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Jaguars in the borderlands: Multinatural conservation for coexistence in the Anthropocene

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Conservation in the human-dominated Anthropocene involves negotiations among diverse stakeholders. However, these stakeholder inclusion schemes are often superficial, leading to unsuccessful interventions. Here we apply the theory of multinaturalism as an operational starting point for stakeholder engagement efforts, to deepen local involvement and work towards coexistence. Multinaturalism posits that natures are multiple and can be known in many ways, and that many natures can coexist in the same geographical space. Using the northern jaguar population in the US-Mexico borderlands as a case study, we investigate, through semi-structured interviews, the natural realities ('natures') of various stakeholders involved in borderland jaguar conservation. We define a nature as an individual's or group's *perceptions, knowledge, values, attitudes, and actions* towards jaguars. We construct each stakeholder group's natural reality of this jaguar population through applied thematic analysis, and we identify which aspects of stakeholders' natures are similar and different, particularly across the international border. For example, we found that many conservationists and activists value the jaguar as an apex predator because its presence signifies ecosystem health and balance, while some ranchers hold existence value for the jaguar's power and beauty, but resent its role as a predator, due to potential for conflict with livestock. This information provides a greater understanding of differences in realities that may cause conflicts over wildlife-related decisions, and can be used by local conservation actors to facilitate collaboration in a complex transboundary region. This interdisciplinary study highlights the importance of investigating the human dimensions of conservation completely, while treating all forms of knowledge about nature seriously and equally. Due to the unique nature of human-wildlife interactions, each conservation situation requires bespoke consideration, and particularly in diverse landscapes, a multinatural approach offers a novel path towards sustainable human-wildlife coexistence.

KEYWORDS

multinaturalism, human-wildlife coexistence, human dimensions, interdisciplinary conservation, transboundary conservation, jaguar (*Panthera onca*), Anthropocene, stakeholder engagement

1 Introduction

1.1 Conservation and coexistence in the Anthropocene

Westernized wildlife conservation strives to save nature in a human-dominated world (Western, 2000). However, the Anthropocene reality, with mankind as a major geological force, challenges attempts to protect ‘wilderness’ – areas of pristine, untouched nature – from human influence (Crutzen and Stoermer, 2000). As humans and wildlife increasingly share space in new ways (e.g. the rise of urban wildlife in North America, McCance et al., 2017 or the return of wolves to Europe for the first time in many human generations, Fenske and Tschofen, 2020), the Anthropocene idea renders obsolete normative ideas of nature as separate from human society. Nonetheless, many novel and working ecosystems still hold high biodiversity value, so our efforts to save nature must be reimagined – with people integral to every ecosystem, and our managed landscapes as a part of, not apart from, nature (Marris, 2011; Ellis, 2013). Here we investigate the natural realities of ten stakeholder groups sharing a landscape with jaguars in the US-Mexico borderlands, applying the anthropological theory of multinaturalism to wildlife conservation. This approach allows us to explore and compare the lived experiences of people coexisting with wildlife in a complete and holistic manner.

The Anthropocene’s emergence has spurred calls for new modes of conservation, with emphases ranging from sustaining human livelihoods (Phang et al., 2019), to biopolitical practice (Lorimer, 2015), and post-capitalist valuation of nature (Buscher and Fletcher, 2020). What each of these proposals shares is a renewed attention to human-wildlife interactions (HWIs). HWIs range from negative (conflict) to neutral (passive tolerance) to positive (coexistence) (Frank, 2016). Historically, conservation focused on mitigation of negative human-wildlife conflicts (HWCs), reducing direct and indirect costs for humans (e.g. livestock depredation and detrimental health effects, Barua et al., 2013) and detrimental impacts on wildlife (e.g. population and species declines, Nyhus, 2016). However, as humans and wildlife continue to enter each other’s traditional spaces, creation of positive coexistence approaches may better enable humans to live with, rather than separate from, wildlife (Madden, 2004).

Though people and wildlife have shared landscapes for millennia, formal study of human-wildlife coexistence is relatively new to conservation biology, and the field lacks a consistent definition of the term (Woodroffe et al., 2005). Carter and Linnell (2016) describe coexistence as a ‘dynamic but sustainable state in which humans and [wildlife] co-adapt to living in shared landscapes’ (p575). Coexistence is complex and context-laden, with varied meanings across landscapes, but this definition highlights three key aspects: coexistence is dynamic, active, and integrated. Dynamic, because coexistence is not a fixed endpoint, with the human-wildlife relationship constantly evolving and negotiated daily (Yurco et al., 2017; Hill, 2021). Active, because coexistence is facilitated by mutual adaptations. Conscious and unconscious behavior changes by humans and wildlife minimize their interactions, allowing them to share time and space (Carter and Linnell, 2016; Connolly et al., 2021). Integrated, because under coexistence, humans and wildlife interact

as parts of a broader whole. The landscape is then, one socioecological entity, a human-wildlife-habitat system, and coexistence arises from the interconnectedness. Emphasizing coexistence over conflict encourages positive solutions to conservation challenges, while appreciating the plurality of stakeholder needs (Peterson et al., 2010; Redpath et al., 2015; IUCN, 2020).

1.2 Deepening stakeholder engagement

In recent decades, stakeholder engagement has become a common practice in conservation, to increase trust among participants and improve wildlife management (Lauber et al., 2012). Stakeholders are ‘the people and organizations who affect or are affected by a decision’, and their involvement may be direct or indirect (Sterling et al., 2017, p160). In theory, inclusion of local stakeholders can lead to improved local livelihoods and success of conservation initiatives, particularly when these groups impact or rely on the target of conservation action (Adams and Hutton, 2007). This is especially important in HWC, where multiple groups are involved in disagreements over wildlife management (Dickman, 2010). However, in practice, stakeholder inclusion is often superficial and passive (Reed, 2008; Madden and McQuinn, 2014). Engagement processes may then fail to identify underlying social conflicts, resulting in ineffective mitigation (Jolibert and Wesselink, 2012; Zimmerman et al., 2020). The promised benefits of participation efforts then go unrealized, fostering disillusionment and further contention amongst practitioners and stakeholders (Reed, 2008; Mbaiwa and Stronza, 2011).

Ultimately, the sustainability of decisions made with stakeholders depends on the perception of fairness in engagement processes and degree of participation by these stakeholders – a concept known as participatory justice (Sterling et al., 2017; McInturff et al., 2021). Interventions borne out of active, collaborative, transparent decision-making are more likely to succeed (Minter et al., 2014). However, well-designed engagement strategies do not always lead to better conservation outcomes, in part because these processes do not occur in a vacuum (Young et al., 2013; Sterling et al., 2017). A range of factors can significantly impact these efforts, from international political conflicts, to local governance regimes, to stakeholders’ preconceptions of each other (Baral and Stern, 2011). Nevertheless, participation processes tailored to local socio-political and environmental contexts can overcome unfavorable circumstances for the benefit of biodiversity (Brooks et al., 2013).

Enhancing our understanding of these social dimensions is critical for conservation in the Anthropocene, as diverse stakeholders share space with wildlife in new ways (Marchini, 2014; Lorimer, 2015). To create human-wildlife coexistence, conservationists must deepen engagement by investigating each stakeholder’s perspective and mitigating these human-human conflicts (Dickman, 2010). This requires consideration of multiple stakeholder knowledges and values, and an understanding of each group’s viewpoints and decision-making processes (Cullman, 2015). To enhance participation, and combat participatory injustice, conservationists must engage with a range of local attitudes and perceptions, to prevent value disconnects from eroding trust and communication (McInturff et al., 2021). Interventions framed around

the views of just one group may not appeal to all relevant stakeholders (Gore and Kahler, 2012).

1.3 Multinaturalism: Theory and opportunities

To describe this theory, we use the term nature to refer to components of the natural world, including wildlife and human experiences of wildlife, and the term culture to refer to human societal traditions and norms. Coined by anthropologist Viveiros de Castro (1998), the theory of multinaturalism may provide a useful framework for investigating differing stakeholder perspectives on wildlife conservation. Viveiros de Castro (1998) noted that Amazonian Amerindians consider some nonhuman species to possess an identical culture, i.e. societal norms, to that of humans, and that each human and nonhuman group apprehends the natural world from their distinct perspective. In this way, the Amerindian ontology is defined by one culture and multiple natures. This multinaturalism differs from multiculturalism, under which there is only one true nature, defined by science, of which groups may hold varied cultural understandings (Descola, 2012). The multiculturalist framework therefore necessarily operates under a mononaturalism, which privileges scientific knowledge and concern as the singular truth and singular nature (Blaser, 2009).

For Latour (2004), a multinatural understanding describes the multiple ways that nature can be perceived, valued and contested. Lorimer (2015) applied this framework to conservation in the Anthropocene, where ‘natures are materially multiple and can be legitimately known in many ways’ (p39). In contrast to Viveiros de Castro, this newer definition allows for both multiple cultures and multiple natures, and can be more usefully applied to stakeholder engagement in wildlife conservation (Lorimer, 2015). This multinaturalism recognizes cultural and ethnic diversity among humans (Lorimer, 2012). Here, cultural differences contextualize the multiple natures held by people in any one area, because values

and attitudes towards nature can stem from community cultural traditions (Martínez-Dueñas et al., 2017). This approach accepts not just multiple cultures but also a multiplicity of complete natural worlds, with each world and each nature containing its own human-wildlife relations (Martínez-Dueñas et al., 2017).

The Anthropocene itself is multinatural, bringing a ‘reflexive awareness of the always-entangled nature of humans with their environments’ (Lorimer, 2015, p4). This multiplicity of diverse peoples and natures sets the stage for how conservation should be carried out – under the framework of multinaturalism. Conservation has progressed from operating under mononaturalism, to multiculturalism, and now to multinaturalism (Figure 1). The field of wildlife conservation arose out of desire to protect nature *from* humans, an ideology exemplified by the creation of American national parks in the late nineteenth century (Nash, 2001). Decades later, the conservation discourse turned to saving nature for people, valuing biodiversity in terms of economic contribution to society (Pearce and Moran, 1994). At the same time, practitioners began to recognize the importance of including a diversity of local communities in conservation initiatives, considering both nature *and* people (Berkes, 2007). However, these perspectives are often sidelined when they contradict the assumptions of scientific goals, because conservationists view themselves as the experts, uniquely able to objectively speak for nature (Blaser, 2009). These inclusion efforts have rarely, if ever, attended to a diversity of realities. Now, conserving in the Anthropocene, we must embrace natures *with* peoples, as entangled and inseparable (Marris, 2011). Recognizing this pluralism acknowledges the novel forms of nature co-produced by people and their environments (Bhagwat, 2018).

Different natures can come into contact because, critically, many worlds and their particular beings exist in the same geographical space (Martínez-Dueñas et al., 2017). This sharing of space is what facilitates interactions between stakeholder realities, sometimes resulting in conflict (Martínez-Dueñas et al., 2017). Typically in such encounters, only one nature is privileged by wildlife management and policy – that of the conservationist, defined by

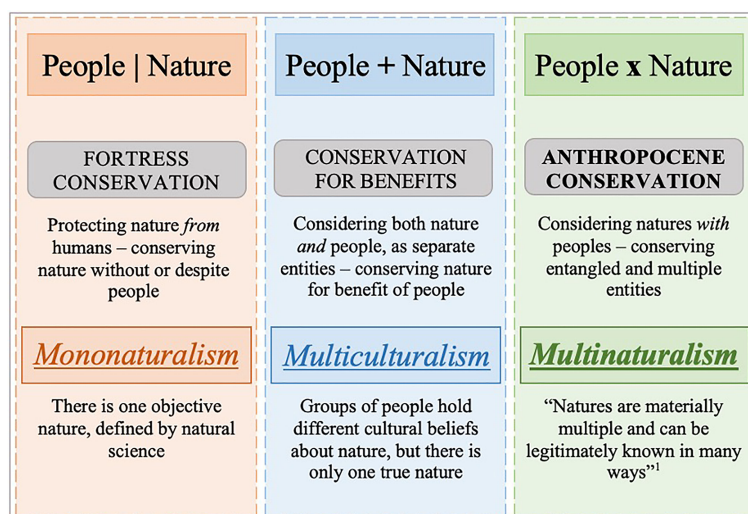


FIGURE 1
From mono to multinaturalism: Frameworks for conservation.¹Lorimer, 2015, p39.

modern science (Blaser, 2009). This leads to stakeholder dissatisfaction in participatory processes, because their worlds are dismissed as simply cultural misinterpretations of an ‘objective’ nature (Blaser, 2009). If conservationists instead accept these different natures to be realities, and seriously investigate them when working with stakeholder groups, we will gain a deeper understanding of what drives stakeholder conflicts and become better equipped to mitigate them. Failure to address the disparities in norms, values, and knowledges that exist between these natures can undermine coexistence (Carter and Linnell, 2016).

Stakeholders’ multiple natures are related to their worldviews, or ‘the multiple truths about, or ways of knowing and understanding the world’ (Alexander and Draper, 2019, p318; Proctor, 1998). Worldviews also encompass beliefs and behaviors towards human and nonhuman beings and phenomena, including wildlife (Koltko-Rivera, 2004). Following Alexander and Draper (2019), our definition of worldview here aligns with the philosophical worldview, reflecting beliefs about fundamental aspects of reality which ‘ground or influence all one’s perceiving, thinking, knowing, and doing’ (p311).

Expanding on this concept, we identify the five components of a stakeholder nature as an individual’s (or group’s) *knowledge, perceptions, valuation, attitudes, and actions* of/towards the natural world. These aspects of a natural reality encompass an individual’s relations with and behavior towards wildlife and their shared landscape (Alexander and Draper, 2019). A stakeholder’s nature encompasses not just their worldview but also their lived experience of and interactions with nature, thereby legitimizing their reality and forcing conservationists to accept it as ‘truth’, something previously reserved for scientific observation. By investigating these five components to characterize and compare stakeholders’ natures, conservationists can gain insight into the root drivers of human-wildlife and human-human conflicts. This understanding can increase the efficacy of coexistence strategies by identifying where and how we can best communicate among stakeholder realities (Pooley et al., 2017; Harrison and Loring, 2020).

1.4 The jaguar (*Panthera onca*) and its conservation

Jaguars (*Panthera onca*) have coexisted with humans across many natures and political boundaries for millennia (Zeller, 2007). The Americas’ largest cat, jaguars historically occurred from southern Argentina to the southwestern United States, and have for centuries held an important place in Indigenous cultures and cosmologies throughout their range (Saunders, 1994). Symbolizing sacred power and beauty across the Americas, jaguar iconography has been woven into religion, art, and cultural rituals since at least the Olmec civilization of 1150 BC (Coe, 2002). The Olmecs, Maya and Aztecs revered and worshipped the jaguar as a warrior and deity (Saunders, 1998). For present-day traditional Maya, the jaguar can see into the spirit world, and modern Mayan shamans are believed to take on a jaguar’s form (Klein et al., 2002).

Today, the iconic spotted cat inhabits 18 Latin American countries plus the United States (where they have been almost eliminated), occupying just 51% of their former range (Guggisberg, 1975; Quigley et al., 2017). Jaguars are typically associated with the

tropics, but in fact occupy a diverse array of habitats covering 11.6 million km² including dry forests, montane grasslands, and xeric shrublands (Zeller, 2007). Because of their high space requirement (adult male home ranges can exceed 230 km²), jaguars act as an umbrella species, supporting high-quality habitat for hundreds of co-occurring mammal species (Morato et al., 2016; Thornton et al., 2016). As apex predators, jaguars also play a role in maintaining ecological systems, predating on over 109 other species (Zeller, 2007). With an estimated population of approximately 173,000 individuals, the jaguar is currently listed as Near Threatened on the IUCN’s Red list, with a decreasing population trend across their entire distribution (Quigley et al., 2017; Jędrzejewski et al., 2018), and listed on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (CITES, 2012).

Major threats to long-term jaguar survival include direct persecution by people, decimation of prey populations, and habitat loss and fragmentation (Zeller, 2007). The most serious, persecution by people, is driven largely by pro-active and retaliatory killing from conflict with humans and livestock (Cavalcanti et al., 2010; Jędrzejewski et al., 2017). Human-jaguar conflict has been documented in each of the 19 jaguar range states, resulting in fear and low tolerance (Sanderson et al., 2002; Tortato et al., 2017). Defaunation is another key threat to jaguars, as important prey populations (e.g. deer, peccaries) are overhunted by humans (WWF, 2020). Lack of natural prey not only contributes to jaguar population declines, but also forces jaguars to prey on livestock, exacerbating human-jaguar conflict (Zeller, 2007). Lastly, habitat loss and fragmentation reduce and isolate jaguar populations, increasing susceptibility to local extinctions and jeopardizing range-wide genetic integrity of the species (Medellín et al., 2016).

1.5 Case study: The northern jaguars – los tigres de la frontera

1.5.1 Historic occurrence in the United States

Jaguars historically roamed across the southwestern United States, primarily in Arizona and New Mexico but also through Texas and California (Brown and López González, 2001). The forests, woodlands and even deserts of the American southwest were jaguar country, and jaguars were documented throughout Arizona, as far north as the Grand Canyon (Brown and López González, 2001). We know this thanks to photographs, physical remains, and accounts of jaguars from hunters and cowboys, and because of their cultural importance among Native tribes of the American southwest (Brown and López González, 2001; Pavlik, 2003). Jaguars were extirpated from this northernmost part of their range in the 1960s, likely due to hunting; the last female was shot in Arizona’s White Mountains in 1963, and two years later the last known resident jaguar was killed in the Patagonia Mountains, south of Tucson, Arizona (Brown and López González, 2000).

After three decades without jaguars, in 1996, two different males were photographed on separate occasions by hunters – the first photos ever taken of live jaguars in the United States (Glenn, 1996; Childs, 1998). The next year, the US Fish and Wildlife Service (USFWS) listed jaguars as endangered in the United States (USFWS, 1997). Over a decade later and after repeated litigation by

local activist groups, USFWS initiated recovery planning, a process to identify critical jaguar habitat in the southwestern United States (USFWS, 2010). After some controversy, the Jaguar Recovery Plan was finalized and made public (USFWS, 2018). The findings suggested that habitat in the US could only support a maximum of six jaguars, too few for a viable population, and recommended that recovery efforts be focused south of the US-Mexico border (USFWS, 2018).

1.5.2 2021 reintroduction proposal

In 2021, two significant papers were published about borderland jaguars, and both received global news coverage (Sanderson et al., 2021a; Sanderson et al., 2021b). The first re-evaluated habitat suitability for jaguars in the American southwest, and the second made the first official call to reintroduce jaguars to the United States (Sanderson et al., 2021a; Sanderson et al., 2021b). Sanderson et al. (2021a) conducted a review of jaguar habitat modelling and assessment efforts over the last 25 years, and focused on previously unconsidered areas north of Interstate-10, in the central mountain ranges of Arizona and New Mexico. These areas were excluded by USFWS in their 2018 Recovery Plan, despite evidence that jaguars had occurred there before the highway was constructed in 1956 (Brown and López González, 2001). These authors found that Arizona and New Mexico could in fact support up to 90–151 adult jaguars, raising the carrying capacity of the US to a viable breeding population level (Sanderson et al., 2021a). Numerous similarly-sized jaguar populations have persisted throughout their range despite relative isolation (Zanin et al., 2015). This substantial increase in potential carrying capacity creates new opportunity for jaguar conservation in the United States.

Rewilding and reintroduction are often discussed in the context of conservation in the Anthropocene (Corlett, 2016). These practices are usually controversial, largely due to the high level of human involvement in physically translocating animals on the landscape (Jørgensen, 2015). Until very recently, the leading view in the borderlands was that jaguars were ‘rewilding themselves’ – returning to the US on their own, with no physical aid from humans (Northern Jaguar Project, 2021). This idea was supported by occasional captures of jaguars very near to and/or north of the border; not common, but frequent enough to fuel hope for the future (Northern Jaguar Project, 2021).

In light of the results from their habitat reassessment, Sanderson et al. called for the reintroduction of jaguars by physical translocation into the United States (2021b). They argued that the landscape is too fragmented to permit natural reestablishment across the border, so active translocations are now ‘essential to species conservation, ecosystem restoration, and rewilding’ (Peters, 2017; Miller, 2019; Sanderson et al., 2021b, p2). Proposed benefits of reintroduction include the addition of a distinctive habitat type in Arizona and New Mexico, Madrean Evergreen Woodland, a zone where subtropical and temperate species meet (Brown, 1994). Restoring jaguars to this habitat would enhance ecological representation for the species, and an additional apex predator could improve ecosystem quality (Sanderson et al., 2002; Sanderson et al., 2021b).

However, many unknown variables remain. The ecological suitability of these areas is uncertain, because existing habitat models are weak on prey availability, and it is not possible to

predict exactly how future climate change will change jaguar distribution (Povilitis, 2015; Sanderson et al., 2021b). It is also unclear where the reintroduced jaguars will be obtained – captive-bred or wild-sourced – particularly because the nearest populations in Sonora are too rare to permit removal of individuals for translocation (Northern Jaguar Project, 2021; Sanderson et al., 2021b). Because the proposal is so new, many ecological, social, economic and political questions must be addressed before any reintroduction efforts can move forward.

This proposal is not the first to reintroduce a large predator to the US. Most famously, gray wolves (*Canis lupus*) were reintroduced to Yellowstone National Park, after a long and controversial negotiation process (Smith et al., 2003). Around the same time, Mexican gray wolves (*C. lupus baileyi*) were reintroduced to Arizona and New Mexico, following a similarly long and complex set of agreements and compromises (Brown and Parsons, 2001). As with the wolves, reintroduction of jaguars to the southwest will require collaboration between many stakeholders: national governments, the USFWS, state game agencies, ranchers, Tribal nations, NGOs, and local citizens (Hernandez et al., 2014). Wolf reintroduction has been fairly successful; Arizona and New Mexico are now home to over 160 Mexican gray wolves (USFWS, 2020). However, poaching still occurs, and existing hostility towards wolves, and USFWS’s reintroduction process, may exacerbate apprehension around the jaguar’s potential return, particularly on Native-owned lands (Gardner, 2018). Because this study was planned and initiated before the reintroduction proposal was published in May 2021 (Sanderson et al., 2021b), it does not center on stakeholder attitudes towards reintroduction. However, information generated here on both stakeholder worldviews and on multinaturalism as an engagement framework can contribute to planning for future reintroduction-focused research.

1.5.3 An opportunity for multinaturalism to facilitate coexistence

Because of the complex binational politics and diverse stakeholder community, we need bespoke approaches to jaguar conservation in the US-Mexico borderlands. This makes the northern jaguar population an ideal case for application of multinaturalism. The borderlands clearly provide a landscape of coexistence and interaction of multiple natures in the same geographical space, with the jaguar inhabiting the worlds of conservationists, activists, and ranchers on both sides of the international border in different ways. We investigated these natures to identify similarities and differences, to better understand stakeholder conflicts and coexistence with jaguars across this binational landscape.

Our primary aim was to examine the usefulness of applying multinaturalism to conservation. We propose multinaturalism as a framework through which we can meaningfully deepen stakeholder engagement in conservation landscapes of the Anthropocene, and use the borderland jaguar population as a case study to showcase potential for wider application. We investigate, through semi-structured interviews, the *perceptions, knowledge, values, attitudes, and actions* towards jaguars of various stakeholders involved in borderland jaguar conservation. We then construct, through applied thematic analysis, each stakeholder group’s natural reality (‘nature’) of this jaguar population. We identify which aspects of

stakeholders' natures are similar and which are different, particularly across the international border, and how these differences may cause conflicts over wildlife-related decisions. Lastly, we consider how differences between natures can be communicated and similarities built upon to facilitate stakeholder collaboration, working towards human-jaguar coexistence.

2 Methods

2.1 Study area

The US-Mexico border runs for 3,145 km from California to Texas (and from Baja California to Tamaulipas) (Figure 2) (IBWC, 2015). The area immediately adjacent to the border in both countries has become known as the borderlands, but the region 'has no one set of defining boundaries' (Uptake, 2013, p3). The dynamic physical and cultural diversity of the borderlands make designating strict edges difficult, but definitions typically include the areas within approximately 300 km on either side of the border (Parcher et al., 2013). Potential jaguar habitat and previous sightings occur primarily in the Arizona and New Mexico (and Sonora and Chihuahua) borderlands, which span a combined length of 890 km (Parcher et al., 2013) (Figure 2). This area is also known as the Madrean Sky Islands, 'named for the 55 pine- and oak-studded mountain "islands" encompassed within and separated by desert and grassland "seas"' (Sky Island Alliance, 2021, p1). The Madrean Sky Islands are a world biodiversity hotspot, studded across the Sonoran and Chihuahuan Deserts to connect the northern end of the Sierra Madre Occidental in Mexico to the southern Colorado Plateau in the US (Warshall, 1995). Home to over 7,000 species of plants and animals, a Madrean Sky Island may cover up to six different plant biomes as it climbs in elevation, from desert scrub, to oak woodland, to fir forest (Sky Island Alliance, 2021).

Because of their ecological uniqueness, the US-Mexico borderlands hold great potential for transboundary conservation

(Brenner and Davis, 2012). However, differences in administrative authority and land tenure, combined with increasing politicization and militarization of the border make binational coordination very challenging. For the last 15 years, this complex situation has been exacerbated by construction of a border wall, as part of anti-immigration efforts from the US. In 2006, President George W. Bush authorized construction of 1,125 km of fence along the southern border (Secure Fence Act, 2006). In doing so, the Department of Homeland Security had to waive protections from federal environmental legislation, including the Endangered Species Act, the Clean Water Act, and the Migratory Bird Treaty Act (Wilson and Donnan, 2012). Construction was largely halted in 2010 under the Obama administration, but from 2016-2020, President Trump oversaw reinforcement of 700 km of existing border fence with taller, thicker barriers, and built an additional 120 km (Giles, 2021). In January 2021, President Biden halted any further construction of the wall. It currently spans approximately 1,200 km, including almost all of the Sky Islands region (The White House, 2021). In addition to heightening political tensions, the border wall and its construction processes have significantly degraded landscape connectivity. The physical barrier disrupts migration and dispersal routes, preventing wildlife from accessing critical resources including food, water and mates (Peters et al., 2018). It is increasingly difficult for large endangered animals such as the jaguar, Mexican gray wolf, and Sonoran pronghorn (*Antilocapra americana sonoriensis*) to disperse across the border, fragmenting already at-risk populations (Peters et al., 2018).

2.2 The northern jaguar population

The nearest breeding population to the US is based in northern Sonora, Mexico; it contains an estimated 80-120 jaguars, approximately 200 km south of the border (Northern Jaguar



FIGURE 2

Map of the US-Mexico border. The borderlands are typically considered to be the areas within 300 km north and south of the border. Jaguar observation data taken from the public US Fish and Wildlife Service's Jaguar Observation Database (jaguardata.info/#). Observations include first-, second-, and third-hand reports of jaguar presence from the 20th and 21st centuries. Created with QGIS 3.16.13.

Project, 2021). These ‘northern jaguars’ are not an official subspecies, but are somewhat genetically and phenotypically distinct from southern populations. Jaguars from Arizona and Sonora possess unique mitochondrial DNA haplotypes and Culver (2016) have hypothesized that these may confer genetic adaptations to the hot, arid conditions of the borderlands. Northern jaguars are also significantly smaller than other jaguars, typically with greyer undersides, lighter orange coloration, and longer fur than their tropical conspecifics (Brown and López González, 2001).

Since 1996, at least seven male jaguars have been captured on camera traps in Arizona, presumably dispersing across the border from northern Sonora (Main, 2017). While cubs have recently been spotted within 8 km of the border in Sonora, indicating likely presence of females, no female jaguars have been recorded in the US since the 1960s (Main, 2021). In the US-Mexico borderlands, jaguars act as a peripheral transboundary species (PTS), with a large portion of their range in one country (Mexico), and a small peripheral portion in an adjacent country (US) (Thornton et al., 2018). PTS are often threatened by asymmetries in protection level across the border; luckily, the jaguar is listed and protected as an endangered species in both the US and Mexico (USFWS, 1997; SEMARNAT, 2011). However, landscape connectivity is increasingly threatened across the US-Mexico border, one of the world’s most politicized international boundaries (Brenner and Davis, 2012). A border wall, intended to control human migration into the United States, hinders transboundary movement for the northern jaguars (Peters et al., 2018). Man-made border security barriers are widely recognized as detrimental to conservation and a threat to wildlife, causing mortality, impeding access to seasonally important resources, and restricting movement, for large carnivores especially (Linnell et al., 2016). In addition, growing development, mining interests, highway construction, and militarization are further fragmenting the landscape in this area, decreasing permeability to natural dispersal. The US-Mexico borderlands represent a unique habitat type in the jaguar’s range (Sanderson et al., 2021b). As climatic conditions shift species distributions, this habitat could serve as a refuge, buffering against environmental degradation further south (Thornton et al., 2018). Maintaining binational connectivity is essential for the northern jaguar’s survival, and the charismatic cat has become emblematic of the need for transboundary conservation in the borderlands.

2.3 Author positionality

Both authors are based in the United Kingdom. Neither author nor their institutions were affiliated with any jaguar-related research in the U.S.-Mexico borderlands region beyond this project during the study. E.C., who contacted stakeholders and conducted the interviews, is originally from the region.

2.4 Stakeholder groups

We identify ten stakeholder groups which may hold distinct natures relevant to conservation of borderland jaguars. Summary information on these stakeholders is located in Table 1.

2.5 Semi-structured interviews

2.5.1 Data collection: Qualitative interviews

Qualitative, semi-structured interviews were selected because they are inductivist and emic-focused, appropriate to deeply investigate and construct differing natural realities (Guest et al., 2012). In a semi-structured interview, the interviewer has prepared a guide of questions and topics to be covered, but the interviewee has leeway in how they respond to questions, and the interviewer has freedom in choosing follow-up questions (Newing, 2011). In conservation, semi-structured interviews have previously been used successfully to investigate stakeholder perceptions of conflict (e.g., Dickman, 2005).

Interviews were conducted throughout June and July 2021, and typically lasted from 45 minutes to one hour. The shortest and longest interviews were 37 minutes and one hour and 50 minutes, respectively. Due to travel restrictions and ethical considerations of the Covid-19 pandemic, all interviews were conducted online, remotely. The majority took place over Zoom video calls and voice-only calls *via* Skype and WhatsApp. Interviews were recorded with a smartphone and transcribed manually. 21 of 50 interviews were conducted in Spanish, then translated to English.

2.5.2 Sampling procedure and participant ethics

This was an exploratory qualitative study, so following qualitative research conventions, we selected a small, nonrandom sample (Poor et al., 2021). Five members from each of ten stakeholder groups were interviewed, for a total of 50 interviews. Five members of each group was deemed sufficient to achieve theoretical saturation under reasonable time constraints of scheduling, conducting, transcribing, and translating interviews (Newing, 2011; Rust et al., 2017). Sample sizes were balanced between groups, to ensure analyses considered each nature equally. 17 of 50 interviewees were women, with at least one woman per group.

Interviewees were identified through a combination of purposive criterion sampling and snowball sampling (Palinkas et al., 2015). Initially, participants were drawn from relevant organizations and institutions involved in jaguar conservation, such as wildlife agencies and local NGOs. Individuals were selected based on knowledge of and experience with borderland jaguars. Selected subjects were asked to recommend future interviewees from their own networks until five participants were found for each stakeholder group. The sampling pool was limited to those who were available during the two-month interview period, and those who were willing and able to use online platforms. Informed consent materials were prepared in English and Spanish, and provided to each interviewee at least one day prior to the interview. If requested, sample questions were provided to review in advance. To build rapport before interviews, E.C. emailed and/or called each interviewee, to introduce the project and answer any questions. E.C. obtained verbal or written consent prior to each interview, and direct quotes, though anonymous, are all used with permission.

2.5.3 Interview guide design

The interview topic guide was prepared in English and Spanish, and underwent several drafts after consultation with local jaguar conservation experts. It was tailored slightly to each stakeholder group for relevance. A sample guide is located in the

TABLE 1 Information describing the ten stakeholder groups interviewed in this study.

Group	Definition	Involvement and interests in jaguar conservation
American conservationists - government agencies	Employees of the U.S. Fish and Wildlife Service (USFWS) - the federal wildlife agency, or the Arizona Game and Fish Department (AZGFD) - the state-level wildlife agency	USFWS is charged with designating and protecting jaguar critical habitat, and enforcing a recovery plan (USFWS, 2018). In the US borderlands, conservation is carried out largely on public land, managed by federal and state agencies (Brenner and Davis, 2012). In 2009, a jaguar named Macho B was captured, injured, and euthanized by AZGFD officials in a failed radio-collaring attempt (US Department of the Interior, 2010). No further attempts have been made to collar a jaguar since, and the idea has become taboo among state and federal officials (AZGFD, 2018).
American conservationists - NGOs, academics	Employees of non-governmental organizations (NGOs) or universities based in the U.S. involved in jaguar conservation	While NGOs and research groups lack the law enforcement power of government agencies, they are freer from bureaucratic constraints, and many focus on communication, outreach, and community-building (Sky Island Alliance, 2021). Because the philanthropic American public is excited by jaguars, US-based NGOs tend to be better-funded than their Mexico-based counterparts (interviewee – US NGO employee, 2021).
Mexican conservationists - government agencies	Employees of the Comisión Nacional de Áreas Naturales Protegidas de los Estados Unidos Mexicanos (CONANP) - the federal wildlife agency, or the Comisión de Ecología y Desarrollo Sustentable del Estado de Sonora (CEDES) - the state-level wildlife agency	In Mexico, federally protected areas are managed by CONANP, with few regulatory powers left to the states (González Ocampo et al., 2014). States do have their own wildlife agencies, for example CEDES in Sonora, Mexico. However, CONANP is underfunded and understaffed, so often unable to enforce wildlife laws (Valdez et al., 2009). Furthermore, the majority of protected areas in northern Sonora are privately or communally-owned (Villareal et al., 2019). The Mexican federal government therefore assumes an advisory role, while ‘private landholders [are] entrusted with the responsibility—perhaps better described as a choice—of conserving the land’ (Sifford and Chester, 2007, p211).
Mexican conservationists - NGOs, academics	Employees of NGOs or universities based in Mexico involved in jaguar conservation	NGOs and academic researchers in Mexico are perceived by some to play a more active role in jaguar conservation, often working directly with landowners and communities to protect land (Rosas-Rosas and Valdez, 2010). Similarly to NGOs in the US, their work tends to emphasize awareness and outreach, to build community trust.
Borderlands activists	Employees of or volunteers with activist NGOs, groups, or collectives which campaign against construction of a wall and other environmentally degrading activities along the U.S.-Mexico border	For many activist groups in both the U.S. and Mexico, saving the charismatic jaguar has become a rallying cry against the border wall, mining, and highway construction (Center for Biological Diversity, 2017). Some organizations are environmental, while others are political, and use jaguar conservation as a supporting argument for their interests. Many of these groups were involved in lawsuits that led to listing the jaguar as endangered in the US, and jaguar images often feature in press releases and protests against destruction of borderlands habitat (Serraglio, 2020).
American ranchers	Ranchers who raise cattle for use, profit, or hobby in the U.S.	Spaniards introduced cattle ranching to the American southwest in the 17th century, and for over 300 years, it was a cornerstone of southern Arizona’s economy (Wagoner, 1949). Ranching has declined in recent decades but cattle still generate significant income (Wagoner, 1949). Many ranchers in the southwest lack tolerance for large predators, whether or not they actually experience livestock depredation (Bickel et al., 2020). However, some ranching organizations, such as the Malpai Borderlands Group, manage their land to support both biodiversity (including predators) and traditional livelihoods (USFWS, 2013).
Mexican ranchers	Ranchers who raise cattle for use, profit, or hobby in Mexico	Similarly, cattle ranching has dominated the northern Sonoran economy since the 17th century (Martínez-Caraza, 1983). Recent severe droughts have resulted in significant livestock losses, exacerbating ranchers’ intolerance to predation, leading to retaliatory killings of jaguars (Rosas-Rosas and Valdez, 2010; Rosas-Rosas et al., 2011; Isaacs, 2014). Wildlife-friendly ranches exist; the NGO Northern Jaguar Project’s Viviendo con Felinos (Living with Cats) program compensates ranchers for camera trap photos of live jaguars and other wild cats (Northern Jaguar Project, 2021). Pay is at or above the going bounty hunting price, making predators more valuable alive than dead (Northern Jaguar Project, 2021).
Indigenous communities - southern Arizona	Members of three of the 22 federally-recognized Native Tribes in Arizona: the Tohono O’odham Nation, the White Mountain Apache Tribe, and the San Carlos Apache Nation (AZED, 2019)	There is evidence in folklore and art that the jaguar ‘has been known to most [southwestern] tribes from the earliest prehistoric period, and that that knowledge continues’ today (Pavlik, 2003, p3). Tohono O’odham land today is split by the US-Mexico border, and numerous jaguars have been reported in the area since the 20th century (Pavlik, 2003). Land owned by both the San Carlos and White Mountain Apache Tribes has recently been identified as potentially suitable jaguar habitat, and at least five jaguars have been killed on or near Apache land in the last 150 years (Brown and López González, 2001; Sanderson et al., 2021a).
Indigenous communities - Sonora	Members of the Yaqui Tribe in Sonora	The Yaqui people in Sonora live on reserved land or neighborhoods, sometimes called Yaqui districts (Luque et al., 2020). While there has been no jaguar habitat assessment equivalent to that in the US, some Yaqui-owned lands fall in historic jaguar range, and local NGOs have begun collaborative conservation work in these areas (Luque et al., 2020).
Día del Jaguar attendees	Attendees of at least one Día del Jaguar festival in Sonora	The annual Día del Jaguar festival brings together conservationists, scientists, ranchers, artists, and locals in Sonora, Mexico, to celebrate the iconic jaguar (Lozano, 2020). The event includes regional food, local music and dances, workshops for ranchers to decrease livestock-jaguar conflict, children’s activities, and speakers (Avila and Millis, 2019). It began to raise awareness and create a positive perception of jaguars in the ranching-dominated community, but is now something bigger, that the community ‘is building together’ (Lozano, 2020, p1).

Supplementary Material. The guide was designed to cover each of the five aspects of a nature, and questions were grouped into five sections accordingly:

1. Knowledge (e.g., *From where do you usually get your information about jaguars?*);
2. Perception (e.g., *How would you describe a jaguar to someone who has never heard of one before?*);
3. Value (e.g., *Do jaguars add value to this landscape? If so, in what ways?*);
4. Attitude (e.g., *How would you feel if jaguars disappeared completely from the borderlands region?*);
5. Action (e.g., *What is the most important next step we can take for jaguars in this region?*);

Due to the semi-structured nature of the interviews, specific topics and follow-up questions varied. However, all five aspects of a nature were discussed in every interview.

2.6 Constructing and comparing natures: Applied thematic analysis

Applied thematic analysis (ATA) is an inductive, exploratory approach to analyzing textual data (Guest et al., 2012). ATA moves beyond counting ‘explicit words or phrases’ and supports phenomenological research: investigating participants’ perceptions and lived experiences in an applied, real-world context (Guest et al., 2012, p21). ATA functions similarly to other forms of qualitative textual analysis, with a specific focus on methodological rigor for inductive theme development (Guest et al., 2012). We employed ATA to identify both implicit and explicit themes surrounding each of the five components of a nature, and construct a wholistic representation of each stakeholder’s natural reality. Interview transcripts were coded according to conceptual codes, participant perspective codes, and participant characteristic codes to organize the data (Vasmoradi et al., 2016). These codes were not predetermined but instead developed

inductively as analysis proceeded. For example, a statement about a jaguar’s beauty or grace could be coded as ‘physical appearance’. Codes were then grouped and transformed into themes. A theme is ‘an implicit topic that organizes a group of repeating ideas’, and themes were developed for each aspect of a nature within each stakeholder group (Vasmoradi et al., 2016, p101). For example, the code ‘physical appearance’ could form part of a theme about ‘aesthetic value’. Themes were then compared between stakeholder groups, to identify similarities and differences in stakeholders’ natural realities of borderland jaguars.

3 Results

This section characterizes each stakeholder’s nature wholistically, by describing the salient themes comprising each of the five aspects (Figure 3). Importantly, heterogeneity existed within each stakeholder group, so multiple themes are reported and described for each component

3.1 American conservationists – government agencies (USFWS, AZGED)

When asked about where and how they read information about jaguars, one USFWS employee responded that it was her ‘duty to read the scientific literature’, to carry out her job. Many considered the ultimate expert resource to be the 2018 USFWS Jaguar Recovery plan, and referred to it frequently. None of the interviewees could correctly answer factual questions about the northern jaguar population, including the current population estimate in Sonora or how many jaguars had been spotted in the US since the 1990s. Interviewees perceived the jaguar as ‘elusive’, ‘strong’, and ‘powerful’. They also all described jaguars as ‘charismatic’, though this usually had a negative connotation, ‘drawing disproportionate attention and funding’ away from other species in need. Each agreed that they value jaguars. One interviewee stated that they value the jaguar ‘the same as all biodiversity’, and another said it was ‘because I value all diversity of

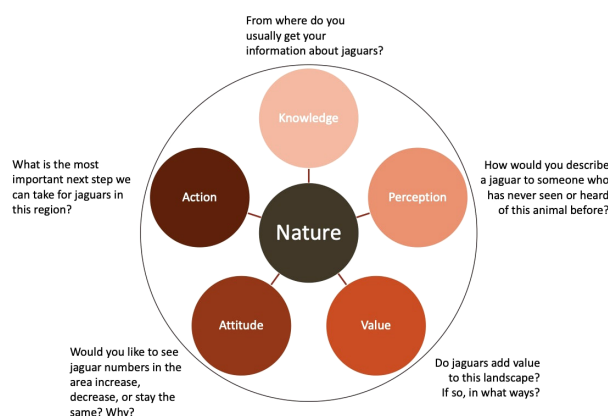


FIGURE 3

Conceptual model of five aspects of an individual’s or a group’s nature: knowledge, perception, value, attitude, and action. Each aspect is represented by a sample question, one of several that were used to investigate that component in each interview.

life'. All five interviewees mentioned the jaguar's role maintaining prey populations in the ecosystem. Three mentioned potential revenue from ecotourism. Describing human-jaguar conflict, most interviewees mentioned that the perceived risk exceeded actual livestock depredation, and their concern for human safety was 'minimal' or 'nonexistent'. Despite low actual risk, one interviewee called human-jaguar relations 'tense', and all five would like to see borderland jaguar numbers remain stable. Interviewees identified 'maintaining connectivity' as the most important contribution to jaguar conservation, and also noted a need to rebuild trust between agencies, NGOs, and ranchers.

3.2 American conservationists – NGOs, academics

Interviewees all mentioned reading scientific literature about jaguars, and communicating within and between organizations about new findings. Most were aware of the number of jaguars captured on US camera traps, and some knew the current northern jaguar population estimate. Interviewees perceived the jaguar as 'elusive', and as 'symbolic of the conservation work we still need to get done'. For all of the interviewees, the jaguar 'represents ecosystem health', because 'if an ecosystem can support a top predator like a jaguar, the prey and forage species must be doing well too'. Two conservationists value the jaguar because 'it belongs here', and three mentioned its usefulness as a 'charismatic umbrella species', where protecting land for the jaguar benefits many other species. Each valued the jaguar's role as an apex predator. The interviewees would like to see jaguar numbers increase or stay the same, but all acknowledged the need for increased local tolerance of jaguars before increasing numbers. Interviewees identified a need to maintain binational connectivity, firstly by removing the border wall, to secure the jaguar's future in the area. All five discussed a need for greater collaboration among organizations and 'especially across the border'.

3.3 Mexican conservationists – government agencies (CONANP)

Interviewees stated that they keep up with scientific publications on jaguars, and also read reports from local NGOs working on jaguars. Some knew factual information about the northern jaguar population, but none knew about jaguar numbers in the US. Interviewees perceived jaguars as a positive symbol of ecosystem health, but 'controversial animals' among landowners and scientists. Four value jaguars because they are native to the region, and the four mentioned revenue from ecotourism. All mentioned the benefits of an apex predator on the landscape. Interviewees would like to see jaguar numbers increase or stay the same, and mentioned that proper livestock management was key to mitigating conflict, 'especially if the population grows'. Each mentioned that jaguar conservation in Mexico needs more resources to be successful, and that we need to collect more data about this jaguar population to understand it.

3.4 Mexican conservationists – NGOs, academics

All five interviewees were aware of current northern jaguar population estimates, and some were familiar with US jaguar numbers. Each mentioned reading scientific literature and keeping up with local NGO reports. Interviewees perceived jaguars as indicators of ecosystem health, and charismatic in a positive light, because 'their charisma can be harnessed for many conservation issues, like habitat and watershed restoration'. Interviewees value jaguars because 'they belong here – they were here before us', and because of their ecosystem roles as an umbrella species and apex predator. All interviewees would like to see jaguar numbers increase, and mentioned that we need to improve both human tolerance and livestock management to minimize conflict. For successful conservation, interviewees identified needs for baseline data collection and collaboration among organizations, both of which will require more resources put towards jaguars.

3.5 Borderlands activists

Activists emphasized interest in online news and popular media articles about jaguars, and mentioned reading scientific literature and reports from NGOs on both sides of the border. Interviewees perceived jaguars as 'elusive' and as a 'symbol of hope for the borderlands'. All mentioned the jaguar's charisma in a positive light, as 'a way to get people to care about this landscape'. One interviewee values the jaguar because to him, the jaguar's presence 'represents a wilderness that is still out there'; another values 'the wildness of the jaguar' because 'that's a rare quality'. Others mentioned the valuing all biodiversity equally, and the value of large predators. All interviewees would like to see jaguar numbers increase, but are concerned about continued degradation 'creating a hostile landscape' for large wildlife. All identified the border wall as the biggest roadblock to the jaguar's success, and mentioned the need for community outreach and binational collaboration.

3.6 American ranchers

Ranchers mentioned coming to know the landscape through 'living on [it] for generations', learning about wildlife from their parents and neighbors. Some interviewees also read reports from local NGOs on jaguar research. None of the interviewees could answer factual questions about jaguar numbers in Sonora or the US. One interviewee was adamant that jaguars 'have not ever and should not now live in the United States'; their answers were therefore very different from the rest of the participants, and are denoted with * in Table 2. Other interviewees perceived the jaguar as 'elusive, because I know he's there but I've never seen him', and 'controversial' among ranchers in the area. One rancher values jaguars because he takes pride in living in a 'working wilderness, where ranchers keep traditional livelihoods alive ... while being a part of conservation'. Others mentioned the value of all biodiversity. Interviewees mentioned the importance of 'smart' livestock management in reducing conflict, and would like to see jaguar numbers remain the

TABLE 2 Summary characteristics of each stakeholder's natural reality of borderland jaguars.

Stakeholder	Knowledge	Perception	Value	Attitude	Action
US conservationists-government	- Scientific literature - Expertise - recovery plan	- Elusive - Charismatic (negative)	- Biodiversity - Ecosystem role - Ecotourism	- Tension - Perceived > actual conflict - Maintain numbers	(Re)build trust - Maintain connectivity
US conservationists-NGOs, academics	- Local NGO network - Scientific literature	- Elusive - Conservation work - Ecosystem health	- Belong here - Apex predator - Umbrella species	- Perceived > actual conflict - Increase or maintain - Need tolerance	- Maintain connectivity - Remove border wall - Collaboration
MX conservationists-government	- Scientific literature - Reports from NGOs	- Ecosystem health - Controversial	- Apex predator - Native - Ecotourism	- Increase or maintain - Livestock management	- Baseline data - Resources
MX conservationists-NGOs, academics	- Local NGO network - Scientific literature	- Ecosystem health - Charismatic (positive)	- Belong here - Umbrella species - Apex predator	- Increase - Need tolerance - Livestock management	- Baseline data - Collaboration - Resources
Borderlands activists	- Scientific literature and media - Reports from NGOs	- Hope - Elusive - Charismatic (positive)	- Biodiversity - Wilderness - Apex predator	- Increase - People creating hostile landscape	- Remove border wall - Collaboration - Outreach
US ranchers	- Multi-generational ranching - Reports from NGOs	- Elusive - Controversial *Not native to US	- Biodiversity - Wilderness *Uninterested	- Livestock management - Maintain *Uninterested	- Maintain open space - Collaboration *None
MX ranchers	- Facebook, - WhatsApp ranch groups - Reports from NGOs	- Balance with nature - Elusive	- Pride - Money - Ecosystem role	- Increase or maintain - Tolerance for some predation	- Outreach - Protect prey species, water
US Indigenous communities	- Scientific literature - Government reports	- Elusive - Powerful - Respect	- Belonging - Native - Biodiversity	- Increase or maintain - Tolerance needed	- Live more sustainably - Protect prey species, water
MX Indigenous communities	Scientific literature and media	- Ecosystem health - Important	- Wilderness - Belonging	- Increase or maintain - Mitigation possible	- Maintain connectivity - Restore habitat
Día del Jaguar participants	- Reports from NGOs - Media	- Strong - Elusive	- Apex predator - Pride - Ecotourism	- Increase - Need tolerance - Livestock management	- Outreach - Maintain prey populations

same. They identified a need to maintain open space for both ranchers and jaguars, and for more NGOs to collaborate with ranching groups, so that more ranchers 'learn about the jaguar's role in the ecosystem'.

3.7 Mexican ranchers

Most interviewees stated that they read information about jaguars online, in local ranching groups, through WhatsApp and Facebook. They also receive information from local NGOs, and were aware of jaguar numbers in Mexico but not the US. Interviewees perceived the jaguar's presence as indicating a 'balance with the natural world', and a good sign that 'biodiversity and ranching are both thriving'. They also perceived the jaguar as elusive, because although many ranchers have captured jaguars on their camera traps, none have seen one in the flesh. Interviewees participating in coexistence initiatives (e.g. *Viviendo con Felinos*, run and funded by the NGO Northern Jaguar Project) described feeling 'proud and excited' when seeing photos of jaguars on their property, and valuing the monetary reward they get for reporting the photos. Some interviewees indicated that they accept some level of predation, as 'paying rent to the land' and a 'cost of sharing [space and resources] with jaguars'. Participants would like to see

jaguar numbers maintain or increase, and all indicated the importance of protecting prey species and water sources.

3.8 Indigenous groups in Arizona

Most interviewees mentioned reading government agency reports about jaguars, and some keep up with scientific literature. All of the interviewees perceive the jaguar as 'powerful' because of their size and strength, and 'deserving of respect'. Interviewees value the jaguar because it is native to and belongs in the ecosystem, and because 'all life is valuable'. They would like to see jaguar numbers maintain or increase, but identify a need to increase tolerance first. Interviewees emphasized that humans must 'live more sustainably' overall for jaguars to come back, and that it is our responsibility to protect shared resources including prey species and water.

3.9 Indigenous groups in northern Sonora

Interviewees mentioned reading scientific literature and popular news articles, but none were aware of jaguar numbers in either country. They perceived jaguars as indicators of good ecosystem

health, and ‘important’ to have on the landscape. They valued jaguars for their association with ‘wilderness and healthy, wild areas’, and because ‘they belong in the ecosystem’. Interviewees would like to see jaguar numbers increase or stay the same, and considered livestock-jaguar conflict an issue, but ‘possible to mitigate’. Interviewees prioritized maintaining connectivity across the border and restoring disturbed habitat for future conservation.

3.10 Día del Jaguar attendees

Two interviewees mentioned receiving reports from local NGOs, and all mentioned reading news articles online about jaguars; some could answer factual questions about northern jaguar numbers. They perceived the jaguar as ‘strong’ and ‘elusive’, with multiple participants emphasizing its jaw strength. Some interviewees stated that they are ‘proud’ and ‘lucky’ to share the landscape with jaguars, and others mentioned its value as an apex predator or for ecotourism. All participants would like to see jaguar numbers increase, and identified needs for both increased tolerance and improved livestock management for coexistence. Interviewees prioritized community outreach, because ‘so many people don’t even believe we have jaguars here [in Sonora]’ and maintenance of prey populations for future conservation action.

4 Discussion

4.1 Comparing natures: Hybridities and clashes between worlds

Here we describe key similarities and differences between specific aspects of stakeholder natures, as are relevant to jaguar conservation and human-jaguar coexistence.

4.1.1 Knowledge: Who speaks for the jaguar?

The northern jaguar population is relatively understudied (Brown and López González, 2001). We only have estimates of population size and density, and know very little about their movement patterns. This is because the only data available is from small-scale camera trapping efforts in Sonora and along the border, and there are few extra resources to attempt larger campaigns (Northern Jaguar Project, 2021). Because of this data deficiency, it is difficult to predict how the population will react to environmental changes, conservation interventions, or potential reintroduction. However, different groups appreciate their own knowledges – how and what they know about jaguars – in different ways, some more confident than others. These differences in knowledge perception affect beliefs and assurance about future conservation actions.

When discussing knowledge of the northern jaguars and future plans for conservation, Mexican conservationists most often pointed out this uncertainty, citing a need to conduct baseline studies and area-wide surveys to investigate population dynamics and make predictions. Many interviewees from Indigenous communities on both sides of the border emphasized the significance of the jaguar’s agency in knowing about itself: the jaguar ‘will do what he wants to do, and go where he wants to go, because he doesn’t know what

conservation is’. One US Tribal member described the jaguar as ‘holding the most power’ in this binational conservation situation, because ‘only the jaguar knows’ where it will disperse – conservationists cannot predict this. Conversely, US ranchers, some US government conservationists, and borderlands activists confidently discussed what jaguars ‘want’ or ‘don’t want’, despite being unable to answer factual questions about population numbers. One rancher stated that jaguars ‘don’t want to live here’, and one government employee stated ‘if they wanted to be here, they would be already’, in discussions about reintroduction and increasing the jaguar population. These contrasting views of what is ‘best for the jaguar’ or what should be done about its conservation may underlie stakeholder conflicts over management decisions.

Most participants considered their local NGOs to be a good and trustworthy source of information about jaguars, in addition to scientific and news articles. Mexican ranchers in particular emphasized the sharing of knowledge amongst themselves, through online social media groups. US government conservationists tended to consider their own agency reports, like the Jaguar Recovery Plan, to be the most accurate source of information on jaguars, referring to the plan as ‘good science’ and ‘the most up-to-date’ data to inform management, indicating confidence in their knowledge and recommendations (USFWS, 2018).

4.1.2 Perception: How do we relate to a rare, elusive predator?

Of 50 total interviewees, many of whom have spent their whole careers studying jaguars, only two had ever seen a live, wild northern jaguar in the flesh. The cats were perceived by many as ‘elusive’ and ‘secretive’. In describing and discussing jaguars, every single participant compared the jaguar to another predator present in the borderlands; the animal that participants relate most to the jaguar provides insight into how they perceive this animal (Figure 4).

Mountain lions were the most frequently mentioned animal. Mountain lions are large cats, the closest in size to the jaguar in the area. While not common, they are not nearly as rare as the jaguar; they are not endangered and not federally protected (Mountain Lion Foundation, 2020). All American conservationists and American ranchers most frequently related jaguars to mountain lions, which are commonly blamed for livestock depredation (Mountain Lion Foundation, 2020). Some interviewees voiced concern that reintroduced jaguars may shoulder the blame for mountain lion depredations, and suffer from retaliatory killing. Indigenous interviewees on both sides of the border mentioned that they know jaguars used to exist on their lands because their spots make them distinguishable from mountain lions, and traditional stories and songs specifically reference a large, spotted cat. Mexican ranchers discussed receiving payments for camera trap photos of mountain lions, but because they are not endangered, the payment is less than for jaguar photos.

The second most common comparison was with the Mexican gray wolf, another large predator which was recently reintroduced to the area (Brown and Parsons, 2001). In light of the 2021 jaguar reintroduction proposal, the parallel to wolf reintroduction was mentioned by Mexican conservationists, Día del Jaguar participants, and Indigenous groups in Arizona. While wolf reintroduction is considered successful, tensions and hostility remain around both

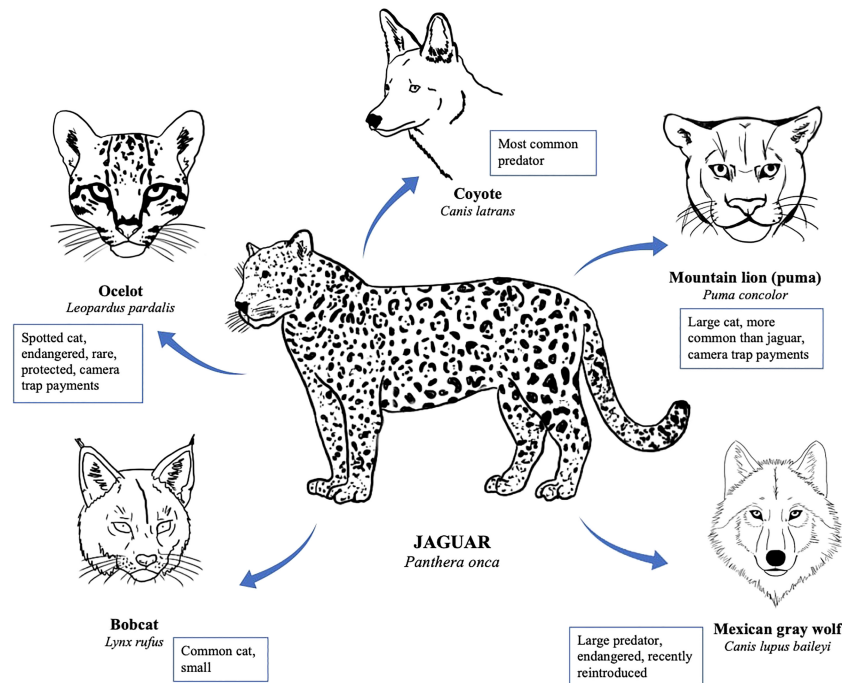


FIGURE 4
How do we relate to a rare, elusive predator? The jaguar's place on the landscape among other native predators.

the predator itself and the way it was reintroduced, which will likely affect perceptions of reintroduced jaguars (Gardner, 2018).

Mexican ranchers and conservationists, mostly NGO-based, often compared the jaguar to the ocelot. They are both rare and endangered spotted cats, and typically the two highest-paid animals in camera trap payment programs, so ranchers described feeling excited when they capture these images (Northern Jaguar Project, 2021). Borderlands activists were the only participants to relate the jaguar to the bobcat, which is a much smaller and more common feline predator in the region. American ranchers were the only group to relate the jaguar to the coyote, which is also a much more common predator in the region. They mentioned the coyote's common presence in contrast to the jaguar's rarity, but still considering both animals a 'nuisance' to have around livestock.

Each animal related here is a predator, indicating that jaguars are largely perceived first and foremost as a predator on the landscape. This is a valuable characteristic for some groups, for varying reasons. For conservationists and activists, because an apex predator represents ecosystem health and balance, and plays a key role regulating prey populations. For Mexican ranchers involved in compensation programs, because jaguar photos bring monetary rewards. However, the jaguar's identity as a predator is more concerning for others, including Indigenous groups and American ranchers, due to potential for conflict and negative experiences with other large predators.

4.1.3 Value: Finding space and place for jaguars in a human-dominated landscape

For humans to coexist with wildlife, we must find adequate space for wildlife to live on the landscape, and find a meaningful place for wildlife in lives of local stakeholders (Western et al., 2020). This is

especially pertinent for large carnivores like the jaguar, which need open, connected spaces and have conflict with local ranching communities. When considering spatial needs of the jaguar, most stakeholders mentioned connectivity and large spaces. Ranchers on both sides of the border emphasized need for sufficient water resources and prey populations on the landscape, recognizing that these are resources that livestock require too. Creating this connected space will require very different processes in the US and Mexico, because of the differences in land tenure. In the US, space will come from the government designating protected habitat, and in Mexico, space will come from private and communal landowners creating safe passage through their lands. Moreover, connectivity from Mexico through to the US is disrupted both physically and politically by the border wall, as emphasized by US activists and conservationists. Willingness to create and share this space will depend on finding a place for these jaguars in the minds and lives of local communities.

Finding a place for jaguars in the borderlands necessitates a sense of belonging in the ecosystem. Most stakeholders hold existence value for jaguars – even though they may never see one, they appreciate the jaguar's presence and enjoy knowing that it exists, because it is 'beautiful' 'powerful' and 'majestic'. Many conservationists and Indigenous interviewees specifically mentioned that the jaguar belongs on this landscape, and that it is valuable simply because it should be here, as a member of the native fauna. Activists and some US ranchers value the jaguar because it represents wildness and wilderness, and those are qualities that they desire for this landscape. Each stakeholder holds a place in their lives for the jaguar for different reasons. Understanding how each group conceives the landscape, and who or what belongs in it, can facilitate large-scale coexistence and creation of further spaces and places for jaguars where they do not yet exist.

4.1.4 Attitude: From conflict to coexistence

Attitudes towards jaguars centered around themes of conflict and coexistence. Many stakeholders mentioned that the perceived threat of livestock-jaguar conflict, and especially human-jaguar conflict, is much higher than in reality, but that the perceived threat is still strong enough to drive retaliatory killing and intolerance. When asked to describe potential conflict with jaguars, all participants mentioned the dominant livestock ranching economy in the borderlands.

However, ranchers in Mexico expressed much greater tolerance of some, presumably low, level of predation, as a natural consequence of sharing space with jaguars. To these ranchers, jaguars were valuable enough either through camera trap compensation programs or as a vital part of the biodiverse ecosystem, to be worth losing a few cattle. These ranchers expressed pride and excitement in the jaguar's presence on their land, and little concern for depredation, because they have faith in their livestock management practices. By contrast, only one US rancher expressed similar pride in sharing space with jaguars, and did not indicate resulting tolerance for any level of depredation. This divergence in attitudes held by ranchers across the border may exist due to differing livestock management practices and understandings of historical jaguar habitat; first steps towards reconciling it could include outreach and education efforts by local conservation actors.

Most interviewees believed that coexistence with jaguars is possible at the current population density, which is very low, particularly in the US (Northern Jaguar Project, 2021). Many ranchers and conservationists believed that coexistence would still be possible with higher jaguars numbers, particularly in Mexico, but that such coexistence would require significant changes in livestock management and increased tolerance for predators. Some ranchers expressed interest in working with NGOs or wildlife agencies to provide insight on issues they face and facilitate these changes, to benefit both ranchers and jaguars.

4.1.5 Action: How should we enact jaguar conservation?

All stakeholder groups emphasized a need for collaboration – between NGOs, between NGOs and the government, between conservationists and ranchers, and between conservationists across the border. Most stakeholders also agreed that maintaining landscape connectivity is a top priority, as well as increasing tolerance range-wide. When considering who should lead such collaborative efforts, the Northern Jaguar Project, an NGO based in Sonora, was named by participants from many stakeholder groups. Chiefly this was because of their success with local ranchers through *Viviendo con Felinos*, compensating them for camera trap photos to deter predator control. This was seen as one of the best models for community involvement, and one that could be replicated elsewhere, including in the US.

Overall, both US- and Mexico-based NGO conservationists had more interest in taking action for jaguar conservation, through reintroduction, education and outreach, or ecological study. Government conservationists conveyed more satisfaction with the current situation; this may be due to the bureaucratic rules and liabilities involved with government agencies. US ranchers typically agreed with a similarly hands-off approach. Additionally, many NGO conservationists expressed distrust in state game agencies due to their 'historically anti-predator stance', but most agreed that USFWS is effective in their role of protecting critical habitat.

When discussing jaguar reintroduction to the US, no stakeholder group supported immediately moving forward. Opinions fell into three categories: against, unsure, and in favor but after further research. Stakeholders who were against reintroduction, including most US ranchers and US government conservationists, cited lack of jaguar habitat north of the border, so they did not believe jaguars could be successful there. Those who were unsure, including most NGO conservationists, Indigenous groups and most Mexican ranchers, either wanted to see more research before making a decision, or were unaware of the proposal and did not have an opinion at the time. Further information requested included more data on the source population, tolerance levels for jaguars in the proposed reintroduction areas, and more detailed prey population analyses; most of these gaps are identified by the authors of the study (Sanderson et al., 2021b). Some participants also questioned the motive of physical translocation – if it would be truly beneficial for conservation, or if it is just motivated by Americans wanting jaguars in their country. Those who supported the reintroduction proposal, including most Día del Jaguar attendees and some conservationists on both sides of the border, still had reservations about the lack of data on source and prey populations, but felt that the idea was realistic and would be beneficial to the species and ecosystem.

4.2 Operational multinaturalism

Operating from a multinatural standpoint allowed us to consider simultaneously many different perspectives on jaguars and their conservation. We were able to meaningfully engage with the viewpoints and realities of multiple stakeholders in a bioculturally diverse and politically-charged transboundary region. The wholistic investigation of an entire nature, rather than just one aspect (e.g. attitudes towards predators), gave stakeholders the time and space to convey a range of thoughts and concerns about jaguar conservation. This in turn facilitated clearer comparisons between different groups of people and their natural realities, elucidating disconnects which may drive stakeholder conflicts, to build a better understanding of coexistence. Understanding similarities in knowledge, perceptions, values, attitudes, and actions can allow local conservation actors to identify common goals and desires to better facilitate collaboration amongst groups, which is something that all stakeholders identified as important. For example, many ranchers, activists, and conservationists on both sides of the border identified open, connected landscapes as important for jaguar conservation, ecosystem health, and livestock success – a shared and mutually beneficial goal.

Multinaturalism holds potential beyond simply participation as an entirely new way of knowing natures, and an opportunity for diverse stakeholders to co-create a shared understanding of the landscape (Martínez-Dueñas et al., 2017). Indigenous peoples and local communities (IPLC) have been historically underrepresented in decision-making processes, forcibly removed from their land, and their understandings of nonhuman nature disregarded (Adams and Mulligan, 2003; Baker et al., 2019). By taking seriously and wholly their value systems and natural realities, rather than treating their unique knowledge as 'data', multinaturalism builds genuine relationships with IPLC, whose environmental stewardship is

critical to biodiversity conservation globally (Brook and McLachlan, 2008; Ellis et al., 2021). For example, (Martínez-Dueñas et al., 2017) found that in Puracé-Coconuco, Colombia, two different worlds coexist and interact: that of the conservationist, and that of the Indigenous Puraceños. For conservationists, the presence of Andean condors (*Vultur gryphus*) represents a key success of Puracé National Natural Park, while for Puraceño ranchers, the condor is sometimes considered a threat to livestock, but is otherwise unimportant in daily life (Martínez-Dueñas et al., 2017). Here, conservationists and Puraceños inhabit different natures, each with their own HWIs, and in which the same animals exist as different entities (Martínez-Dueñas et al., 2017).

‘To decolonize the past, IPLC should be empowered through knowledge production involving local realities’ (Acabado and Martin, 2020, p182). A multinatural approach requires not only engagement with diverse knowledge systems, but also treatment of these ways of knowing as expert perspectives (Trisos et al., 2021). Such recognition of Indigenous and localized expertise significantly widens the pool of available information, strengthening the evidence-base, legitimacy, and inclusivity of conservation interventions (Tengö et al., 2017; Pedersen et al., 2020). Flattening this knowledge hierarchy creates opportunities for bottom-up conservation, led by the coexisting communities themselves. In this application to conservation, ‘multinaturalism is not a description of how the world is ... but a call for a form of thinking’, one which can aid conservationists in meaningfully deepening stakeholder engagement (Kohn, 2015, p320). Multinaturalism ‘allows differences to be held together’ rather than collapsed (Kohn, 2015, p321). This offers a way for diverse stakeholders to relate which communicates ‘by differences’, preserving the plurality of worlds that simultaneously exist in the same space, and retaining agency of IPLC in defining their own realities (Viveiros de Castro, 2004, p10).

A multinatural perspective necessarily changes the way conservationists interact with diverse stakeholders, valuing equally all knowledges and realities. By asking each stakeholder group the same questions to investigate their realities, (instead of, for example, stereotypically considering conservationists the primary holders of expert knowledge, or only discussing conflict scenarios with ranchers), we gained insight into how jaguars inhabit the specific worlds of each group. Despite discrepancies in knowledge about jaguar population numbers and historical range, many stakeholders confidently expressed ideas about how jaguar conservation should best be enacted. And while all stakeholders held existence value for jaguars, appreciating their presence on the wider landscape because of their beauty and ecosystem services, only some groups considered the local presence of a large predator to be positive. Mexican ranchers described higher tolerance for some predation in exchange for sharing space with jaguars than US ranchers, possibly due to differences in livestock management, camera trap payment schemes, and familiarity with large predators. A multinatural perspective facilitates investigation of these specific differences in stakeholders’ natural realities of coexisting with jaguars, providing more detailed insight than traditional stakeholder engagement approaches.

4.3 Transboundary conservation: Natures across borders

Many natures often coexist and overlap across international borders, in transboundary conservation areas (TBCAs). This is because species ranges and ecological processes rarely coincide with socio-political divisions (Runge et al., 2014). Indeed, 53.8% of terrestrial bird, mammal, and amphibian populations span an international border, including 21% of all threatened species (Mason et al., 2020). Wildlife occupying transboundary ranges or migrating across such boundaries are exposed to different management and governance regimes, a variety of legal and institutional structures, and various socio-cultural contexts (Vasilijević et al., 2015). They may also be impacted by complex relations between countries, and the lack of coordinated management across such borders can undermine conservation efforts (Bartón et al., 2019).

Recognition of the need for large-scale ecosystem connectivity and cooperation across political divides is growing (Rands et al., 2010; Thornton et al., 2018). Transboundary conservation initiatives represent a practical way to overcome socio-political differences through international cooperation, by working towards shared conservation goals to better protect species (Mason et al., 2020). TBCAs have proven effective for protection of many species worldwide, including leopards (*Panthera pardus*) in Africa (Searle et al., 2020), brown bears (*Ursus arctos*) in Europe (Recio et al., 2020), Persian leopards (*P. pardus saxicolor*) in Asia (Farhadinia et al., 2021), and grey wolves (*Canis lupus*) in North America (Chester, 2015). TBCAs have even shown success along borders affected by conflict, as exemplified in the Greater Virunga landscape, where mountain gorilla (*Gorilla beringei beringei*) numbers increased despite civil wars in the region, thanks to collaboration between Rwanda, Uganda, and the Democratic Republic of Congo (Plumptre et al., 2007). Ecological benefits of TBCAs include enhanced resilience, connectivity and dispersal opportunities, protection for migratory species, and greater genetic exchange among populations (Vasilijević et al., 2015).

But while geopolitical borderlands typically hold high biodiversity, they are difficult to protect (Farhadinia et al., 2021). Transboundary conservation initiatives must navigate dynamic socio-cultural and economic transitions, and sometimes armed conflict or political instability (Mason et al., 2020). Conservation work across borders in such diverse situations requires skillful coordination and cooperation on-the-ground between local stakeholders (Zbicz, 1999; Zbicz, 2003). Such coordinated management of species and ecosystems across boundaries is increasingly recognized as important in the evolving post-2020 global biodiversity frameworks (CBD, 2019). Maintaining and strengthening ecosystem resilience across the increasingly-fragmented landscapes of the Anthropocene is also critical in the face of climate change. As species ranges shift with changing environmental conditions, some will inevitably cross political borders (Hannah, 2010). Transboundary conservation governance in such cases will become even more complex, as wildlife encounter new and more diverse stakeholders (Ruter et al., 2014; Lim, 2016).

Multinaturalism offers a framework for bottom-up transboundary conservation initiatives. For example, the Kgalagadi Transfrontier Park in Botswana and South Africa emerged informally, when park rangers across the border began to work together to manage the entire ecosystem (Schoon, 2013). This allowed for efficient collaboration and strong adaptive capacity to respond to the park's daily changes and challenges (Schoon, 2013). Successful transboundary conservation projects are built upon strong community engagement practices, tailored to meet the unique needs of local stakeholders and their realities (e.g. the Yellowstone to Yukon initiative, Chester, 2015). A multinatural standpoint requires conservationists to consider the many worlds coming into contact in a transboundary area, inclusive of their social, cultural and political contexts. This framework can facilitate cooperation among diverse stakeholders in transboundary landscapes, providing an inclusive, engaging way to collaborate for conservation and coexistence.

Loss of connectivity in increasingly human-dominated landscapes is a characteristic of the Anthropocene, and must be addressed to ensure the jaguar's survival. Recent genetic work has indicated widespread dispersal between jaguar populations across their entire range (Eizirik et al., 2001). Landscape connectivity is essential to this dispersal and to ensuring genetic variation in the species, so maintaining existing corridors between populations is critical for the jaguar's long-term persistence on the American landscape (Rabinowitz and Zeller, 2010; Zeller et al., 2011). This new genetic understanding prompted two complementary range-wide conservation efforts: Panthera's Jaguar Corridor Initiative (JCI) and the Jaguar 2030 Roadmap (Panthera, 2018). Both aim to link key populations with corridors throughout the species' entire range, maintaining connectivity and gene flow through human-dominated landscapes from Argentina to Mexico (Panthera, 2018; Jaguar 2030 Roadmap, 2020). Over 50 transboundary areas have been identified as important core populations or corridors, presenting a diverse landscape of experts and stakeholders, each with their own natures, coexisting and potentially coming into conflict (Jaguar 2030 Roadmap, 2020).

While the JCI is a large spatial-scale initiative, the diversity of socio-economic contexts and heterogeneous communities covered necessitates working at multiple levels of engagement, from the international level down to the local landowner (Zeller et al., 2013). Human geography and land uses present a diverse landscape across jaguar range, so jaguars may coexist with people holding many natural realities, including different attitudes and tolerances for wildlife (Cavalcanti et al., 2010). In a recent review of 17 human-jaguar conflict case studies, the authors found that 'no single situational factor' could predict farmer's perceptions of jaguars or responses to conflict, and noted that observed patterns in conflict were only meaningful for informing action only at a local scale (Zimmerman et al., 2021, p9). Each case of human-jaguar conflict is likely unique, needing individual treatment and a custom solution to create coexistence (Zimmerman et al., 2021). Local stakeholder analysis and engagement, with strategies tailored to each individual landscape and combination of natures, are therefore essential for planning and understanding jaguar conservation (Marchini et al., 2019; WWF, 2020). To scale-up coexistence across the jaguar's range, conservationists should study 'processes rather than predictive rules' (Zimmerman et al., 2021, p11). Practicing effective processes for stakeholder engagement and community collaboration will allow us to better understand and incorporate perspectives of the people who

share space with jaguars, creating more intuitive and sustainable coexistence solutions. Multinaturalism could facilitate such processes.

To understand and change how people relate to jaguars, conservationists must attend to the human dimensions of conflict: the values, relationships, and social perceptions of jaguars that constitute a natural reality (Marchini, 2010). Few studies focus on stakeholder perceptions of jaguar conservation beyond quantification of livestock depredation, which may not be the ultimate motivator of retaliatory persecution (Cavalcanti et al., 2010; Bredin et al., 2015). Coexistence requires working across multiple disciplines; for example, employing social science methods to consider how communities perceive the threat of jaguar predation (Cavalcanti et al., 2010; Pooley et al., 2017; Zimmerman et al., 2020). Tensions between stakeholder groups with opposing values can exacerbate conflict, so differences between stakeholders' complete natures and social relationships behind conflicts over jaguars need to be considered for consensus building on the nature of successful conservation strategies (Dickman et al., 2013).

5 Conclusions

This study presents multinaturalism as a mechanism to deepen stakeholder engagement in carnivore conservation across an important international boundary through a new philosophical approach to knowledge about nature. The extent to which conservationists might be willing to embrace a multinatural approach remains unknown and subject to further study, but here we show its usefulness in elucidating varied stakeholder worldviews on coexistence with a large predator. The greatest material cost to conservationists of engaging with multiple natures is the time required for data collection and analysis. But ultimately, if intensive planning and engagement leads to more sustainable coexistence solutions, time investments should pay off. Moreover, investing time into building meaningful relationships with stakeholders will only improve relations and potential for conservation action, particularly in diverse transboundary areas. Our specific results should be interpreted with caution due to limitations in our sample size and degree of stakeholder interaction over online platforms, resulting from Covid-19 travel restrictions.

Managing human-wildlife interactions is one of conservation's most fundamental charges, and in the crowded reality of the Anthropocene, it is increasingly urgent to understand how humans and wildlife can share space (Nair et al., 2021). Conflicts between people and wildlife are being exacerbated by growing overlap between human populations and wildlife ranges. Underlying conflicts between people over wildlife are becoming more complex, as stakeholders diversify and more people participate in conservation and management (Marchini, 2014). Understanding the social dynamics between these diverse groups of people, who each exist in their own worlds and realities of nature, is essential for creating coexistence (Redpath et al., 2015). The theory of multinaturalism can allow conservationists to investigate these human dimensions holistically and completely, facilitating deep stakeholder involvement and co-creation of management solutions. Due to the unique nature of human-wildlife interactions, each conservation situation requires bespoke consideration, and a multinatural approach offers a novel way to create sustainable coexistence.

Data availability statement

The datasets presented in this article are not readily available because the interview transcripts from this study are anonymized and protected in line with the Data Protection Act of 1998. A sample interview guide is available in the [Supplementary Material](#). Requests to access the datasets should be directed to EC, connolly.erinlizbeth@gmail.com.

Ethics statement

The studies involving human participants were reviewed and approved by University of Cambridge Department of Geography. The participants provided their written informed consent to participate in this study.

Author contributions

EC conceived the original idea. EC and HN discussed the idea and planned the interviews. EC recruited the participants, carried out the interviews, and analyzed the transcripts. EC wrote the manuscript with support and contributions from HN. HN supervised the project. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that this research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fcsc.2023.851254/full#supplementary-material>

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