By Resistance. Evolution 60:1551.

Medellin R, Equihua C, Chetkiewicz C, Junior Crawshaw P., Rabinowitz KH, Redford H, Robinson JG, Sanderson EW, Taber AB, editors. 2002. El jaguar en el nuevo milenio. Fondo de Cultura Económica, Universidad Nacional Autónoma de México, Wildlife Conservation Society, Mexico, D.F.

Medellín R, de la Torre A, Zarza H, Chávez C, Ceballos G, editors. 2016. El jaguar en el siglo XXI. La perspectiva continental. Ediciones Científicas Universitarias., México D.F., México.

Mena JL, Yagui H, Tejeda V, Cabrera J, Pacheco-Esquivel J, Rivero J, Pastor P. 2020. Abundance of jaguars and occupancy of medium- and large-sized vertebrates in a transboundary conservation landscape in the northwestern Amazon. Global Ecology and Conservation 23:e01079.

Menchaca A et al. 2019. Population genetic structure and habitat connectivity for jaguar (Panthera onca) conservation in Central Belize. BMC Genetics 20:1-13.

Meyer NF V. et al. 2019. Effectiveness of Panama as an intercontinental land bridge for large mammals. Conservation Biology 0:1-13.

Meyer NF V., Moreno R, Reyna-Hurtado R, Signer J, Balkenhol N. 2020. Towards the restoration of the Mesoamerican Biological Corridor for large mammals in Panama: comparing multi-species occupancy to movement models. Movement Ecology 8:1-14.

Miller DA, Nichols JD, McClintock BT, Grant EHC, Bailey LL, Weir LA. 2011. Improving occupancy estimation when two types of observational error occur: non-detection and species misidentification. Ecology 92:1422–1428.

Mishra C, Allen P, McCarthy T, Madhusudan MD, Bayarjargal A, Prins HHT. 2003. The role of incentive programs in conserving the snow leopard. Conservation Biology 17:1512–1520.

Mishra C, Young JC, Fiechter M, Rutherford B, Redpath SM. 2017. Building partnerships with communities for biodiversity conservation: lessons from Asian mountains. Journal of Applied Ecology 54:1583–1591.

Montalvo VH, Sáenz-Bolaños C. 2023. A review of environmental and anthropogenic variables used to model jaguar occurrence 18:31–51.

Mora JM, Polisar J, Portillo H, Castañeda F. 2016. Estado de conservación del jaguar (Panthera onca) en Honduras. Pages 137–167 in Medellín R, de la Torre A, Zarza H, Chávez C, Ceballos G, editors. El jaguar en el siglo XXI La perspectiva continental. Ediciones Científicas Universitarias.

Moraga AD, Martin AE, Fahrig L. 2019. The scale of effect of landscape context varies with the species' response variable measured. Landscape Ecology 34:703–715.

Morato RG et al. 2016. Space use and movement of a Neotropical top predator: the endangered jaguar. PLOS ONE 11:e0168176.

Morato RG et al. 2018. Resource selection in an apex predator and variation in response to local landscape characteristics. Biological Conservation 228:233–240.

Moreno R, Meyer N, Olmos M, Hoogesteijn R, Hoogesteijn A. 2015. Causes of jaguar killing in Panama - a long term survey using interviews. CATnews 62:40–42.

Mukherjee T, Sharma LK, Saha GK, Thakur M, Chandra K. 2020. Past, Present and Future: Combining habitat suitability and future landcover simulation for long-term conservation management of Indian rhino. Scientific Reports 10:606.

Mulder MB, Kwiyega JL, Beccaria S, Bwasama SS, Fitzherbert E, Genda P, Caro T. 2019. Lions, Bylaws, and Conservation Metrics. BioScience 69:1008–1018.

Munn Z, Peters MDJ, Stern C, Tufanaru C, Mcarthur A, Aromataris E. 2018. Systematic review or scoping review ? Guidance for authors when choosing between a systematic or scoping review approach. BMC Medical Research Methodology 18:1–7.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Naito R, Zhao J, Chan KMA. 2022. An integrative framework for transformative social change: a case in global wildlife trade. Sustainability Science 17:171–189.

Niedballa J, Sollmann R, Courtiol A, Wilting A. 2016. camtrapR: an R package for efficient camera trap data management. Methods in Ecology and Evolution 7:1457-1462.

Niemiec RM et al. 2021. Integrating social science into conservation planning. Biological Conservation 262:09298.

Nuñez R. 2006. Área de actividad, patrones de actividad y movimiento del jaguar (Panthera onca) y del puma (Puma concolor), en la Reserva de la Biosfera "Chamela-Cuixmala", Jalisco. Universidad Nacional Autónoma de México.

O'Brien K et al. 2013. You say you want a revolution? Transforming education and capacity building in response to global change. Environmental Science and Policy 28:48–59.

Olsoy PJ, Zeller KA, Hicke JA, Quigley HB, Rabinowitz AR, Thornton DH. 2016. Quantifying the effects of deforestation and fragmentation on a range-wide conservation plan for jaguars. Biological Conservation 203:8–16.

Olsson P, Galaz V, Boonstra WJ. 2014. Sustainability transformations: A resilience perspective. Ecology and Society 19:1.

Palmer C, McShane K, Sandler R. 2014. Environmental ethics. Annual Review of Environment and Resources 39:419–442.

Parsons JJ. 1955. The miskito pine savanna of nicaragua and honduras. Annals of the Association of American Geographers 45:36–63.

Paviolo A et al. 2016. A biodiversity hotspot losing its top predator: The challenge of jaguar conservation in the Atlantic Forest of South America. Scientific Reports 6:1–16.

Pe'er G, Henle K, Dislich C, Frank K. 2011. Breaking Functional Connectivity into Components: A Novel Approach Using an Individual-Based Model, and First Outcomes. PLoS ONE 6:e22355.

Pelling M. 2010. Adaptation to climate change from resilience to transformation. Routledge. Taylor & Francis Group, London, UK.

Peterman WE. 2018. ResistanceGA: An R package for the optimization of resistance surfaces using genetic algorithms. Methods in Ecology and Evolution 9:1638–1647.

Peterman WE, Connette GM, Semlitsch RD, Eggert LS. 2014. Ecological resistance surfaces predict fine-scale genetic differentiation in a terrestrial woodland salamander. Molecular Ecology 23:2402–2413.

Petracca LS et al. 2018. Robust inference on large-scale species habitat use with interview data: The status of jaguars outside protected areas in Central America. Journal of Applied Ecology 55:723–734.

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344:1–10.

Portanier E, Léger F, Henry L, Gayet T, Queney G, Ruette S, Devillard S. 2022. Landscape genetic connectivity in European wildcat (Felis silvestris silvestris): a matter of food, shelters and demographic status of populations. Conservation Genetics 23:653–668.

Powers RP, Jetz W. 2019. Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. Nature Climate Change 9:323–329. Springer US. Available from http://dx.doi.org/10.1038/s41558-019-0406-z.

Quevedo M, Echegaray J, Fernández-Gil A, Leonard J, Naves J, Ordiz A, Revilla E. 2019. Lethal management may hinder population recovery in Iberian wolves. Biodiversity and Conservation 28:415–432.

Quigley H, Foster R, Petracca L, Payan E, Salom R, Harmsen B. 2017. Panthera onca. Available from https://www.iucnredlist.org/es/species/15953/123791436#bibliography.

Rabelo RM, Aragón S, Bicca-Marques JC. 2019. Prey abundance drives habitat occupancy by jaguars in Amazonian floodplain river islands. Acta Oecologica 97:28–33.

Rabinowitz A, Zeller KA. 2010. A range-wide model of landscape connectivity and conservation for the jaguar, Panthera onca. Biological Conservation 143:939–945.

Rabinowitz AR, Nottingham BG. 1986. Ecology and behaviour of the Jaguar (Panthers onca) in Belize, Central America. Journal of Zoology 210:149–159.

Redford KH. 1992. The Empty Forest. BioScience 42:412–422.

Reding DM, Cushman SA, Gosselink TE, Clark WR. 2013. Linking movement behavior and fine-scale genetic structure to model landscape connectivity for bobcats (Lynx rufus). Landscape Ecology 28:471–486.

Redo DJ, Grau HR, Aide TM, Clark ML. 2012. Asymmetric forest transition driven by the interaction of socioeconomic development and environmental heterogeneity in Central America. Proceedings of the National Academy of Sciences of the United States of America 109:8839–44.

Redpath SM et al. 2017. Don’t forget to look down – collaborative approaches to predator conservation. Biological Reviews 92:2157–2163.

Richard Y, Armstrong DP. 2010. Cost distance modelling of landscape connectivity and gap-crossing ability using radio-tracking data. Journal of Applied Ecology 47:603–610.

Richie L, Oppenheimer JD, Clark SG. 2012. Social process in grizzly bear management: Lessons for collaborative governance and natural resource policy. Policy Sciences 45:265–291.

Ripple WJ et al. 2014. Status and ecological effects of the world’s largest carnivores. Science 343.

Roelke ME, Martenson JS, O’Brien SJ. 1993. The consequences of demographic reduction and genetic depletion in the endangered Florida panther. Current Biology 3:340–350.

Romero-Muñoz A et al. 2019. Habitat loss and overhunting synergistically drive the extirpation of jaguars from the Gran Chaco. Diversity and Distributions 25:176–190.

Rondinini C et al. 2011. Global habitat suitability models of terrestrial mammals. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 366:2633–41.

Roques S et al. 2016. Effects of habitat deterioration on the population genetics and conservation of the jaguar. Conservation Genetics 17:125–139.

Roques S, Furtado M, Jácomo ATA, Silveira L, Sollmann R, Tôrres NM, Godoy JA, Palomares F. 2014. Monitoring jaguar populations Panthera onca with non-invasive genetics: a pilot study in Brazilian ecosystems. Oryx 48:361–369.

Row JR, Knick ST, Oyler-McCance SJ, Lougheed SC, Fedy BC. 2017. Developing approaches for linear mixed modeling in landscape genetics through landscape-directed dispersal simulations. Ecology and Evolution 7:3751–3761.

Ruiz-Garcia M, Payán E, Murillo A, Alvarez D. 2006. DNA microsatellite characterization of the jaguar (Panthera onca) in Colombia. Genes and Genetic Systems 81:115–127.

Rutherford MB, Clark SG. 2014. Improving Governance for people and large carnivores. Large carnivore conservation. University of Chicago Press.

Saif O, Keane A, Staddon S. 2022. Making a case for the consideration of trust, justice, and power in conservation relationships. Conservation Biology 36:1–12.

Salom-Pérez R, Carrillo E, Saénz JC, Mora JM. 2007. Critical condition of the jaguar Panthera onca population in Corcovado National Park, Costa Rica. Oryx 41:51–56.

Salom-Pérez R, Corrales-Gutiérrez D, Araya-Gamboa D, Espinoza-Muñoz D, Finegan B, Petracca LS. 2021. Forest cover mediates large and medium-sized mammal occurrence in a critical link of the Mesoamerican Biological Corridor. PLOS ONE 16:e0249072.

Salvatori V et al. 2021. Are large carnivores the real issue? Solutions for improving conflict management through stakeholder participation. Sustainability (Switzerland) 13:1–24.

Salvatori V, Balian E, Blanco JC, Ciucci P, Demeter L, Hartel T, Marsden K, Redpath SM, von Korff Y, Young JC. 2020. Applying participatory processes to address conflicts over the conservation of large carnivores: Understanding conditions for successful management. Frontiers in Ecology and Evolution 8:1–14.

Sandel M. 1989. The mating tactics and spacing patterns of solitary carnivore. Pages 164–182 in Gittleman JL, editor. Carnivore behavior, ecology, and evolution. Cornell University Press, New York. US.

Sanderson EW, Chetkiewicz C-LB, Medellín RA, Rabinowitz AR, Redford KH, Taber AB. 2002a. Un análisis geográfico del estado de conservación y distribución de los jaguares a través de su área de distribución. Pages 551–600 in Medellín RA, Equihua C, Chetkiewicz C-LB, Crawshaw PGJ, Rabinowitz AR, Redford KH, Robinson JG, Sanderson EW, Taber AB, editors. El jaguar en el nuevo milenio1a. Ediciones Científicas Universitarias. Serie Texto Científico Universitario, Mexico, D.F.

Sanderson EW, Redford KH, Chetkiewicz C-LB, Medellin RA, Rabinowitz AR, Robinson JG, Taber AB. 2002b. Planning to save a species: the Jaguar as a model. Conservation Biology 16:58–72.

Sartor CC, Wan HY, Pereira JA, Eizirik E, Trigo TC, de Freitas TRO, Cushman SA. 2022. Landscape genetics outperforms habitat suitability in predicting landscape resistance for congeneric cat species. Journal of Biogeography 0:1–12.

Schmidt C, Domaratzki M, Kinnunen RP, Bowman J, Garroway CJ. 2020. Continent-wide effects of urbanization on bird and mammal genetic diversity. Proceedings of the Royal Society B: Biological Sciences 287:20192497.

Schwab AC, Zandbergen PA. 2011. Vehicle-related mortality and road crossing behavior of the Florida panther. Applied Geography 31:859–870.

Shirk AJ, Wallin DO, Cushman SA, Rice CG, Warheit KI. 2010. Inferring landscape effects on gene flow: a new model selection framework. Molecular Ecology 19:3603–3619.

Sjölander-Lindqvist A, Johansson M, Sandström C. 2015. Individual and collective responses to large carnivore management: The roles of trust, representation, knowledge spheres, communication and leadership. Wildlife Biology 21:175–185.

Sjölander-Lindqvist A, Risvoll C, Kaarhus R, Lundberg AK, Sandström C. 2020. Knowledge claims and struggles in decentralized large carnivore governance: Insights from Norway and Sweden. Frontiers in Ecology and Evolution 8:120.

Sonam K, Dorjay R, Khanyari M, Bijoor A, Lobzang S, Sharma M, Suresh S, Mishra C, Suryawanshi KR. 2022. A Community-based conservation initiative for wolves in the Ladakh Trans-Himalaya, India. Frontiers in Ecology and Evolution 10:1–8.

Spear SF, Balkenhol N, Fortin M-J, Mcrae BH, Scribner K. 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Molecular Ecology 19:3576–3591.

Srbek-Araujo AC, Mendes SL, Chiarello AG. 2015. Jaguar (Panthera onca Linnaeus, 1758) roadkill in Brazilian Atlantic Forest and implications for species conservation. Brazilian Journal of Biology 75:581–586.

Steffen W et al. 2018. Trajectories of the Earth System in the Anthropocene. Proceedings of the National Academy of Sciences of the United States of America 115:8252–8259.

Sunquist ME, Sunquist FC. 1989. Ecological constraints on predation by large felids. Pages 283–301 in Gittleman JL, editor. Carnivore behavior, ecology and evolution. Cornell University Press, New York, USA.

Taylor PD, Fahrig L, Henein K, Merriam G. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571.

Temper L, Walter M, Rodriguez I, Kothari A, Turhan E. 2018. A perspective on radical transformations to sustainability: resistances, movements and alternatives. Sustainability Science 13:747–764.

Tengö M, Hill R, Malmer P, Raymond CM, Spierenburg M, Danielsen F, Elmqvist T, Folke C. 2017. Weaving knowledge systems in IPBES, CBD and beyond—lessons learned for sustainability. Current Opinion in Environmental Sustainability 26:17–25.

Terborgh J et al. 2001. Ecological meltdown in predator-free forest fragments. Science 294, 1923-1926.

Termeer CJAM, Dewulf A, Biesbroek GR. 2017. Transformational change: governance interventions for climate change adaptation from a continuous change perspective. Journal of Environmental Planning and Management 60:558–576.

Tesson SVM, Edelaar P. 2013. Dispersal in a changing world: Opportunities, insights and challenges. Movement Ecology 1:1–6.

Thatte P, Chandramouli A, Tyagi A, Patel K, Baro P, Chhattani H, Ramakrishnan U. 2020. Human footprint differentially impacts genetic connectivity of four wide-ranging mammals in a fragmented landscape. Diversity and Distributions 26:299–314.

Thatte P, Joshi A, Vaidyanathan S, Landguth E, Ramakrishnan U. 2018. Maintaining tiger connectivity and minimizing extinction into the next century: Insights from landscape genetics and spatially-explicit simulations. Biological Conservation 218:181–191.

Thompson JJ et al. 2021. Environmental and anthropogenic factors synergistically affect space use of jaguars. Current Biology 31:3457-3466.e4.

Thompson JJ, Martí CM, Quigley H. 2020. Anthropogenic factors disproportionately affect the occurrence and potential population connectivity of the Neotropic's apex predator: The jaguar at the southwestern extent of its distribution. Global Ecology and Conservation 24:e01356.

Thornton D, Zeller K, Rondinini C, Boitani L, Crooks K, Burdett C, Rabinowitz A, Quigley H. 2016. Assessing the umbrella value of a range-wide conservation network for jaguars (Panthera onca). Ecological Applications 26:1112–1124.

Tilman D, Clark M, Williams DR, Kimmel K, Polasky S, Packer C. 2017. Future threats to biodiversity and pathways to their prevention. Nature 546:73–81.

Tischendorf L, Fahrig L. 2000. On the usage and measurement of landscape connectivity. Oikos 90:7–19.

Tobler MW, Garcia Anleu R, Carrillo-Percastegui SE, Ponce Santizo G, Polisar J, Zuñiga Hartley A, Goldstein I. 2018. Do responsibly managed logging concessions adequately protect jaguars and other large and medium-sized mammals? Two case studies from Guatemala and Peru. Biological Conservation 220:245–253.

Toncheva S, Fletcher R, Turnhout E. 2022. Convivial Conservation from the bottom up: Human-Bear cohabitation in the Rodopi Mountains of Bulgaria. Conservation and Society 20:124–135.

Torrents-Ticó M, Fernández-Llamazares Á, Burgas D, Cabeza M. 2021. Convergences and divergences between scientific and Indigenous and Local Knowledge contribute to inform carnivore conservation. Ambio 50:990–1002.

Tucker MA et al. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. Science (New York, N.Y.) 359:466–469.

Turrini T, Dörler D, Richter A, Heigl F, Bonn A. 2018. The threefold potential of environmental citizen science - Generating knowledge, creating learning opportunities and enabling civic participation. Biological Conservation 225:176–186.

Tyre AJ, Tenhumberg B, Field SA, Niejalke D, Parris K, Possingham HP. 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. Ecological Applications 13:1790–1801.

UNEP-WCMC, IUCN. 2021. World Database on Protected Areas-WDPA. Available from https://www.protectedplanet.net/en/thematic-areas/wdpa?tab=WDPA (accessed January 15, 2021).

Valsecchi J, Monteiro MCM, Alvarenga GC, Lemos LP, Ramalho EE. 2022. Community-based monitoring of wild felid hunting in Central Amazonia. Animal Conservation 26:189-198.

Vickers TW, Sanchez JN, Johnson CK, Morrison SA, Botta R, Smith T, Cohen BS, Huber PR, Ernest HB, Boyce WM. 2015. Survival and mortality of pumas (Puma concolor) in a fragmented, urbanizing landscape. PLoS ONE 10:1–18.

Villalva P, Palomares F. 2022. A continental approach to jaguar extirpation: A tradeoff between anthropic and intrinsic causes. Journal for Nature Conservation 66:126145.

Visseren-Hamakers IJ et al. 2021. Transformative governance of biodiversity: insights for sustainable development. Current Opinion in Environmental Sustainability 53:20–28.

Visseren-Hamakers IJ, Kok MT, editors. 2022. Transforming Biodiversity Governance. Cambridge University Press, Cambridge, UK.

Volski L, McInturff A, Gaynor KM, Yovovich V, Brashares JS. 2021. Social Effectiveness and Human-Wildlife Conflict: Linking the Ecological Effectiveness and Social Acceptability of Livestock Protection Tools. Frontiers in Conservation Science 2:1–17.

Vynne C, Keim JL, Machado RB, Marinho-Filho J, Silveira L, Groom MJ, Wasser SK. 2011. Resource Selection and Its Implications for Wide-Ranging Mammals of the Brazilian Cerrado. PLoS ONE 6:e28939.

Warton DI, Stoklosa J, Guillera-Arroita G, MacKenzie DI, Welsh AH. 2017. Graphical diagnostics for occupancy models with imperfect detection. Methods in Ecology and Evolution 8:408–419.

Westley F et al. 2011. Tipping toward sustainability: Emerging pathways of transformation. Ambio 40:762–780.

White RM, Schmook B, Calmé S, Giordiano AJ, Hausser Y, Kimmel L, Lecuyer L, Lucherini M, Méndez-Medina C, Peña-Mondragón JL. 2023. Facilitating biodiversity conservation through partnerships to achieve transformative outcomes. Conservation Biology DOI: https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.14057.

Whyte KP, Brewer JP, Johnson JT. 2016. Weaving Indigenous science, protocols and sustainability science. Sustainability Science 11:25–32.

Wikramanayake E, Mcknight M, Dinerstein E, Joshi A, Gurung B, Smith D. 2004. Designing a Conservation Landscape for Tigers in Human-Dominated Environments. Conservation Biology 18:839–844.

Willi Y, Kristensen TN, Sgro CM, Weeks AR, Ørsted M, Hoffmann AA. 2022. Conservation genetics as a management tool: The five best-supported paradigms to assist the management of threatened species. Proceedings of the National Academy of Sciences of the United States of America 119:1–10.

Wilson SM, Bradley EH, Neudecker GA. 2017. Learning to live with wolves: Community based conservation in the Blackfoot Valley of Montana. Human-Wildlife Interactions 11:245–257.

Woiwode C, Schäpke N, Bina O, Veciana S, Kunze I, Parodi O. 2021. Inner transformation to sustainability as a deep leverage point : fostering new avenues for change through dialogue and reflection. Sustainability Science 16:841–858.

Wolf C, Ripple WJ. 2017. Range contractions of the world's large carnivores. Royal Society Open Science 4: 170052.

World Bank. 2020. Human population, DataBank Microdata Data Catalog. Available from https://data.worldbank.org/indicator/SP.POP.TOTL (accessed February 26, 2020).

Wright S. 1942. Isolation by distance. Genetics 28:114–138.

Wultsch C, Caragiulo A, Dias-Freedman I, Quigley H, Rabinowitz S, Amato G. 2016. Genetic diversity and population structure of Mesoamerican Jaguars (Panthera onca): Implications for conservation and management. PLOS ONE 11:e0162377.

Young JC et al. 2021. Community-based conservation for the sustainable management of conservation conflicts: Learning from practitioners. Sustainability 13:1-20.

Zanin M, Palomares F, Brito D. 2015. The jaguar's patches: Viability of jaguar populations in fragmented landscapes. Journal for Nature Conservation 23:90–97.

Zeller KA. 2007. Jaguars in the New Millennium Data Set Update: The State of the Jaguar in 2006. Maryland.

Zeller KA, McGarigal K, Whiteley AR. 2012. Estimating landscape resistance to movement: A review. Landscape Ecology 27:777–797.

Zeller KA, Nijhawan S, Salom-Pérez R, Potosme SH, Hines JE. 2011. Integrating occupancy modeling and interview data for corridor identification: A case study for jaguars in Nicaragua. Biological Conservation 144:892–901.

Zeller KA, Rabinowitz A, Salom-Perez R, Quigley HB. 2013. The Jaguar Corridor Initiative: A range-wide conservation strategy. Pages 629–657 in Ruiz-García M, J S, editors. Molecular population genetics, evolutionary biology and biological conservation of Neotropical carnivores. Nova Science Publishers, Inc., New York, USA.

Zeller KA, Wultsch C, Welfelt LS, Beausoleil RA, Landguth EL. 2023. Accounting for sex-specific differences in gene flow and functional connectivity for cougars and implications for management. Landscape Ecology 38:223–237.

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SUPPLEMENTARY INFORMATION

Appendices - Chapter 2

Appendix S1: Study area

Central America spans the tropics and subtropics. It encompasses the countries of Guatemala, Belize, Honduras, El Salvador, Nicaragua, Costa Rica, and Panama; all of which –with the exception of El Salvador- are jaguar range countries (Fig. 1). The climate is, in general terms, considered dry-winter tropical (Portig 1965), with a dominant dry winter/summer regime. Nonetheless the complex and diverse topography of the region, for which the elevational gradient is 0 to 5252.61 meter asl, produces significant climate modifications at the sub regional scale. The region's annual mean temperature is 24.7°C, with small temperature ranges across the year that span from 2°C in the south and the coastal zones, to exceeding 4°C to the north (Yucatan to Honduras; Taylor & Alfaro, 2005).

Central America holds a high biological diversity and represents a hotspot of plant and animal endemism (Myers et al. 2000). However, it also holds one the highest deforestation rates and the highest proportional forest degradation worldwide (Redo et al. 2012), being Guatemala and Nicaragua the countries with the highest loss of woody vegetation (Aide et al. 2013). The region is characterized by a highly diverse pattern of land uses and a high human density of 94.27 ind./km2 (World Bank 2020). A little over 60% of the region is covered by broadleaved evergreen and deciduous trees (61%), as well as mosaics of natural vegetation with croplands (21%). The rest of the region is represented by a diverse matrix of land uses in which the main categories are croplands (6%), secondary growth forests (4%), grasslands (3%), wetlands (1%) and urban areas (0.5%, ESA, 2015).

Appendix S2: Research teams who collected the camera trap data used for analysis in this research, their members and institutional affiliations. The site removed from the occupancy analysis included the data from two camera traps collected by the Panthera-Guatemala team on the years 2015 and 2016

Team	Country	Affiliated institutions	Research Team Members	Stations	Years
Panthera - Southampton	Belize	Panthera, University of Southampton, University of Belize Environmental Research Institute	Rebecca Foster, Bart Harmsen, Patrick Doncaster, Yahaira Urbina	199	2009-2015
WCS - Washington	Guatemala	Wildlife Conservation Society –WCS-, Washington State University	Rony Garcia-Anleu, Roan McNab, Dan Thornton,	74	2005, 2008
CECON	Guatemala	Centro de Estudios Conservacionistas –CECON- from San Carlos University -USAC-, Fundación Defensores de la Naturaleza and Tikal National Park	Manolo García, Raquel Leonardo, Cristel Pineda	62	2014-2017
Panthera - Guatemala	Guatemala	Former Panthera, currently Leibniz Institute for Zoo and Wildlife Research	Ana Patricia Calderón	28	2014-2016
Panthera - Nicaragua	Nicaragua	Panthera	Sandra Hernández	152	2015-2018
Panthera - Costa Rica	Costa Rica	Panthera	Roberto Salom-Perez, Javier Carazo-Salazar, Daniel Corrales-Gutiérrez, Daniela Araya-Gamboa, Alvaro Sauma Rossi, David Mattey Trigueros, Luis Mariano Barrantes-Núñez	226	2011-2013
Coastal Jaguar Conservation	Costa Rica	Coastal Jaguar Conservation	Stephanny Arroyo-Arce, Ian Thomson	62	2012-2017
Yaguará-Panamá	Panamá	Yaguará-Panamá, Smithsonian Tropical Research Institute, University of Newcastle, Albert-Ludwigs-Universität Freiburg	Ricardo Moreno, Ninon Meyer	679	2006, 2011-2017

Appendix S3: Camera trap data availability across study years and countries in Central America, with number of months surveyed per year[6].

Country	Year												
	2005	2006	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Belize				3	4	5	4	4	4	4			
Guatemala	2		2				7	🟩	3	3	5	5	
Costa Rica						3	7	12	12	12	12	6	
Nicaragua										3			3
Panama	1	2				2	5	5	4	6	6	5	

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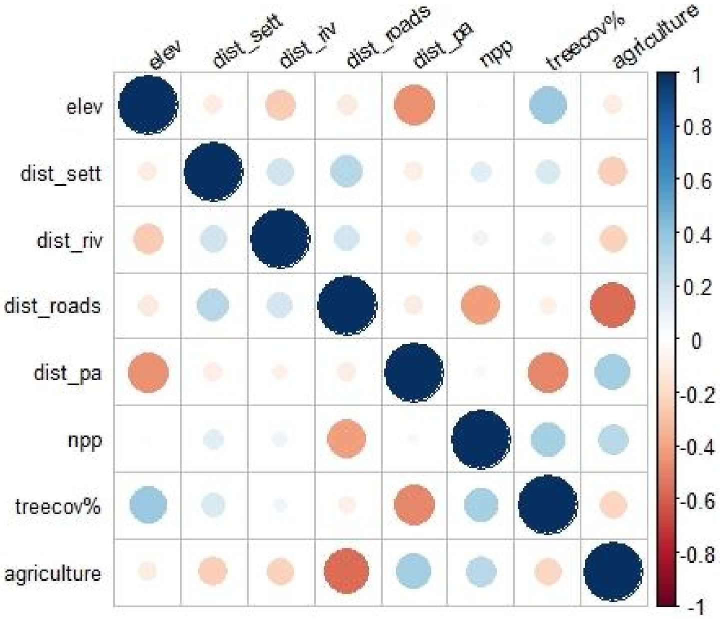
[6] The removal of one site from analysis did not affect the number of months surveyed per year in this table

Appendix S4: Study species

The jaguar (*Panthera onca*) is the largest carnivore in the Neotropics. It regulates trophic dynamics and contributes to ecosystem's integrity and functionality (Terborgh et al. 2001). Additionally, it serves as an effective focal species in environmental management as an umbrella species (Thornton et al. 2016), indicator of functional ecosystems, and planning basis for reserve design and management (Rabinowitz & Zeller 2010b). The jaguar is a near threatened species with 91% of all of their subpopulations under medium and high levels of threat (de la Torre et al. 2017). Priority areas (jaguar conservation units -JCUs-), where populations of jaguars can be sustained in the long term, have been therefore delineated, as well as corridors to connect them throughout the species range, and represent areas of high conservation priority and concern (Rabinowitz & Zeller, 2010; main text Fig. 1).

Throughout their range, jaguar distribution has been strongly and positively related to prey abundance (Rabelo et al. 2019), amount of forest cover (Conde et al. 2010; Foster et al. 2010; Petracca et al. 2018) and wetlands (Figel et al. 2019); and negatively related to human disturbance (Morato et al. 2018; McBride & Thompson 2019). Furthermore, ecosystem productivity has been positively related to jaguar presence, with populations surviving better in humid, productive environments (Jędrzejewski et al. 2017b). Productivity in turn may also be related to prey richness (Melis et al. 2009; Jetz & Fine 2012; Ripple & Beschta 2012), which influences positively jaguar occupancy (Petracca et al. 2018; Rabelo et al. 2019).

Appendix S5: Correlation matrix of the predictor variables used for the occupancy modelling for jaguar in Central America[7]



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[7] This correlation matrix does not include the data removed for occupancy analysis.

Appendix S6: Predictor variables for the occupancy modelling for jaguar in Central America[a]

Variable name	**Description**	**Reference**	***Expected effect***
treecov%	Percentage of forest	MODIS yearly imagery at 250m resolution, from 2005 to 2018 (https://modis.gsfc.nasa.gov/data/)	+
npp	Net primary productivity	MOD17A3 v055 MODIS/Terra Net Primary Production Yearly L4 Global 1 km SIN Grid at 1Km resolution, from 2005 to 2018 (https://lpdaac.usgs.gov/products/mod17a3v055/)	+
dist_pa	Distance to protected areas	Euclidian distance raster at 36 km^2 resolution created from the original dataset of Protected Planet (https://www.protectedplanet.net/)	-
dist_roads	Distance to roads	Euclidian distance raster at 36 km^2 resolution created from the original dataset of Global patterns of current and future road infrastructure, which used data of roads between the scales of 1:100 000 and 1:500 000 resolution (Meijer et al., 2018; https://iopscience.iop.org/article/10.1088/1748-9326/aabd42/meta)	+
dist_sett	Distance to settlements	Euclidian distance raster at 36 km^2 resolution created from the original dataset of the European Commission (https://ghsl.jrc.ec.europa.eu/). Human settlements are recorded by the presence of any constructed, man-made object (e.g. buildings and associated structures, civil constructions)	+
agriculture	Area of agricultural lands	ESA Climate Change Initiative Yearly Global Land Cover at 300m resolution, from 2005 to 2018 (http://www.esa-landcover-cci.org/?q=node/158)	-
dist_riv	Distance to dist_rivers	Euclidian distance raster at 36 km^2 resolution created from the original dataset of 'A simple global dist_river bankfull width and depth database' at 1Km resolution (Andreadis et al. 2013, https://doi.org/10.1002/wrcr.20440)	-
elev	Elevation	USGS EROS Archive - Digital Elevation - Shuttle Radar Topography Mission SRTM, 90m resolution (https://www.usgs.gov/centers/eros/science/usgs-eros-archive-digital-elevation-shuttle-radar-topography-mission-srtm-1-arc?qt-science_center_objects=0#qt-science_center_objects)	-
*dist_pa * dist_sett*	Interaction between mean distance to protected areas and mean distance to settlements	Same source as the *dist_pa* and *dist_sett* datasets described above	+
*treecov% * agriculture*	Interaction between percentage of forest and area of agricultural lands	Same source as the *treecov%* and *agriculture* datasets described above	-

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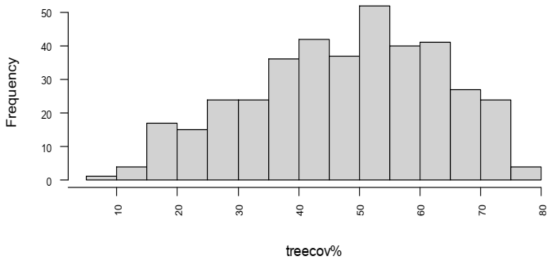
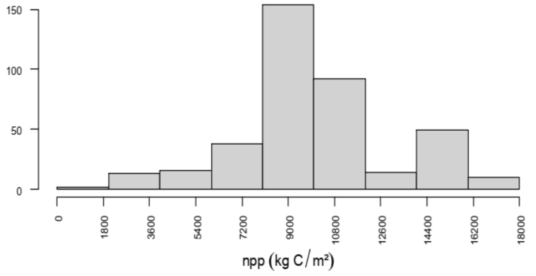
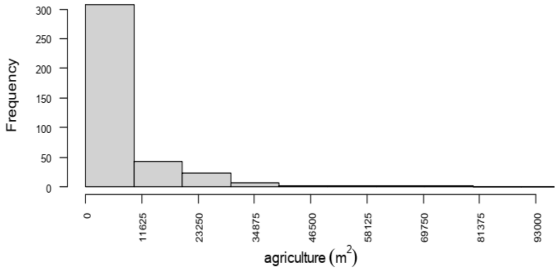
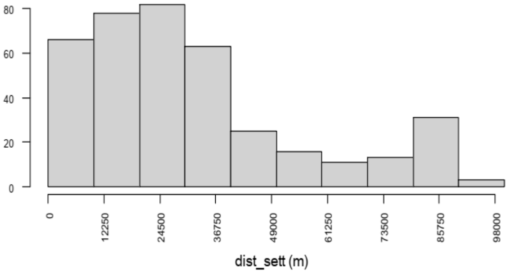
[a] Abbreviation shown in text (Variable name), description of the variable (Description), expected effect to jaguar habitat use according to the literature (Expected effect), and whether the variables were used as predictors of habitat use (Ψ) or detection (p). All raster datasets were converted to a 36 km^2 resolution by bilinear interpolation of the downloaded resolution using function 'resample' (package 'raster', Hijmans & Etten, 2012) in R-4.0.4 (R Core Team, 2021).

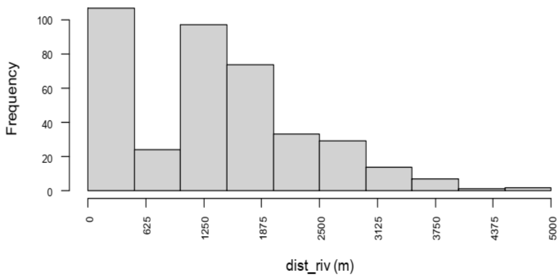
Appendix S7: Environmental space of the predictor variables used for the occupancy modelling for jaguar in Central America

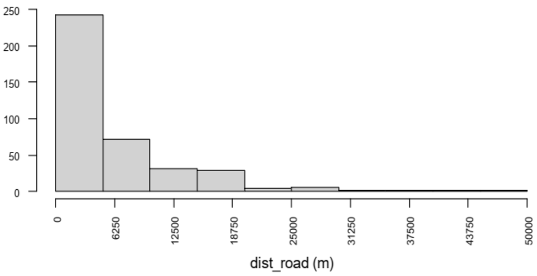


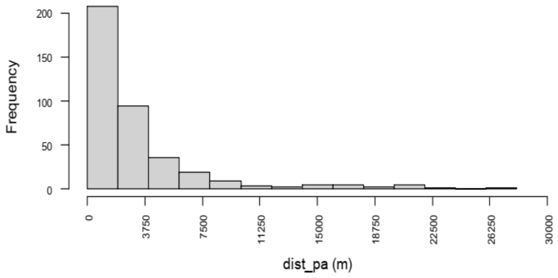












Appendix S8: Spatial aggregation of predictor variables for jaguar occupancy and detection

The environmental variables of elevation *(elev)*, tree cover percent *(treecov%),* distance to dist_rivers *(dist_riv)* and primary net productivity *(npp)* were obtained from MODIS yearly imagery at 250m and 1km^2 resolution, for the respective years of 2006 to 2018, USGS EROS Archive - Shuttle Radar Topography Mission –SRTM- at 90m resolution, and Andreadis et al. (2013) at 1Km resolution. All the covariate raster maps were re-sampled using bilinear interpolation and setting the output resolution at 36km2 before extracting their values at the sampling grid locations. When data was not available for a particular year, we used data from the closest year available.

Regarding the variables related to human disturbance, all the original datasets of roads, protected areas and settlements were used to create distance rasters using the 'Euclidian distance' tool in ArcGIS 10.8, from which the required distances between each grid cell to the feature of interest were calculated and for which the output raster resolution was set to 36km2. To get the area of agriculture within the 36km2 grid cells out of the land use land cover rasters, we first reclassified the rasters into 1 (agriculture) and 0 (all other land classes). The land use classes considered as agricultural areas were rain-fed cropland, irrigated cropland, mosaic cropland (>50%) with natural vegetation (tree, shrub, herbaceous cover, <50%), mosaic natural vegetation (tree, shrub, herbaceous cover, >50%) with cropland (<50%). The classes of roads included for analysis were Highways, primary and secondary roads (Meijer et al. 2018). All the processing and analysis of the spatial data was performed in R unless otherwise stated (R Core Team 2021).

Appendix S9: Occupancy analysis

Hierarchical site occupancy models are hierarchical logistic regression models that account for imperfect detection, modelling occurrence probability jointly with the probability of detection, using occurrence data collected through repeated sampling (MacKenzie et al. 2002). Two important assumptions of site-occupancy models are a lack of false-positive errors (i.e. all individuals must be identified correctly) and population closure (i.e. the occupancy state at a site must not change during survey period). We controlled carefully for false positive errors in our dataset, by collecting data from well-established scientific teams which work permanently in jaguar research, conservation, and monitoring in each of the surveyed countries. Given that we were unable to meet the population closure assumption in the present study, we interpret here the probability of occurrence (Ψ) as 'probability of habitat use' (Kéry & Schaub 2012).

From our occurrence data we created two different databases: (1) a record table that integrated all jaguar detection records with their associated date, camera trap id, responsible research team and grid cell-coordinates; and (2) a camera trap database that included camera traps with data on the period for which each of them was active, when it was malfunctioning, grid-cell-coordinates, and the responsible research team for that survey. These databases are the required inputs of *camtrapR* (Niedballa et al. 2016) to create the detection history and camera operation files for running the occupancy analysis in unmarked (Fiske & Chandler 2011).

We fitted single-state, single-season occupancy models treating each site-year combination sampled ('grid cell – year') as independent sites. We used a static approach because we were interested in the static occupancy patterns of jaguars across the region, rather than the turnover rates between years; and temporal replication was limited due to grid cells not being surveyed consistently on the same years (72% of the grid cells had data on one year only, 19% on two years, and the rest on three to six years). Models with uninformative parameters were deleted from the model list to avoid AIC cannibalization of non-competing models (Arnold 2010).

We expected 'year' to be more related to changes in the environment across time than on the jaguar habitat use per se, and that this variability would be accounted for by matching the covariate values to the respective year of camera-trapping or the closest year available (e.g. for grids cells sampled on 2018, the covariate values used were those of the year 2018 or the closest year available). However we also tested for any potential year effects by running a model version with 'year' as random effect for each of the models in the candidate set (Appendix S11). We used the R package *ubms* (Kellner 2021), which fits occupancy models in a Bayesian framework using the programming language Stan (Carpenter et al. 2017).

For each model we ran three chains, 30,000 iterations, and a target average proposal acceptance probability (adapt_delta) of 0.99 for the adaptation period. We reviewed R-hat values and traceplots to confirm convergence of Markov chain Monte Carlo chains. Model selection was performed using the expected log point predictive density (ELPD), in which the top ranked model is selected based on the lowest value and the remaining models are evaluated against the former in pairwise comparisons. The selected top model was evaluated with a goodness of fit test using posterior predictive checks and the leave-one-out cross validation. Results can be found in Appendix S12.

Appendix S10: Model validation using an independent dataset

We used a published dataset of global jaguar records (Jędrzejewski et al. 2018) as a validation set, selecting those records available for Central America (n= 310: presences= 221, absences= 89). Presence points in this dataset corresponded to jaguar records from Zeller (2007) which were located inside the most recent IUCN jaguar range map at the time of the study. Absence records were points located inside a buffer of 200 km outside the current jaguar range. We then used these records to create different habitat suitability probability thresholds between 0 to 1, in 0.05 increments, recording detections and non-detections at each threshold and constructing a two-by-two confusion matrix. The confusion matrix displays four different aspects of the model for each probability threshold, a) sensitivity (fraction of correctly predicted positive); b) specificity (fraction of correctly predicted negative); c) commission errors (fraction of falsely predicted positives); and d) omission errors (fraction of falsely predicted negatives). Sensitivity was plotted against the commission error (1 – specificity) for each habitat use probability threshold, and the area under this curve (AUC score) was calculated using the formula for the area of a trapezoid. The AUC score was calculated by the sum of the product of the height of the trapezoid times its width, where the height was calculated by:

$$h = \frac{TPR\,(-1) + TPR\,(-L(TPR)\,)}{2}$$

where *TPR* is the true positive rate *(sensitivity)* and *L* is the number of habitat use probability thresholds

And width was calculated by:

$$w\ = -\Delta\,(1 - TNR)$$

where *TNR* is the true negative rate *(specificity)*

Appendix S11: Candidate models of a priori hypotheses explaining jaguar occupancy by natural habitat, human influence, and mixture of both variable sets. Model selected for habitat use prediction in Central America in bold

Model	**AIC**	**Model Likelihood**	**AIC Weight**	**LL**
Natural habitat models				
p (team + eff), psi (npp + dist_riv)	1469.641	0.000	0.000	-722.821
p (team + eff), psi (treecov + dist_riv)	1481.093	0.000	0.000	-728.546
p (team + eff), psi (npp + elev)	1482.432	0.000	0.000	-729.216
p (team + eff), psi (treecov + npp)	1483.781	0.000	0.000	-729.890
p (team + eff), psi (npp + elev + dist_riv)	1437.713	0.000	0.000	-705.857
Human influence models				
p (team + eff), psi (pa)	1486.566	0.000	0.000	-732.283
p (team + eff), psi (dist_sett)	1423.649	0.000	0.000	-700.824
p (team + eff), psi (dist_sett + pa)	1425.556	0.000	0.000	-700.778
p (team + eff), psi (dist_sett + dist_roads)	1425.563	0.000	0.000	-700.782
p (team + eff), psi (dist_sett + dist_roads + pa)	1427.502	0.000	0.000	-700.751
p (team + eff), psi (dist_sett + pa + dist_sett * pa)	1424.720	0.000	0.000	-699.360
p (team + eff), psi (dist_sett + dist_roads + pa + dist_sett * pa)	1426.560	0.000	0.000	-699.280
Natural habitat and Human influence models				
p (team + eff), psi (npp + dist_sett + dist_riv)	**1407.999**	**1.000**	**0.886**	**-691.000**
p (team + eff), psi (npp + treecov + dist_sett + dist_riv + agri_area + treecov * agri_area)	1412.364	0.113	0.100	-690.182
p (team + eff), psi (treecov + dist_sett + dist_riv)	1417.745	0.008	0.007	-695.872
p (team + eff), psi (treecov + dist_sett + dist_riv + elev)	1419.239	0.004	0.003	-695.619
p (team + eff), psi (treecov + dist_sett + dist_riv + elev + dist_roads + pa)	1420.807	0.002	0.001	-694.404
p (team + eff), psi (elev + dist_sett + dist_roads + dist_riv + pa + dist_sett * pa)	1420.990	0.002	0.001	-694.495
p (team + eff), psi (treecov + agri_area + treecov * agri_area)	1490.275	0.000	0.000	-732.138

Appendix S12: Candidate models of a priori hypotheses explaining jaguar occupancy by natural habitat, human influence, and mixture of both variable sets including year as random effect

<table>
<tr><th>Model</th><th>ELPD</th><th>nparam</th><th>ELPD diff</th><th>SE diff</th><th>weight</th></tr>
<tr><td>Null models</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>p (team + eff), psi (~)</td><td>-745.306</td><td>14.703</td><td>-38.5445</td><td>9.937</td><td>0.083</td></tr>
<tr><td>p (team + eff), psi (~ + (1|year))</td><td>-815.252</td><td>10.338</td><td>-108.490</td><td>15.470</td><td>0.032</td></tr>
<tr><td>Natural habitat models</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>p (team + eff), psi (npp + elev + river)</td><td>-722.393</td><td>18.659</td><td>-15.631</td><td>9.554</td><td>0.046</td></tr>
<tr><td>p (team + eff), psi (npp + elev + river + (1|year))</td><td>-723.555</td><td>21.748</td><td>-16.793</td><td>9.630</td><td>0.085</td></tr>
<tr><td>p (team + eff), psi (npp + river + (1|year))</td><td>-736.666</td><td>22.705</td><td>-29.904</td><td>9.070</td><td>0.000</td></tr>
<tr><td>p (team + eff), psi (npp + river)</td><td>-737.307</td><td>15.839</td><td>-30.545</td><td>9.148</td><td>0.034</td></tr>
<tr><td>p (team + eff), psi (treecov + river + (1|year))</td><td>-742.679</td><td>23.974</td><td>-35.917</td><td>9.664</td><td>0.000</td></tr>
<tr><td>p (team + eff), psi (treecov + river)</td><td>-743.384</td><td>16.554</td><td>-36.622</td><td>9.363</td><td>0.000</td></tr>
<tr><td>p (team + eff), psi (npp + elev)</td><td>-744.384</td><td>17.006</td><td>-37.622</td><td>9.549</td><td>0.000</td></tr>
<tr><td>p (team + eff), psi (treecov + npp)</td><td>-744.671</td><td>16.442</td><td>-37.909</td><td>9.689</td><td>0.000</td></tr>
<tr><td>p (team + eff), psi (npp + elev + (1|year))</td><td>-745.900</td><td>21.645</td><td>-39.138</td><td>9.715</td><td>0.000</td></tr>
<tr><td>p (team + eff), psi (treecov + npp + (1|year))</td><td>-746.148</td><td>22.204</td><td>-39.386</td><td>9.758</td><td>0.000</td></tr>
<tr><td>Human influence models</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>p (team + eff), psi (builtup)</td><td>-714.706</td><td>15.628</td><td>-7.945</td><td>4.253</td><td>0.089</td></tr>
<tr><td>p (team + eff), psi (builtup + (1|year))</td><td>-715.573</td><td>18.313</td><td>-8.811</td><td>4.472</td><td>0.088</td></tr>
<tr><td>p (team + eff), psi (builtup + grip + (1|year))</td><td>-715.651</td><td>17.541</td><td>-8.890</td><td>4.486</td><td>0.015</td></tr>
<tr><td>p (team + eff), psi (builtup + pa)</td><td>-715.780</td><td>16.893</td><td>-9.018</td><td>4.332</td><td>0.000</td></tr>
<tr><td>p (team + eff), psi (builtup + grip)</td><td>-715.820</td><td>16.875</td><td>-9.058</td><td>4.342</td><td>0.001</td></tr>
<tr><td>p (team + eff), psi (builtup + grip + pa + builtup * pa)</td><td>-716.500</td><td>19.645</td><td>-9.738</td><td>5.443</td><td>0.048</td></tr>
<tr><td>p (team + eff), psi (builtup + pa (1 | year))</td><td>-716.902</td><td>19.859</td><td>-10.140</td><td>4.530</td><td>0.000</td></tr>
<tr><td>p (team + eff), psi (builtup + pa)</td><td>-717.097</td><td>18.296</td><td>-10.335</td><td>4.403</td><td>0.000</td></tr>
<tr><td>p (team + eff) psi (builtup + pa + builtup * pa + (1|year))</td><td>-717.307</td><td>22.566</td><td>-10.545</td><td>5.588</td><td>0.099</td></tr>
<tr><td>p (team + eff) psi (builtup + grip + pa + builtup * pa)</td><td>-718.058</td><td>21.397</td><td>-11.296</td><td>5.507</td><td>0.000</td></tr>
</table>

Continuation Appendix S12: Candidate models of a priori hypotheses explaining jaguar occupancy by natural habitat, human influence, and mixture of both variable sets

<table>
<tr><th>Model</th><th>ELPD[a]</th><th>nparam</th><th>ELPD diff[b]</th><th>SE diff[b]</th><th>weight</th></tr>
<tr><td>Human influence models</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>p (team + eff), psi (builtup + grip + pa + (1|year))</td><td>-718.200</td><td>21.299</td><td>-11.438</td><td>4.635</td><td>0.000</td></tr>
<tr><td>p (team + eff), psi (builtup + grip + pa + builtup*pa + (1|year))</td><td>-718.571</td><td>23.989</td><td>-11.809</td><td>5.683</td><td>0.000</td></tr>
<tr><td>p (team + eff), psi (pa)</td><td>-746.301</td><td>15.817</td><td>-39.539</td><td>9.968</td><td>0.000</td></tr>
<tr><td>p (team + eff), psi (pa + (1|year))</td><td>-746.455</td><td>21.556</td><td>-39.693</td><td>10.149</td><td>0.009</td></tr>
<tr><td>Natural habitat and Human influence models</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>p (team + eff), psi (npp + builtup + river)[c]</td><td>-706.762</td><td>17.147</td><td>0.000</td><td>0.000</td><td>0.147</td></tr>
<tr><td>p (team + eff), psi (npp + builtup + river + (1|year))</td><td>-707.823</td><td>19.773</td><td>-1.061</td><td>0.967</td><td>0.041</td></tr>
<tr><td>p (team + eff), psi (npp + treecov + builtup + river + agri_area + treecov * agri_area)</td><td>-709.818</td><td>20.899</td><td>-3.056</td><td>1.786</td><td>0.014</td></tr>
<tr><td>p (team + eff), psi (npp + treecov + builtup + river + agri_area + treecov * agri_area + (1|year))</td><td>-711.466</td><td>24.321</td><td>-4.704</td><td>2.131</td><td>0.000</td></tr>
<tr><td>p (team + eff), psi (treecov + builtup + river)</td><td>-712.395</td><td>18.527</td><td>-5.633</td><td>2.838</td><td>0.000</td></tr>
<tr><td>p (team + eff), psi (treecov + builtup + river + (1|year))</td><td>-713.032</td><td>23.149</td><td>-6.270</td><td>3.078</td><td>0.071</td></tr>
<tr><td>p (team + eff), psi (builtup + pa + (1|year))</td><td>-719.051</td><td>27.440</td><td>-12.289</td><td>3.666</td><td>0.025</td></tr>
<tr><td>p (team + eff), psi (elev + builtup + grip + river + pa + builtup*pa)</td><td>-719.541</td><td>27.651</td><td>-12.779</td><td>3.840</td><td>0.018</td></tr>
<tr><td>p (team + eff), psi (elev + builtup + grip + river + pa + builtup*pa + (1|year))</td><td>-719.559</td><td>30.082</td><td>-12.798</td><td>3.816</td><td>0.000</td></tr>
<tr><td>p (team + eff), psi (treecov + builtup + river + elev + grip + pa + (1|year))</td><td>-720.786</td><td>32.320</td><td>-14.024</td><td>4.051</td><td>0.006</td></tr>
<tr><td>p (team + eff), psi (treecov + agriculture + treecov * agriculture)</td><td>-749.399</td><td>19.106</td><td>-42.637</td><td>9.762</td><td>0.000</td></tr>
<tr><td>p (team + eff), psi (treecov + agriculture + treecov * agriculture + (1|year))</td><td>-750.420</td><td>25.682</td><td>-43.659</td><td>9.873</td><td>0.000</td></tr>
</table>

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[a] Expected log pointwise predictive density

[b] The values in these columns are computed by making pairwise comparisons between each model and the model with the largest ELPD

[c] Model selected for habitat use prediction in Central America

Appendix S13: Top model of jaguar habitat use in Central America fitted in the Bayesian framework

Parameter estimates of the top model ran using three chains, 30,000 iterations, and a target average proposal acceptance probability (adapt_delta) of 0.99 for the adaptation period.

Covariate	Estimate	SD	2.50%	97.50%	n_eff	Rhat
Occupancy						
Intercept	2.285	0.453	1.474	3.260	24414	1
npp	0.677	0.228	0.256	1.160	34494	1
dist_sett	4.114	0.692	2.849	5.570	23989	1
dist_river	1.022	0.261	0.537	1.560	30637	1
Detection						
Intercept	-1.037	0.245	-1.525	-0.556	12397	1
eff	0.635	0.082	0.476	0.799	42740	1
Site (Team) effects:						
Coastal-Jaguar-Conservation	0.777	0.280	0.232	1.334	14429	1
Yaguará-Panamá	0.135	0.295	-0.443	0.716	15652	1
Panthera-Costa Rica[a]	-1.125	0.497	-2.125	-0.170	25274	1
Panthera-Guatemala	-1.416	0.893	-3.381	0.152	30636	1
Panthera-Nicaragua	-0.746	0.371	-1.488	-0.027	19656	1
Panthera-Southampton-UB-ERI[a]	1.380	0.282	0.832	1.940	14277	1
WCS-Washington	0.539	0.327	-0.099	1.183	17180	1

Results of model evaluation using the MacKenzie-Bailey Chi-square goodness of fit test (X^2) and leave-one-out cross-validation *(LOO)*

Model Evaluation test	**Estimate**	**Posterior predictive *p***	**Estimate**	**SE**
X^2				
	15938.590	0.921		
LOO[11]				
elpd[12]_loo			-706.800	40.500
p_loo[13]			17.100	1.600
looic[14]			1413.500	81.000

---

[11] All Pareto k estimates were below 0.7, evidencing good model accuracy

[12] Expected log pointwise predictive density

[13] Effective number of parameters

[14] Leave-one-out cross-validation Information Criterion

References

Aide TM, Clark ML, Grau HR, López-Carr D, Levy MA, Redo D, Bonilla-Moheno M, Riner G, Andrade-Núñez MJ, Muñiz M. 2013. Deforestation and reforestation of Latin America and the Caribbean (2001-2010). Biotropica 45:262–271.

Andreadis KM, Schumann GJ-P, Pavelsky T. 2013. A simple global river bankfull width and depth database. Water Resources Research 49:7164–7168.

Arnold TW. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. The Journal of Wildlife Management 74:1175–1178.

Carpenter B, Gelman A, Hoffman MD, Lee D, Goodrich B, Betancourt M, Brubaker M, Guo J, Li P, Riddell A. 2017. Stan : A Probabilistic Programming Language. Journal of Statistical Software 76:1–32. Available from http://www.jstatsoft.org/v76/i01/ (accessed November 12, 2021).

Conde DA, Colchero F, Zarza H, Christensen NL, Sexton JO, Manterola C, Chávez C, Rivera A, Azuara D, Ceballos G. 2010. Sex matters: Modeling male and female habitat differences for jaguar conservation. Biological Conservation 143:1980–1988.

de la Torre JA, Núñez JM, Medellín RA. 2017. Habitat availability and connectivity for jaguars (Panthera onca) in the Southern Mayan Forest: Conservation priorities for a fragmented landscape. Biological Conservation 206:270–282.

ESA. 2015. ESA CCI Global Land cover. Available from https://www.esa-landcover-cci.org/?q=node/164 (accessed June 26, 2019).

Figel JJ, Botero-Cañola S, Forero-Medina G, Sánchez-Londoño JD, Valenzuela L, Noss RF. 2019. Wetlands are keystone habitats for jaguars in an intercontinental biodiversity hotspot. PLOS ONE 14:e0221705.

Fiske I, Chandler R. 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1-23.

Foster RJ, Harmsen BJ, Doncaster CP. 2010. Habitat use by sympatric jaguars and pumas across a gradient of human disturbance in Belize. Biotropica 42:724–731.

Jędrzejewski W et al. 2018. Estimating large carnivore populations at global scale based on spatial predictions of density and distribution - Application to the jaguar (Panthera onca). PLoS ONE 13:1–25.

Jędrzejewski W et al. 2017. Predicting carnivore distribution and extirpation rate based on human impacts and productivity factors; assessment of the state of jaguar (Panthera onca) in Venezuela. Biological Conservation 206:132–142.

Jetz W, Fine PVA. 2012. Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. PLoS Biology 10:e1001292.

Kellner K. 2021. Package ubms: Bayesian models for data from unmarked animals using “Stan.” Available from https://kenkellner.com/ubms/.

Kéry M, Schaub M. 2012. Estimation of occupancy and species distributions from detection/nondetection data in metapopulation designs using Site-Occupancy Models. Bayesian Population Analysis using WinBUGS.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Andrew Royle J, Langtimm CA. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

McBride RT, Thompson JJ. 2019. Spatial ecology of Paraguay’s last remaining Atlantic forest jaguars (Panthera onca): implications for their long-term survival. Biodiversity 20:20–26.

Meijer JR, Huijbregts MAJ, Schotten KCGJ, Schipper AM. 2018. Global patterns of current and future road infrastructure. Environmental Research Letters 13:064006.

Melis C et al. 2009. Predation has a greater impact in less productive environments: variation in roe deer, Capreolus capreolus, population density across Europe. Global Ecology and Biogeography 18:724–734.

Morato RG et al. 2018. Resource selection in an apex predator and variation in response to local landscape characteristics. Biological Conservation 228:233–240.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Niedballa J, Sollmann R, Courtiol A, Wilting A. 2016. camtrapR: an R package for efficient camera trap data management. Methods in Ecology and Evolution 7:1457-1462.

Petracca LS et al. 2018. Robust inference on large-scale species habitat use with interview data: The status of jaguars outside protected areas in Central America. Journal of Applied Ecology 55:723–734.

Portig WH. 1965. Central American Rainfall. Geographical Review 55:68. Available from https://www.jstor.org/stable/212856?origin=crossref (accessed September 18, 2020).

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.r-project.org/.

Rabelo RM, Aragón S, Bicca-Marques JC. 2019. Prey abundance drives habitat occupancy by jaguars in Amazonian floodplain river islands. Acta Oecologica 97:28–33.

Rabinowitz A, Zeller KA. 2010. A range-wide model of landscape connectivity and conservation for the jaguar, Panthera onca. Biological Conservation 143:939–945.

Redo DJ, Grau HR, Aide TM, Clark ML. 2012. Asymmetric forest transition driven by the interaction of socioeconomic development and environmental heterogeneity in Central America. Proceedings of the National Academy of Sciences of the United States of America 109:8839–44.

Ripple WJ, Beschta RL. 2012. Large predators limit herbivore densities in northern forest ecosystems. European Journal of Wildlife Research 58:733–742.

Taylor MA, Alfaro EJ. 2005. Central America and the Caribbean, Climate of. Pages 183–189 Encyclopedia of World Climatology. Springer Netherlands. Available from http://link.springer.com/10.1007/1-4020-3266-8_37 (accessed September 18, 2020).

Terborgh J et al. 2001. Ecological Meltdown in Predator-Free Forest Fragments. Ecological meltdown in predator-free forest fragments. Science 294, 1923-1926

Thornton D, Zeller K, Rondinini C, Boitani L, Crooks K, Burdett C, Rabinowitz A, Quigley H. 2016. Assessing the umbrella value of a range-wide conservation network for jaguars (Panthera onca). Ecological Applications 26:1112–1124.

World Bank. 2020. Human population, DataBank Microdata Data Catalog. Available from https://data.worldbank.org/indicator/SP.POP.TOTL (accessed February 26, 2020).

Zeller KA. 2007. Jaguars in the New Millennium Data Set Update: The state of the jaguar in 2006. Maryland, US.

Appendices - Chapter 3

Appendix S1: Polymorphic nDNA microsatellite loci used for individual identification of the jaguar samples collected in the study region

Ind ID	FCA032		FCA075		FCA096		FCA100		FCA124		FCA126		FCA132		FCA208		FCA212		FCA225		FCA229		FCA275	
BZJ01	198	198	123	123	191	193	106	106	127	127	156	160	171	171	305	305	104	106	231	237	166	170	123	123
BZJ02	200	200	117	117	191	191	108	108	125	127	150	156	171	171	301	319	106	106	227	227	162	168	123	129
BZJ03	198	200	115	121	191	197	112	112	123	127	152	156	171	171	301	315	104	106	237	241	162	168	123	123
BZJ04	198	198	117	125	191	191	108	110	123	123	160	160	171	173	305	319	104	106	237	237	162	168	123	133
BZJ05	198	198	127	127	191	197	108	108	127	127	154	156	171	173	305	319	106	106	237	237	162	166	133	133
BZJ06	200	200	115	115	191	197	108	112	125	125	150	154	171	171	301	305	106	106	237	237	168	168	129	129
BZJ07	198	198	115	121	191	197	108	112	125	125	156	156	171	171	305	319	104	104	241	241	168	168	123	123
BZJ08	196	196	123	123	0	0	108	112	123	127	150	156	171	171	0	0	106	106	0	0	166	170	129	129
BZJ09	192	198	115	115	181	185	108	108	125	127	152	156	171	171	309	315	104	104	227	237	162	170	123	129
BZJ10	198	200	115	121	191	191	108	108	125	125	150	156	171	171	301	313	106	106	237	237	166	168	123	133
BZJ11	200	200	121	123	193	197	112	112	127	127	152	156	171	171	301	305	104	106	231	237	168	170	133	133
BZJ12	192	200	113	117	181	191	108	112	125	125	156	156	171	171	301	319	104	106	237	241	162	168	123	133
BZJ13	200	200	115	123	191	193	108	108	125	125	150	156	171	171	305	309	106	106	237	237	162	168	123	133
BZJ14	196	200	117	127	191	197	112	112	125	127	150	156	171	171	301	305	106	106	227	231	162	166	123	129
BZJ15	198	200	111	117	181	197	108	112	127	127	152	156	171	171	315	319	106	106	231	237	160	162	129	129
BZJ16	200	200	103	123	195	197	106	112	123	123	150	160	171	171	305	305	106	106	237	237	162	166	123	133
BZJ17	198	200	111	123	181	193	112	114	127	127	152	156	171	171	305	315	106	106	231	231	162	170	129	133
BZJ18	198	200	123	127	193	193	106	108	123	127	156	156	171	171	305	315	106	106	237	237	170	170	123	123
BZJ19	198	200	115	115	191	197	112	114	123	127	152	156	171	171	313	319	106	106	231	237	166	168	123	129
BZJ20	198	200	123	123	0	0	108	112	125	127	152	156	171	171	0	0	104	106	0	0	166	168	133	133
BZJ21	200	200	105	111	191	197	112	112	125	127	150	160	171	171	301	313	106	106	237	237	168	168	123	123
BZJ22	196	198	111	127	0	0	108	112	125	125	0	0	171	171	0	0	104	106	0	0	0	0	123	133
BZJ23	192	200	117	117	193	193	108	112	123	125	152	156	171	171	0	0	106	106	231	237	0	0	123	133
BZJ24	196	198	123	123	191	193	112	112	123	127	156	160	171	171	0	0	106	106	0	0	162	162	129	129
BZJ25	192	200	115	115	193	193	108	112	125	125	154	154	171	171	301	305	106	106	227	237	166	168	133	133
BZJ26	196	200	123	123	193	197	114	114	123	125	156	160	171	171	305	319	106	106	231	237	162	166	123	129
BZJ27	198	200	117	117	197	197	108	112	125	127	154	156	171	171	315	319	106	106	227	237	162	170	133	133
BZJ28	196	200	121	127	197	197	108	108	127	127	150	156	171	171	315	319	106	106	231	237	168	168	123	133
BZJ29	200	200	117	117	185	197	108	112	127	127	156	160	171	171	0	0	106	106	237	237	168	168	123	129
BZJ30	198	200	115	123	181	197	106	108	125	125	156	156	171	171	315	315	106	106	237	237	162	166	123	123
BZJ31	200	200	117	121	197	197	108	112	125	127	156	156	171	171	317	319	106	106	231	237	166	168	123	123
BZJ32	200	200	111	117	191	197	112	112	0	0	0	0	171	171	0	0	106	106	0	0	162	162	123	129
BZJ33	196	200	111	123	191	193	108	112	123	127	150	152	171	171	301	305	104	104	231	237	162	162	123	133
BZJ34	196	198	103	111	191	193	108	112	123	127	156	156	171	173	305	305	106	106	227	237	162	170	133	133

Continuation Appendix S1: Polymorphic nDNA microsatellite loci used for individual identification of the jaguar samples collected in the study region

Ind ID	FCA032		FCA075		FCA096		FCA100		FCA124		FCA126		FCA132		FCA208		FCA212		FCA225		FCA229		FCA275	
BZJ35	198	198	127	127	191	197	108	108	123	127	150	150	171	171	305	319	104	106	227	237	168	168	123	129
BZJ36	198	198	115	127	181	197	108	108	125	125	150	156	171	171	305	315	106	106	227	227	162	168	123	123
BZJ37	200	200	115	121	191	197	108	112	125	127	150	156	171	171	305	315	0	0	237	237	162	168	123	133
BZJ38	196	200	121	127	191	197	108	112	125	125	150	156	171	171	305	313	106	106	237	237	168	168	133	133
BZJ39	200	200	111	115	191	193	112	112	121	125	154	156	171	171	305	315	106	106	231	241	168	168	123	129

Appendix S2: Summary statistics of genetic diversity for jaguars in the study region[15]

Country	**n**	**N_A**	**A_R**	**H_O**	**H_E**	**F_{IS}**	**95% CI [LL,UL]**
Guatemala	15	4.33	3.35	0.67	0.6	-0.08	(-0.15,0.00)
Belize	50	5	3.38	0.54	0.6	0.12	(0.03,0.18)
Honduras	7	3.92	3.55	0.62	0.58	-0.01	(-0.13,0.18)

---

[15] Summary includes number of individuals (n), number of alleles (N_A), rarefied allelic richness (A_R), observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coeffcient (F_{IS}) and 95% confidence intervals (CI; 1,000 bootstraps) with lower (LL) and upper (UL) limits; Wultsch et al. (2016).

Appendix S3: Variables used to model gene flow of jaguar populations in Northern Central America and that have been shown to be significant for habitat use (Calderon et al. 2022)

Variable name	**Description**	**Reference**	***Expected effect***
treecov%	Percentage of forest cover	MODIS Vegetation Continuous Fields, yearly imagery at 250m resolution, (https://modis.gsfc.nasa.gov/data/)	+
non-vegetation%	Percentage of non-vegetation cover	MODIS Vegetation Continuous Fields, yearly imagery at 250m resolution, (https://modis.gsfc.nasa.gov/data/)	-
npp	Net primary productivity	MOD17A3 v055 MODIS/Terra Net Primary Production Yearly L4 Global 1 km SIN Grid at 1Km resolution, (https://lpdaac.usgs.gov/products/mod17a3v055/)	+
dist_roads	Distance from roads	Euclidian distance raster created from the original dataset of Global patterns of current and future road infrastructure, which used data of roads between the scales of 1:100 000 and 1:500 000 resolution (Meijer et al., 2018; https://iopscience.iop.org/article/10.1088/1748-9326/aabd42/meta)	+
built-up	Human constructed areas	Euclidian distance raster created from the original dataset of the European Commission (https://ghsl.jrc.ec.europa.eu/). Human settlements are recorded by the presence of any constructed, man-made object (e.g. buildings and associated structures, civil constructions)	-
dist_water	Distance from lakes, reservoirs and wetlands	Global database of lakes, reservoirs and wetlands, (Lehner & Döll 2004); https://www.sciencedirect.com/science/article/abs/pii/S0022169404001404	+
dist_riv	Distance from rivers	Euclidian distance raster created from the original dataset of 'A simple global dist_river bankfull width and depth database' at 1Km resolution (Andreadis et al. 2013, https://doi.org/10.1002/wrcr.20440)	+
elev	Elevation	USGS EROS Archive - Digital Elevation - Shuttle Radar Topography Mission SRTM, 90m resolution (https://www.usgs.gov/centers/eros/science/usgs-eros-archive-digital-elevation-shuttle-radar-topography-mission-srtm-1-arc?qt-science_center_objects=0#qt-science_center_objects)	-
ruggedness	Terrain complexity	Terrain Ruggedness Index (TRI), calculated from elevation raster using ArcGIS10	-

Appendix S4: Detailed Methods

We assessed the scale of effect of each of our variables (Jackson & Fahrig 2015; Mcgarigal et al. 2016) on jaguar gene flow, given that gene flow processes and functional connectivity are spatial-scale dependent (Cushman & Landguth 2010; Cushman et al. 2016). To identify the optimal scale for each variable, we smoothed each variable raster using a Gaussian kernel and varied its bandwidth across six scales: 1,000m; 3,000m; 6,000m; 8,000m; 16,000m; 32,000m (Fig 2a). These scales were chosen based on previous knowledge on the selected variables' scale of effect (Alvarenga et al. 2021), and the reported movement capabilities of jaguars (average net displacement 12.5 km/day; McBride & Thompson, 2018; Morato et al., 2016). Smoothing was performed with the R package 'smoothie' (Gilleland 2013). Each landscape variable at the above scales was transformed into a gene flow resistance surface hypothesis, converting the raw variable's values into resistance values using seven transformational forms (Peterman 2018), as to avoid assuming *a priori* a relationship between the raw values of an environmental variable and resistance to gene flow. The transformations tested were linear, monomolecular convex and monomolecular concave functions, in both their positive and negative forms, as well as the inverse Ricker transformation. Positive transformations represented cases in which resistance increased with increasing values of a variable; negative ones represented decreased resistance with increasing values of a variable; and the inverse Ricker represented lowest resistance at moderate values of a variable. This procedure generated 378 univariate resistance hypotheses (each variable with a specific scale of effect and a specific transformation).

Landscape resistance modelling

To optimize landscape resistance values and evaluate how landscape features affect jaguar gene flow in our study region, we evaluated scenarios of isolation-by-distance (IBD; Wright, 1942) and isolation by resistance (IBR; McRae, 2006; Peterman et al., 2014; Fig 2b). For this we created Euclidean, genetic and resistance distance matrices, calculating pairwise distances among all 72 individuals. All analyses were run in R v. 4.1.2. unless explicitly noted (R Core Team 2021). We calculated Euclidean distances with the 'rdist' package (Blaser 2020), genetic distances with 'ecodist' (Goslee & Urban 2007), and resistance distances across each univariate resistance hypothesis with the 'gdistance' package (van Etten 2017).

To test our scenarios of isolation, we ran linear mixed effects models using the maximum likelihood population-effects method (MLPE; Clarke et al., 2002). We used the code provided in the 'resistancega' R package (Peterman 2018), setting the restricted maximum likelihood to false. For the IBR models, our response variable was the genetic distance matrix and our predictors were the resistance and Euclidean distance matrices. To account for the autocorrelation of the pairwise distance matrices and thus increase model performance, we included Euclidean distance as a predictor in all of our IBR models (Row et al. 2017). To test the IBD scenario, we ran a model with genetic distance as our response, including Euclidean distance as the only predictor (null model).

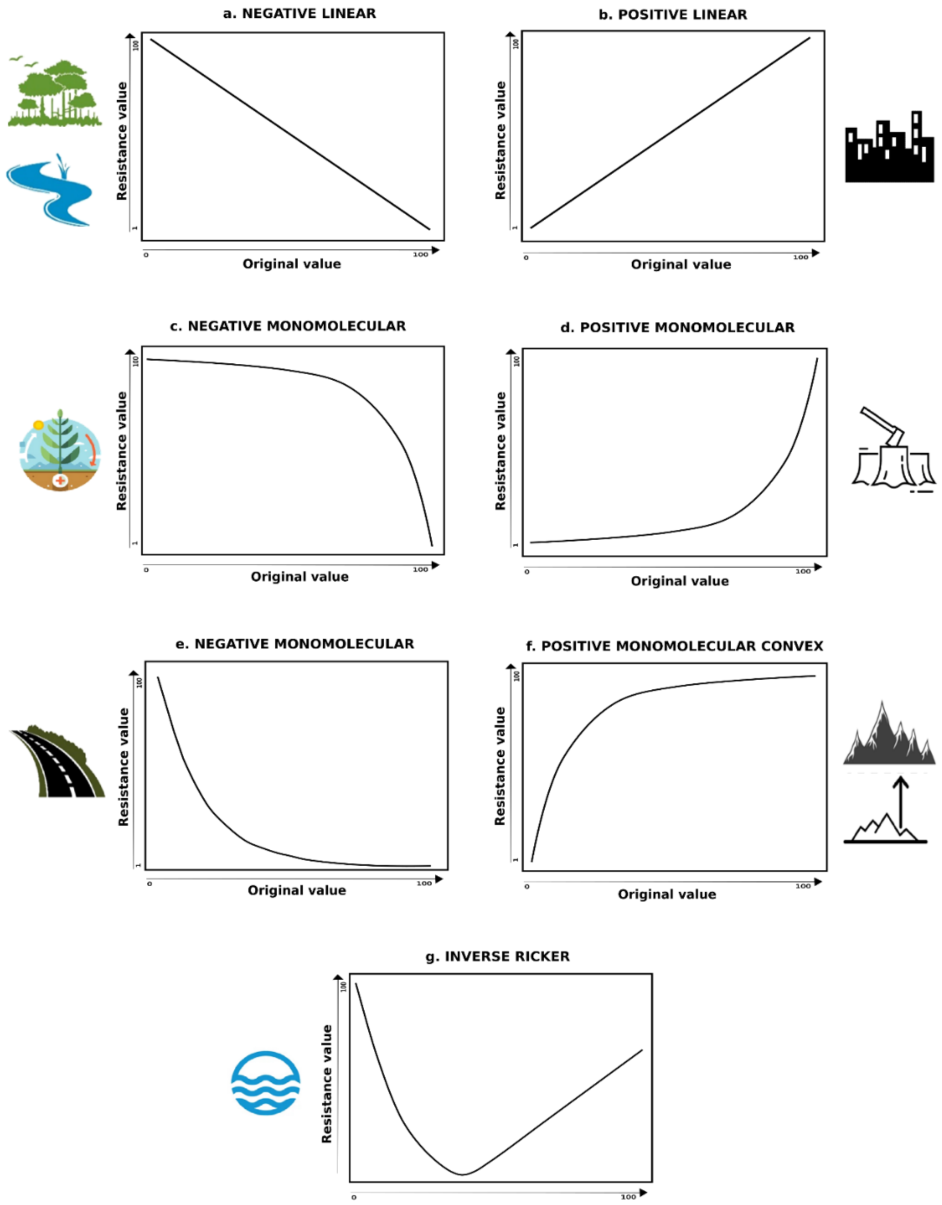
Our modelling sequence was as follows. We first identified the optimal scale and transformation for each covariate by running univariate models across all scales and transformational forms (Fig 2a). We evaluated these models using Akaike's Information Criterion corrected for small sample sizes AICc (Burnham & Anderson 2002) and retained the model with the lowest AICc value for each covariate. Secondly, we assessed correlations among predictors by running partial Mantel correlations between the covariates' resistance distance matrices using the 'vegan' R-package (Oksanen et al. 2022). Thirdly, we combined all non-correlated covariates (Pearson's moment correlation; $|r| < 0.6$) at their optimal scale and transformation to create multi-variable, multi-scale models of resistance (Fig 2b). For these multivariate models, we summed all variables in each model to create a single composite resistance surface across which resistance distances were calculated. We did so because animals do not experience elements separately while moving through a landscape, thus composite surfaces better reflect animal's responses to aggregated landscapes (Peterman & Pope 2021). All composite surfaces were rescaled from 1 to 100. Lastly, we evaluated the empirical support of each candidate model and retained the one with the lowest AICc value for all subsequent analysis. We report AICc, Bayesian Information Criterion BIC and both marginal and conditional R2 values for all univariate and multivariate resistance models as well as for the null model of isolation-by-distance.

Functional connectivity analysis

We assessed connectivity of jaguar populations using cumulative resistant kernels, a synoptic modelling approach which predicts and maps expected functional connectivity as a continuous surface, accounting for species' dispersal abilities (Fig 2c). For this we created a spatial layer of 2000 source locations from which to calculate resistant kernels across the study region. Source locations were obtained by sampling the region with the 'spatially balanced point tool' in ArcGIS 10.8.0 (ESRI 2022), using the linear inverse of the top resistance surface (rescaled from 0-1) as the probability of sampling inclusion. This allowed us to obtain a higher frequency of source locations in areas of low gene flow resistance while still providing good sampling coverage across the region. Resistant kernels were estimated with UNICOR software (Landguth et al. 2012) using the top resistance surface, source location layer, and the cost-distance threshold. The cost-distance threshold was calculated by multiplying the average daily net displacement reported for jaguars (in meters), by the intermediate resistance surface cost in our study landscape (12,500*95= 1,187,500).

For our subsequent connectivity analysis based on habitat suitability estimates, we repeated the above procedure and estimated resistant kernels for a new resistance surface created from the inverse of a recently developed jaguar habitat suitability map (Calderón et al. 2022). For this, a new source location layer with the same number of sampling locations was created (n= 2,000), and the cost-distance was specified at 6250 (12,500*0.5), adjusting to the scale of values of this new resistance surface.

Appendix S5: Top transformational forms[16] for each of the landscape covariates used for modelling jaguar gene flow in Northern Central America



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[16] Tree cover and distance from rivers (a), built-up area (b), net primary productivity (c), non-vegetation (d), distance from roads (e), elevation and terrain complexity (f), distance from lakes, reservoirs and wetlands (g).

Appendix S6: Multivariate resistance models of gene flow for jaguar populations in Northern Central America, including the isolation-by-distance model for reference (IBD) and the top model in bold

No.	Model	AIC	BIC	resistBeta	mR2	cR2
1	**dist_lakes + treecov + builtup + nonveg**	**-1084.17**	**-1054.96**	**0.65**	**0.69**	**0.83**
2	dist_lakes + treecov + builtup	-1083.40	-1054.19	0.65	0.69	0.83
3	treecov + builtup + nonveg	-1080.16	-1050.95	0.58	0.70	0.84
4	treecov + builtup	-1080.04	-1050.83	0.57	0.70	0.84
5	dist_rivs + treecov	-1065.78	-1036.57	1.24	0.69	0.83
6	dist_lakes + dist_rivs + treecov	-1055.72	-1026.52	1.18	0.67	0.82
7	dist_rivs + treecov + builtup	-1052.63	-1023.42	1.27	0.70	0.84
8	dist_lakes + dist_rivs + treecov + builtup	-1033.32	-1004.11	1.21	0.68	0.83
9	dist_lakes + builtup + npp	-1030.50	-1001.30	-0.62	0.68	0.83
10	dist_lakes + npp	-1029.37	-1000.16	-0.63	0.69	0.83
11	treecov + nonveg	-1009.28	-980.07	0.59	0.68	0.82
12	builtup + npp	-1000.22	-971.01	-0.57	0.68	0.84
13	dist_lakes + treecov + nonveg	-990.02	-960.81	0.63	0.65	0.81
14	dist_lakes + treecov	-988.02	-958.81	0.63	0.65	0.81
15	dist_lakes + dist_rivs + builtup	-966.43	-937.22	-0.82	0.66	0.83
16	dist_lakes + treecov + npp + elev	-964.23	-935.02	-0.94	0.54	0.76
17	dist_lakes + dist_rivs	-960.69	-931.48	-0.86	0.67	0.83
18	treecov + npp	-943.02	-913.81	0.98	0.68	0.83
19	builtup + npp + elev	-938.35	-909.14	-0.44	0.67	0.83
20	npp + elev	-935.54	-906.33	-0.43	0.67	0.83
21	dist_rivs + builtup	-861.70	-832.49	-0.96	0.63	0.83
22	dist_lakes + dist_roads	-850.14	-820.93	-0.51	0.65	0.82
23	dist_lakes + builtup + dist_roads	-847.12	-817.91	-0.49	0.64	0.82
24	treecov + elev	-825.76	-796.56	0.64	0.71	0.85
25	treecov + builtup + npp + elev	-822.36	-793.15	-0.72	0.50	0.75
26	treecov + nonveg + elev	-818.74	-789.53	0.65	0.71	0.85
27	dist_roads + elev	-816.07	-786.86	-0.30	0.65	0.82
28	builtup + dist_roads + elev	-813.21	-784.00	-0.30	0.64	0.82
29	treecov + npp + elev	-800.85	-771.65	-0.71	0.49	0.74
30	treecov + builtup + npp	-786.88	-757.67	1.02	0.68	0.83
31	treecov + builtup + elev	-774.25	-745.04	0.69	0.72	0.85
32	treecov + dist_roads	-773.76	-744.56	1.03	0.59	0.77
33	treecov + builtup + nonveg + elev	-768.52	-739.31	0.70	0.71	0.85
34	dist_lakes + treecov + dist_roads	-764.61	-735.41	1.25	0.57	0.76
35	builtup + nonveg + elev	-758.36	-729.15	-0.27	0.64	0.82
36	builtup + elev	-754.69	-725.49	-0.27	0.63	0.82
37	builtup + dist_roads	-752.58	-723.37	-0.34	0.62	0.81
38	nonveg + elev	-742.70	-713.49	-0.27	0.63	0.82
39	treecov + builtup + dist_roads	-740.64	-711.43	1.03	0.60	0.78

Continuation Appendix S6: Multivariate resistance models of gene flow for jaguar populations in Northern Central America, including the isolation-by-distance model for reference (IBD) and the top model in bold

No.	Model	AIC	BIC	resistBeta	mR2	cR2
40	builtup + ruggedness	-734.76	-705.55	-0.25	0.63	0.81
41	dist_lakes + treecov + builtup + dist_roads	-720.30	-691.09	1.23	0.58	0.76
42	dist_lakes + builtup + nonveg	-627.89	-598.69	-0.66	0.53	0.76
43	dist_lakes + treecov + npp	-610.13	-580.92	1.05	0.52	0.75
44	dist_lakes + builtup	-595.22	-566.01	-0.61	0.53	0.76
45	builtup + nonveg	-594.28	-565.07	-0.33	0.55	0.81
46	dist_lakes + nonveg	-502.04	-472.83	-0.42	0.55	0.77
47	dist_lakes + treecov + builtup + npp	-495.59	-466.38	1.03	0.53	0.74
48	dist_lakes + treecov + builtup + dist_roads + elev	-354.35	-325.14	-0.72	0.33	0.70
49	treecov + builtup + dist_roads + elev	-268.34	-239.13	-0.49	0.32	0.69
50	treecov + dist_roads + elev	-235.38	-206.17	-0.44	0.30	0.68
51	treecov + ruggedness	-197.28	-168.08	0.21	0.34	0.64
52	treecov + builtup + ruggedness	-163.65	-134.45	0.13	0.30	0.63
53	IBD	-146.14	-122.77	0.19	0.26	0.63

References

Alvarenga GC et al. 2021. Multi-scale path-level analysis of jaguar habitat use in the Pantanal ecosystem. Biological Conservation 253:108900.

Blaser N. 2020. rdist: Calculate Pairwise Distances.

Burnham KP, Anderson DR. 2002. Model Selection and Multimodel Inference - A Practical Information-Theoretic Approach. Second. Springer-Verlag New York, New York, USA. Available from http://www.springer.com/us/book/9780387953649 (accessed May 30, 2015).

Calderón AP et al. 2022. Occupancy models reveal potential of conservation prioritization for Central American jaguars. Animal Conservation 25:680–691.

Clarke RT, Rothery P, Raybould AF. 2002. Confidence limits for regression relationships between distance matrices: Estimating gene flow with distance. Journal of Agricultural, Biological, and Environmental Statistics 7:361–372.

Cushman SA, Elliot NB, Macdonald DW, Loveridge AJ. 2016. A multi-scale assessment of population connectivity in African lions (Panthera leo) in response to landscape change. Landscape Ecology 31:1337–1353.

Cushman SA, Landguth EL. 2010. Scale dependent inference in landscape genetics. Landscape Ecology 25:967–979.

ESRI. 2022. ArcGIS Desktop. Environmental Systems Research Institute, Redlands, CA.

Gilleland E. 2013. Two-dimensional kernel smoothing: Using the R package smoothie. Available from https://opensky.ucar.edu/islandora/object/technotes:514.

Goslee SC, Urban DL. 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software 22:1–19.

Jackson HB, Fahrig L. 2015. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24:52–63.

Landguth EL, Hand BK, Glassy J, E. SAC, Sawaya MA. 2012. UNICOR: a species connectivity and corridor network simulator. Ecography 35:9–14.

Lehner B, Döll P. 2004. Development and validation of a global database of lakes, reservoirs and wetlands. Journal of Hydrology 296:1–22.

McBride RT, Thompson JJ. 2018. Space use and movement of jaguar (Panthera onca) in western Paraguay. Mammalia 82: 540-549.

Mcgarigal K, Yi H, Zeller KA, Timm BC, Cushman SA. 2016. Multi-scale habitat selection modeling : a review and outlook. Landscape Ecology 31:1161–1175.

McRae BH. 2006. Isolation by resistance. Evolution 60:1551.

Morato RG et al. 2016. Space use and movement of a Neotropical top predator: the endangered jaguar. PLOS ONE 11:e0168176.

Oksanen JARI et al. 2022. vegan: Community Ecology Package. R package version 2.5–7.

Peterman WE. 2018. ResistanceGA: An R package for the optimization of resistance surfaces using genetic algorithms. Methods in Ecology and Evolution 9:1638–1647.

Peterman WE, Connette GM, Semlitsch RD, Eggert LS. 2014. Ecological resistance surfaces predict fine-scale genetic differentiation in a terrestrial woodland salamander. Molecular Ecology 23:2402–2413.

Peterman WE, Pope NS. 2021. The use and misuse of regression models in landscape genetic analyses. Molecular Ecology 30:37–47.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.r-project.org/.

Row JR, Knick ST, Oyler-McCance SJ, Lougheed SC, Fedy BC. 2017. Developing approaches for linear mixed modeling in landscape genetics through landscape-directed dispersal simulations. Ecology and Evolution 7:3751–3761.

van Etten J. 2017. R package gdistance: Distances and routes on geographical grids. Journal of Statistical Software 76:1–21. Available from https://doi.org/10.18637/jss.v076.i13.

Wright S. 1942. Isolation by distance. Genetics 28:114–138.

Wultsch C, Caragiulo A, Dias-Freedman I, Quigley H, Rabinowitz S, Amato G. 2016. Genetic Diversity and Population Structure of Mesoamerican Jaguars (Panthera onca): Implications for Conservation and Management. PLOS ONE 11:e0162377.

Appendices - Chapter 4

Appendix S1: Top studies, Articles that matched selected criteria and were used for analysis

Alexander JS, Agvaantseren B, Gongor E, Mijiddorj TN, Piaopiao T, Redpath S, Young J, Mishra C. 2021. Assessing the Effectiveness of a Community-based Livestock Insurance Program. Environmental Management 68:87–99.

Alexander JS, Bijoor A, Gurmet K, Murali R, Mishra C, Suryawanshi KR. 2022. Engaging women brings conservation benefits to snow leopard landscapes. Environmental Conservation 49:180–186.

Boronyak L, Jacobs B, Wallach A, McManus J, Stone S, Stevenson S, Smuts B, Zaranek H. 2022. Pathways towards coexistence with large carnivores in production systems. Agriculture and Human Values 39:47–64.

Chausson A, Gurd H, Foley J, Bhalla S, Lekilelei J, Otieno T, Lejale B, Lenasalia P, Milner-Gulland EJ. 2022. Evaluating the impact of Warrior Watch: Behaviour change to promote human-lion coexistence. Biological Conservation 271: 109571.5. de la Torre, J. A., Camacho, G., Arroyo-Gerala, P., Cassaigne, I., Rivero, M., & Campos-Arceiz, A. (2021). A cost-effective approach to mitigate conflict between ranchers and large predators: A case study with jaguars in the Mayan Forest. Biological Conservation, 256(March). https://doi.org/10.1016/j.biocon.2021.109066

Espinosa S, Jacobson SK. 2012. Human-wildlife conflict and environmental education: evaluating a community program to protect the Andean Bear in Ecuador. Journal of Environmental Education 43:55–65.

Hazzah L, Dolrenry S, Naughton L, Edwards CTT, Mwebi O, Kearney F, Frank L. 2014. Efficacy of two lion conservation programs in Maasailand, Kenya. Conservation Biology 28:851–860.

Marino A, Ciucci P, Redpath SM, Ricci S, Young J, Salvatori V. 2021a. Broadening the toolset for stakeholder engagement to explore consensus over wolf management. Journal of Environmental Management 296:113125.

Martin JV. 2021. Peace in the valley? Qualitative insights on collaborative coexistence from the Wood River Wolf Project. Conservation Science and Practice 3:1–16.

Mishra C, Allen P, McCarthy T, Madhusudan MD, Bayarjargal A, Prins HHT. 2003. The role of incentive programs in conserving the snow leopard. Conservation Biology 17:1512–1520.

Mulder MB, Kwiyega JL, Beccaria S, Bwasama SS, Fitzherbert E, Genda P, Caro T. 2019. Lions, Bylaws, and Conservation Metrics. BioScience 69:1008–1018.

Richie L, Oppenheimer JD, Clark SG. 2012. Social process in grizzly bear management: Lessons for collaborative governance and natural resource policy. Policy Sciences 45:265–291.

Salvatori V et al. 2021. Are large carnivores the real issue? Solutions for improving conflict management through stakeholder participation. Sustainability (Switzerland) 13:1–24.

Sonam K, Dorjay R, Khanyari M, Bijoor A, Lobzang S, Sharma M, Suresh S, Mishra C, Suryawanshi KR. 2022. A Community-based conservation initiative for wolves in the Ladakh Trans-Himalaya, India. Frontiers in Ecology and Evolution 10:1–8.

Wilson SM, Bradley EH, Neudecker GA. 2017. Learning to live with wolves: Community based conservation in the Blackfoot Valley of Montana. Human-Wildlife Interactions 11:245–257.

Young JC et al. 2021. Community-based conservation for the sustainable management of conservation conflicts: Learning from practitioners. Sustainability 13:1-20.