frontiers | Frontiers in Conservation Science

TYPE Systematic Review
PUBLISHED 14 April 2023
DOI 10.3389/fcosc.2023.1094443

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Animal Conservation, a section of the journal Frontiers in Conservation Science

RECEIVED 10 November 2022
ACCEPTED 23 March 2023
PUBLISHED 14 April 2023

CITATION
Bhatt TR, Castley JG, Baral HS and Chauvenet A (2023) A synthesis of priorities, patterns, and gaps in large carnivore corridor research. *Front. Conserv. Sci.* 4:1094443. doi: 10.3389/fcosc.2023.1094443

A synthesis of priorities, patterns, and gaps in large carnivore corridor research

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Introduction: Conservation research plays an integral role in the effort to conserve biodiversity globally. However, research gaps can limit conservation research's potential contribution to addressing global biodiversity problems such as habitat fragmentation. While a synthesis of the research literature does not attain effective conservation action by itself, it can inform future research and corridor conservation planning and practices.

Methods: We used a systematic search of peer-reviewed research articles in Scopus, Web of Science, and grey literature in the Connectivity Conservation Specialist Group library published before December 2020. Our review assessed research on the identification and use of corridors, a primary instrument used to address the threats of habitat fragmentation, for large carnivores to identify patterns, priorities, and gaps in the literature. We focused on large carnivores because they are frequently used for connectivity planning owing to their higher sensitivity to habitat fragmentation and their importance as conservation flagship species.

Results and discussion: We found that peer-reviewed studies primarily focused on single-species corridors with a strong preference toward apex predators, whereas grey literature focused on multi-species corridors. More than 80% of studies included one of the following five species, the mountain lion (n=46 studies), American black bear (n=31 studies), jaguar (n=25 studies), tiger (n=25 studies), and brown bear (n=18 studies). Although research on the identification of corridors was relatively more common in the past, we found an increasing trend in the publication of studies assessing the use of corridors by large carnivores in recent years. The published research is predominantly from North America (47%) and Asia (30%), with comparatively fewer studies from Africa (4%), despite having several large carnivore species. While climate change and human-wildlife conflict are considered major concerns for large carnivore conservation, these were seldomly considered in corridor research. Corridor research collaborations exist between academia, government, and non-government institutions, but the involvement of the private sector is lacking.

Conclusions: Our review shows that there is scope for future corridor research to (i) focus on areas where geographical gaps exist, (ii) target multi-species corridors, (iii) include climate change and human-wildlife conflict scenarios, and iv) increase collaboration with the private sector to better inform connectivity solutions.

KEYWORDS

habitat fragmentation, connectivity, umbrella species, predators, climate change

Introduction

Conservation research is integral to global biodiversity conservation efforts because it provides a scientifically valid basis for solving conservation problems (Wilson et al., 2016a). However, gaps in conservation research can limit our ability to make an informed decision or action to conserve biodiversity effectively (Velasco et al., 2015; Williams et al., 2020). Research gaps can arise for a variety of reasons, including, but not limited to, a misalignment of priorities and interests among academic researchers and the needs of practitioners on critical issues affecting biodiversity and solutions to mitigate them (Pullin et al., 2009; Laurance et al., 2012; Jarvis et al., 2015) or inadequate research on a conservation topic (Jarvis et al., 2015; Walsh et al., 2015). For example, the knowledge generated by academic researchers for rhinoceros conservation using ex-situ laboratory approaches had little value for practitioners focusing on developing in-situ conservation action plans (Linklater, 2003). This misalignment of the priorities delayed the development of necessary ecological knowledge and management tools to effectively and efficiently address the problem of the rapid decline in the rhinoceros population due to poaching and the illegal wildlife trade of its horn.

Similarly, the inadequacy of research on specific topics of ecological problems, such as habitat fragmentation (Wilson et al., 2016b), road ecology (Collinson et al., 2019), and climate change (Kabisch et al., 2016), has been well documented across geographical areas (Reboredo Segovia et al., 2020), and taxonomic groups (Donaldson et al., 2017). Such gaps limit the potential contribution of conservation research to addressing global biodiversity problems (Jarvis et al., 2015; Walsh et al., 2015) and widen the '*research-implementation gap*' relating to the poor translation of research findings into meaningful conservation actions (Knight et al., 2008; Wilson et al., 2016a). While a synthesis of the research literature does not directly address the research-implementation gap, it does provide a direct and objective approach to identifying important areas where information gaps limit our ability to make decisions for a specific conservation topic and guiding future actionable research.

Habitat loss and fragmentation are major threats to global biodiversity (Haddad et al., 2015; Tilman et al., 2017; Newmark and McNeally, 2018), which negatively affects biodiversity through the combined reduction in habitat, creation of novel habitat configurations and increased isolation (Didham et al., 2012; Haddad et al., 2015). The global impact of habitat fragmentation is so extensive that more than 70% of the world's forests are already within 1 km of a habitat edge (Haddad et al., 2015), and it threatens species' survival by restricting their movement for foraging, dispersal, reproduction, or migration (Crooks et al., 2017; Tilman et al., 2017). However, a review of the literature on habitat fragmentation (Fardila et al., 2017) concluded that the research gaps, e.g., taxonomic and geographical gaps, could potentially affect our ability to develop and implement effective management strategies for fragmented landscapes. Similarly, research gaps can equally be found when attempting to assess the performance of conservation interventions. For example, a review of studies evaluating conservation interventions applied to mitigate the impacts of dams on freshwater turtles identified that fewer studies (~10% of the identified literature) evaluated the effectiveness of the interventions resulting in an information gap to guide the effective management of the problem (Bárcenas-García et al., 2022). Therefore, it is important to synthesize the literature on the solutions adopted to mitigate fragmentation threats i.e. corridors.

Improving connectivity, an attribute that measures how easily a species can move among habitat fragments (Kindlmann and Burel, 2008), through functional corridors is a widely adopted solution to mitigate fragmentation threats (Haddad et al., 2015; Hilty et al., 2020). As such, there has been considerable research focus on improving habitat connectivity by establishing corridors (Gilbert-Norton et al., 2010; Wade et al., 2015; Ayram et al., 2016). In simple terms, a corridor is a part of the landscape that is specifically managed to maintain ecological processes, including the movement of species between intact habitat areas (Wade et al., 2015; Hilty et al., 2020). Nevertheless, given that connectivity is species-specific (Beier et al., 2008; Kindlmann and Burel, 2008), corridors managed for a single species may not meet the connectivity needs of other species in the landscape. Consequently, there has been a push for wildlife corridors that can provide connectivity for multiple species (Gilbert-Norton et al., 2010; Brodie et al., 2015; Wang et al., 2018; Hilty et al., 2020). Selecting focal species that are highly sensitive to habitat fragmentation, have large area requirements, and represent the connectivity requirements of other cohabiting species, such as an umbrella species (Breckheimer et al., 2014), or those that attract conservation funding and public support as a flagship species, i.e. species useful for marketing conservation agendas (Dalerum et al., 2008; Macdonald et al., 2017) provides a reasonable solution to this problem. Large carnivores are one guild of species that meets these criteria as many have small and declining populations (Ripple et al., 2014; Wolf and Ripple, 2017), large area requirements (Thornton et al., 2016; Ward et al., 2020), but also important roles in maintaining ecosystem functions (Ripple et al., 2014). Furthermore, large carnivores are often threatened by poaching and human persecution during dispersal (Ripple et al., 2014; Arlettaz et al., 2021; Bleyhl et al., 2021) yet can attract conservation funding and public support (Dalerum et al., 2008; Macdonald et al., 2017). As such, they are frequently used as focal species for connectivity research and planning.

However, not all carnivores meet the above criteria; some are poor connectivity surrogates because of specific habitat requirements or connectivity not being among the primary threats to their survival. For example, being a forest obligate and sensitive to roads, the American black bear (*Ursus americanus*) poorly represented the connectivity requirements of species not dependent on forest cover for movement in the Northern Rocky Mountains of the USA (Cushman and Landguth, 2012). Previous synthesis of the corridor literature identified carnivores as a primary focal species for connectivity research among a suite of plants and animal species (Ayram et al., 2016). While a comprehensive review of multi-taxa corridor research efforts would be useful, this was beyond the scope of this research, and we focused our synthesis on

large carnivores to highlight the patterns, priorities, and gaps within the corridor research literature.

Here, we aim to review and synthesize knowledge on large carnivore corridor research to understand the current patterns and priorities related to the research focus within the scientific and grey literature to identify gaps that require future research attention. The review also assessed the extent of research collaboration between academics and practitioners as a measure of linking research and implementation. For large carnivore corridor research, we specifically asked; a) where is research conducted; b) which species within the large carnivore guild are the focus of studies; c) what is the spatial scale of studies; d) what are the important variables considered for corridor research; e) how have large carnivore corridor research progressed over time; f) what are the major threats to existing large carnivore corridors g) what is the status of collaboration between different sectors for large carnivore corridor research, and h) what generalizations can be made from this body of work?

Methods

We conducted a systematic search of all (i.e. no specific start date) peer-reviewed research articles published until December 2020 in two scientific publication databases, Web of Science-core collections (https://www.webofscience.com/wos/woscc/, indexed from 1900) and Scopus (https://www.scopus.com/search/form.uri#basic, earliest publication date 1788), as well as a database hosted by the Connectivity Conservation Specialist Group (CCSG) (https://conservationcorridor.org/, earliest publication date 1990). Following the threshold of >15 kg body weight used by Ripple et al. (2016) to group large carnivores, we focused our review on 27 large terrestrial carnivore species (Table 1). Our systematic search of the peer-reviewed literature included default search parameters containing keywords "corridor*" and "connectivit*" in combination with the scientific name and common name of large carnivore species for each species (Supplementary File S1). We limited the search of Titles, Abstracts, and Keywords to research articles published in peer-reviewed journals and within the subject of Agricultural and Biological Sciences and Environmental Sciences in Scopus and Ecology, Zoology, Environmental Sciences, Environmental Studies, and Biodiversity Conservation in Web of Science. Searches for individual species resulted in 1051 and 1146 scholarly articles from Scopus and Web of Science, respectively.

The literature review followed the PRISMA protocol (Moher et al., 2009) that included stages for identification, screening and assessment of eligibility for papers before arriving at a final list of papers included in the analysis (Supplementary File S2). At the first screening stage, we removed duplicate articles across species and databases to generate a set of 958 unique papers from the two core databases for further analysis (Figure 1). We also included grey literature from the CCSG database, which is a global network of academics, practitioners, policymakers, and professional experts dedicated to improving and disseminating knowledge in the field of connectivity conservation. Grey literature, i.e., literature not published in traditional academic journals and frequently in a non-English language that is an important part of conservation evidence and knowledge synthesis (Amano and Sutherland, 2013; Haddaway and Bayliss, 2015). We assessed the suitability of all 799 publications on the CCSG website published until 2020 for inclusion in our review using the same selection criteria for identifying peer-reviewed literature. It is estimated that roughly 36% of conservation literature is published in the non-English language (Amano et al., 2016). However, we could not incorporate non-English publications in our review due to the language barrier that remains a common problem affecting most scientific evidence syntheses (Christie et al., 2021).

Selection criteria for identifying relevant publications

We identified a final set of publications by selecting only eligible studies that included at least one of the 27 large carnivore species and focused on identifying or assessing the use of corridors by large carnivores. As such, we excluded studies that i) did not specifically focus on habitat corridors, for example, studies involving landscape permeability or genetic relatedness between sub-populations, or habitat suitability of the landscape, that did not relate to specific corridors, ii) focused on species diversity, distribution, or behavior, and those studies focusing on connectivity methodologies and habitat restoration and, iii) focused on landscape elements that are not explicitly identified or managed as corridors, such as roadside vegetation, river valleys. To avoid duplication of previous work, we excluded studies on the identification, design, or use of wildlife crossing structures across roads, because the topic, which also includes large carnivores, has been thoroughly reviewed (Ree et al., 2007; Glista et al., 2009; Denneboom et al., 2021). After applying the eligibility and selection criteria, we identified 135 publications from the Scopus and Web of Science databases suitable for the review and 40 publications from the CCSG library database (Figure 1). We also used forward and backward citation tracking of all publications included in the review to identify any missing studies relevant to this review. We found three additional academic publications pertinent to our review. Therefore, the final set of studies used for the review was 178 articles (Supplementary File S3).

Data extraction and analysis

We categorized each study as focusing on the identification of corridors by researchers or assessing the use of existing corridors by large carnivores based on the stated or implied objectives of the research. We also collected data relating to the geographical location of the research (country and continent), year of publication, the affiliations of all authors (academic, government, non-governmental or private institutions), the species included in the research, the rationale for selection of species, the spatial extent of the study area (in sq. km.). We used linear regression analysis in R to examine the relationship between the number of species present and the number of studies conducted in a country. We

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TABLE 1 Terrestrial large carnivore species selected for review. Mean body weight data from Ripple et al. (2016). Conservation status from IUCN Redlist (2022).

Common name	Scientific name	Mean weight (kg)	IUCN Redlist category
Canidae			
African wild dog	*Lycaon pictus*	22	EN
dhole	*Cuon alpinus*	16	EN
dingo	*Canis dingo*	15	–
Ethiopian wolf	*Canis simensis*	15	EN
grey wolf	*Canis lupus*	33	LC
maned wolf	*Chrysocyon brachyurus*	23	NT
red wolf	*Canis rufus*	25	CR
Felidae			
cheetah	*Acinonyx jubatus*	59	VU
clouded leopard	*Neofelis nebulosa*	20	VU
Eurasian lynx	*Lynx lynx*	18	LC
jaguar	*Panthera onca*	87	NT
leopard	*Panthera pardus*	53	VU
lion	*Panthera leo*	156	VU
mountain lion	*Puma concolor*	52	LC
snow leopard	*Panthera uncia*	33	VU
Sunda clouded leopard	*Neofelis diardi*	20	VU
tiger	*Panthera tigris*	161	EN
Ursidae			
American black bear	*Ursus americanus*	111	LC
Andean black bear	*Tremarctos ornatus*	105	VU
Asiatic black bear	*Ursus thibetanus*	104	VU
brown bear	*Ursus arctos*	299	LC
giant panda	*Ailuropoda melanoleuca*	134	VU
sloth bear	*Melursus ursinus*	102	VU
sun bear	*Helarctos malayanus*	46	VU
Hyaenidae			
brown hyena	*Hyaena brunnea*	43	NT
spotted hyena	*Crocuta crocuta*	52	LC
striped hyena	*Hyaena hyaena*	27	NT

Red List categories are LC (Least Concern), NT (Near Threatened), VU (Vulnerable), EN (Endangered), CR (Critically Endangered).

categorized studies based on whether corridors connected two protected areas (PA-PA), more than two protected areas (PA-MPA), a protected area to non-protected habitat (PA-NPA), or between two non-protected habitats (NPA-NPA). We also recorded the environmental and anthropogenic variables considered by researchers in corridor studies. For studies focusing on the use of corridors, we also extracted information on existing threats to corridors and recommendations to mitigate such threats.

We used information on the author's affiliated institutions and countries for 158 large carnivore corridor studies, for which such information could be extracted, to assess research collaboration among different sectors and across continents using VOSviewer (van Eck and Waltman, 2010; v1.6.16). In VOSviewer, research networks can be mapped based on co-citation, co-occurrence, or co-authorship of keywords, important terms, journals, individual publications, authors, countries, or organizations.

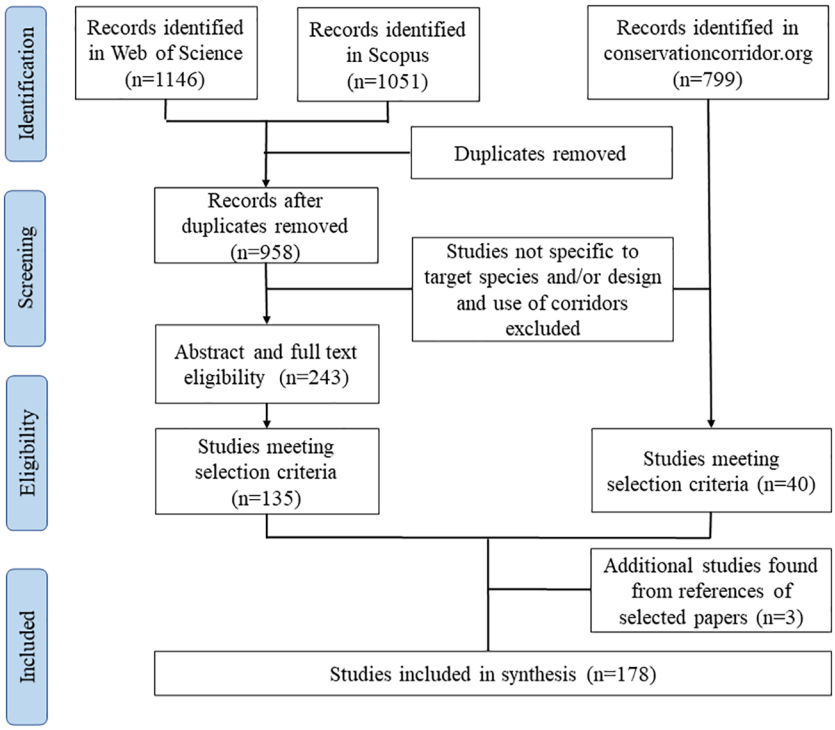

FIGURE 1
Preferred Reporting Items for Systematic reviews and Meta-analyses (PRISMA) flow diagram showing a stepwise selection of literature for the large carnivore connectivity review. Adapted from Moher et al. (2009).

Results

Identification versus the use of large carnivore corridors

The temporal pattern of studies reviewed indicates that there has been an increase in corridor research for large carnivores since 2005. A maximum number of 18 studies relevant to this review were identified for 2017, followed by 17 studies in 2020. We found a stronger preference for research on the identification of corridors connecting habitats occupied by large carnivores (n=143 studies) than those evaluating their use by large carnivores (n=35 studies) (Figure 2). However, since 2015, there has been a marked increase in the number of studies focusing on corridor use by large carnivores (Figure 2).

Studies evaluating the use of the corridors reported on the contribution of the corridor for the dispersal and movement of species (n=27 studies), maintaining a viable metapopulation (n=10 studies), facilitating the genetic exchange between sub-populations (n=6 studies), or reducing human-wildlife conflict (n=2 studies). However, roads and infrastructure (n=17 studies), overexploitation (n=11 studies), habitat encroachment (n=9 studies), habitat degradation and deforestation (n=9 studies), and human-wildlife conflict (n=9 studies) are major threats present within the corridors that may limit their effectiveness in delivering conservation outcomes. Additionally, an increase in traffic intensity (n=2 studies), invasive species (n=1 study), and disturbance due to tourism-related activities (n=1 study) are other threats reported to decrease the effectiveness of corridors at providing connectivity. Habitat restoration (n=11 studies), reducing anthropogenic disturbance (n=9 studies), and strengthening the protection status of corridor habitats (n=8 studies), for example, through designation as protected forest/habitat, were suggested as key strategies to improve the conservation outcomes. Furthermore, studies recommended reducing existing and potential human-wildlife conflicts along the corridors (n=7 studies), putting mechanisms in place to ensure future development activities within corridors are avoided (n=6 studies), and minimizing the effects of road networks (e.g., through crossing structures) (n=4 studies) to improve corridor effectiveness.

Spatial extent and configuration of corridors

Most studies (n=174 studies) included protected areas (PA) as core elements in the identification and use of corridor networks. Nearly 89% (n=158 studies) of studies also focused on corridors across a sizable landscape (i.e., >1000 km^2), accounting for the substantial area requirements of large carnivores (Figure 3). More studies focused on connectivity across multiple protected areas (73%, n=130 studies) compared to connectivity between two protected areas (18%, n=32 studies). In addition, few studies also focused on the connectivity between protected areas and non-

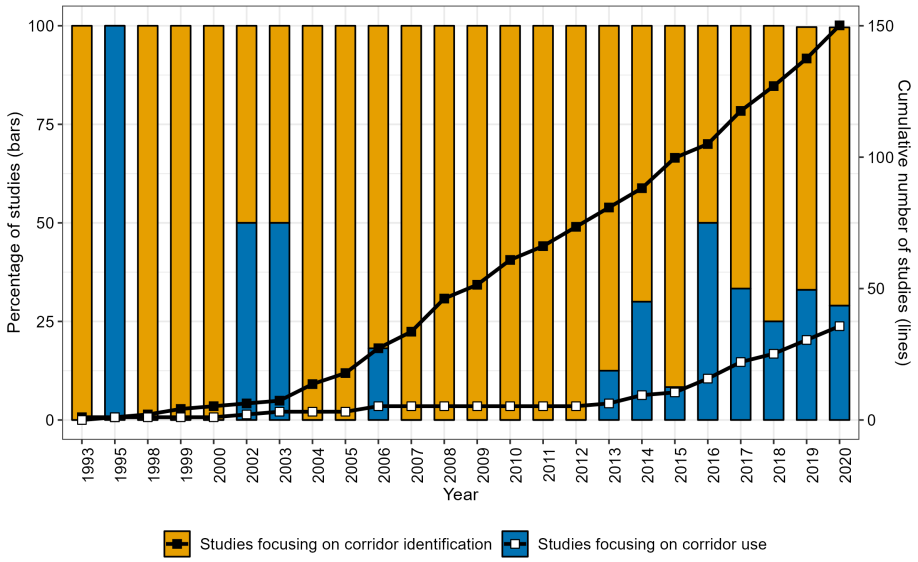

FIGURE 2
Cumulative number of studies focusing on corridor identification and use (line) and proportion of studies on corridor identification and use in the stacked bar for each year.

protected habitats (7%, n=12 studies) and entirely across non-protected habitats (2%, n=2 studies), highlighting the importance of protecting habitats outside the protected areas network for large carnivores.

Priority species for corridor studies

Of the 27 species included in this review, only 22 species were found to be included in corridor research. Research on the identification or use of corridors was missing for the dingo, Ethiopian wolf, maned wolf, brown hyena, and spotted hyena. More than 80% of studies on large carnivore corridors included at least one of only five species, the mountain lion (n=46 studies), American black bear (n=31 studies), jaguar (n=25 studies), tiger (n=25 studies), and brown bear (n=18 studies) (Figure 4). Studies predominantly selected charismatic and apex predators for the study region as the focal species of the research. For example, fewer studies focused on leopards in the Indian sub-continent, where the tiger is the apex predator. In contrast, more studies focused on leopards in central Asia, where it is the apex predator. We found similar patterns for the jaguar and mountain lion in

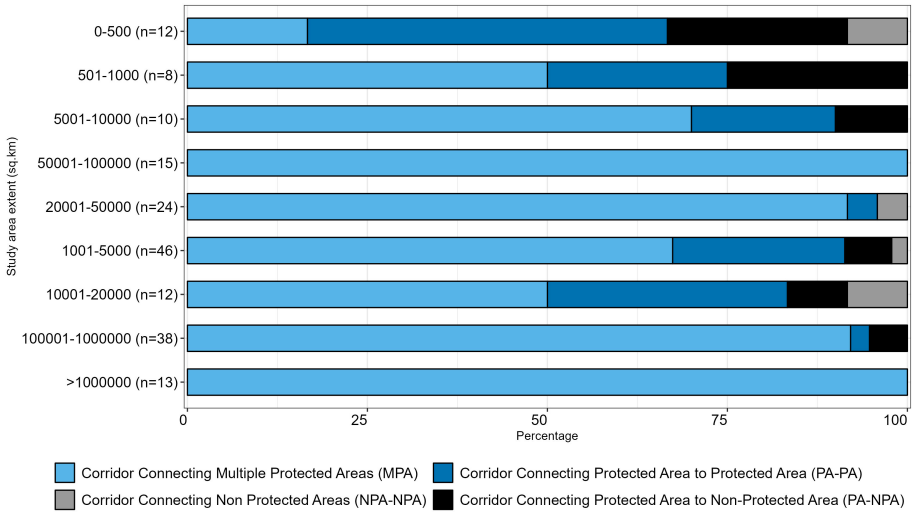

FIGURE 3
Study area extent and habitat elements considered by corridor studies. The approximate area was estimated from the study area maps for studies where the extent was not provided.

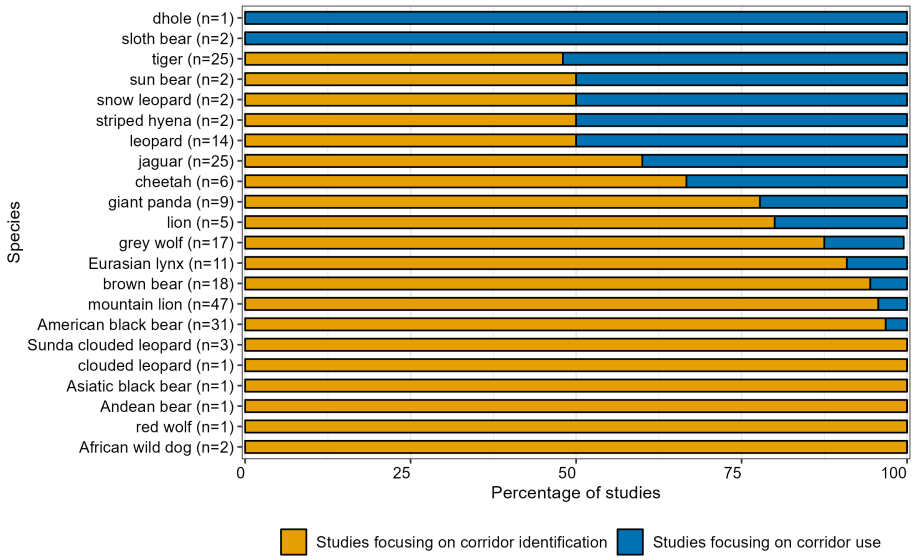

FIGURE 4
Proportion of studies focusing on corridor identification or use for each species.

South America, where more studies focused on the jaguar as the apex predator for the region, despite both species having significant range and habitat overlap.

Studies focusing on single-species corridors were in the majority (n=106 studies) compared to those assessing multiple species (n=72 studies). There was also a difference in the research approach for selecting focal species between academic and grey literature. More than three-quarters (n=105 studies) of all academic publications focused on a single species. In contrast, almost all studies (n=39 studies), except one, from the grey literature, selected more than one focal species for corridor research. Of the 72 studies that focused on multiple species, 37 studies focused on two or more large carnivores. The remaining 35 studies included other species in addition to at least one of the large carnivores, such as elephants, oncillas, Malay civets, peccaries, wild boars, tapirs, blue bulls, as well as reptiles, amphibians, and invertebrate species. While conservation practitioners have been using the multi-species approach for corridor planning since 2000, more than 70% of academic studies focusing on two or more species have been conducted after 2015, suggesting a growing interest in multi-species corridor research in recent years.

Geographical coverage of studies

Despite habitat fragmentation being a major conservation threat for large carnivores across most of their habitat range, corridor research was missing from several countries where large carnivores are found. The 27 large carnivore species reviewed here are found in 147 countries (IUCN, 2022), of which 66 countries had research on either the identification or use of corridors by these species (Supplementary File S4). Using simple linear regression, we found that the number of species present significantly predicted the number of studies conducted in a country ($\beta = 0.9328$, $p < 0.05$; Supplementary File S5). Despite the prevalence of large carnivores in Sub-Saharan Africa, Africa had the lowest representation in corridor research compared to other continents. Studies were concentrated more in North America (47%), followed by Asia (30%), Europe (10%), South America (9%), and Africa (4%). Of the 47 African countries where large carnivores are found, research on either corridor identification or use was conducted in only ten countries (21%). Contrastingly, the proportion of South American countries was 92%, North American countries 82%, Asian countries 63%, and European countries 29% where corridor research was conducted. We did not find any studies focusing on corridor identification or use by dingos in Australia (Figure 5). On a country scale, the United States, India, and China were most represented in research, with 23%, 7%, and 5% of all studies considered respectively for each country.

A research gap existed between species range distribution and where studies were conducted at the country level. It was particularly noticeable for species with a wide distribution, a broad diet, and habitat overlap with other apex predators. For example, generalist predators such as the grey wolf and leopard are the most widely distributed large carnivores found across 68 and 63 countries, respectively, but each was considered only in 9 and 14 countries for corridor studies, respectively. Although the clouded leopard and snow leopard had the highest geographical coverage for corridor studies, this was due to a small number of studies covering their entire range.

Variables considered by corridor studies

Among the 50 environmental and anthropogenic variables considered by researchers, the most frequently used variables were land use/land cover (81%), elevation (54%), presence of transportation infrastructure (46%), distance to roads/railways

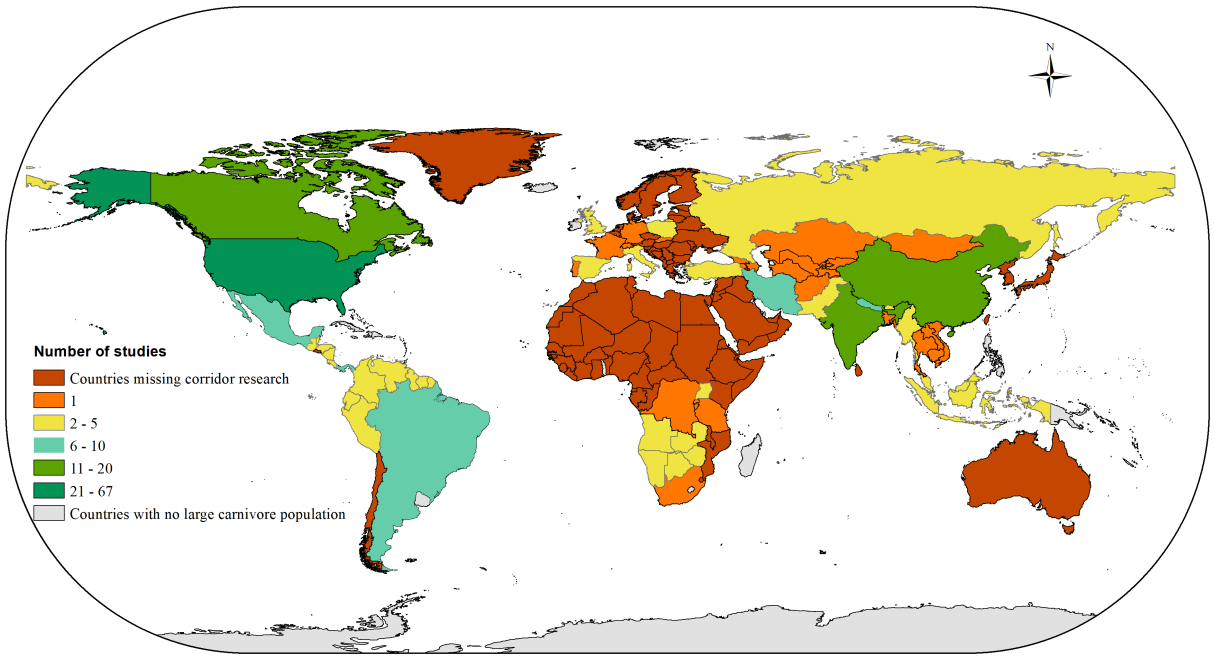

FIGURE 5
Geographical gaps in scientific research on the identification and use of corridors for large carnivore conservation. The geographic distribution of large carnivore species used to identify these gaps is based on IUCN Red List data (IUCN, 2022). The cumulative number of studies conducted for all species across their geographic distribution is presented.

(29%), and slope (29%). All these variables were used disproportionally among studies, with combinations of these variables considered more frequently by studies focusing on the identification of corridors than those assessing the use of corridors by large carnivores (Figure S6). Despite being a major threat to large carnivores, data on human-wildlife conflict incidences (5%) and future climate change scenarios (3%) have been used in only a few studies.

Research collaboration

We found notable cross-sector collaboration for large carnivore corridor research. Of the 158 studies for which author information was collected, 58 studies (37%) were conducted by authors affiliated with only one sector, while the remaining 100 studies (63%) had cross-sector collaborations among authors. Of the 58 studies, the authors of 39 studies were affiliated with academic institutions, 10 studies with the government, and nine studies with non-governmental institutions. For studies having cross-sector collaboration, academics had a slightly greater collaboration with the authors affiliated with government institutions (n=39 studies) than with non-governmental institutions (n=35 studies), whereas 16 studies were conducted by authors affiliated with all three institutions. Only one study for which the authors from government and non-governmental institutions collaborated. While academics sometimes collaborated with the private sector (n=3 studies), the collaboration between authors from government or non-government institutions with the private sector was missing. Authors from academia and the private sector collaborated with the government in four studies and non-governmental institutions in two studies. We noted that academics contributed to advancing knowledge in large carnivore corridors and connectivity through research but also facilitated extended collaboration among various sectors for corridor research.

Mapping connections between the location of the lead author's institutional affiliation and study region showed that the authors affiliated with institutions in Asian and South American countries conducted corridor research predominantly within their region. In contrast, European, North American, and Australian authors conducted research across continents (Figure 6). At a country level, the United States was the major research collaborator with the rest of the world for research on the identification and use of large carnivore corridors (Figure 7; Table S7).

Discussion

We conducted the first global synthesis of research literature that specifically focuses on identifying corridors and their use by large carnivores, a primary focal group for connectivity research. We identified potential gaps related to the disproportionate distribution of studies for species across geographies and institutions and the mismatch of research priorities within the published peer-reviewed and grey literature for corridor research focusing on the identification and use of corridors by large carnivores. We found a greater historical research emphasis on the identification of corridors. However, recent studies are focusing

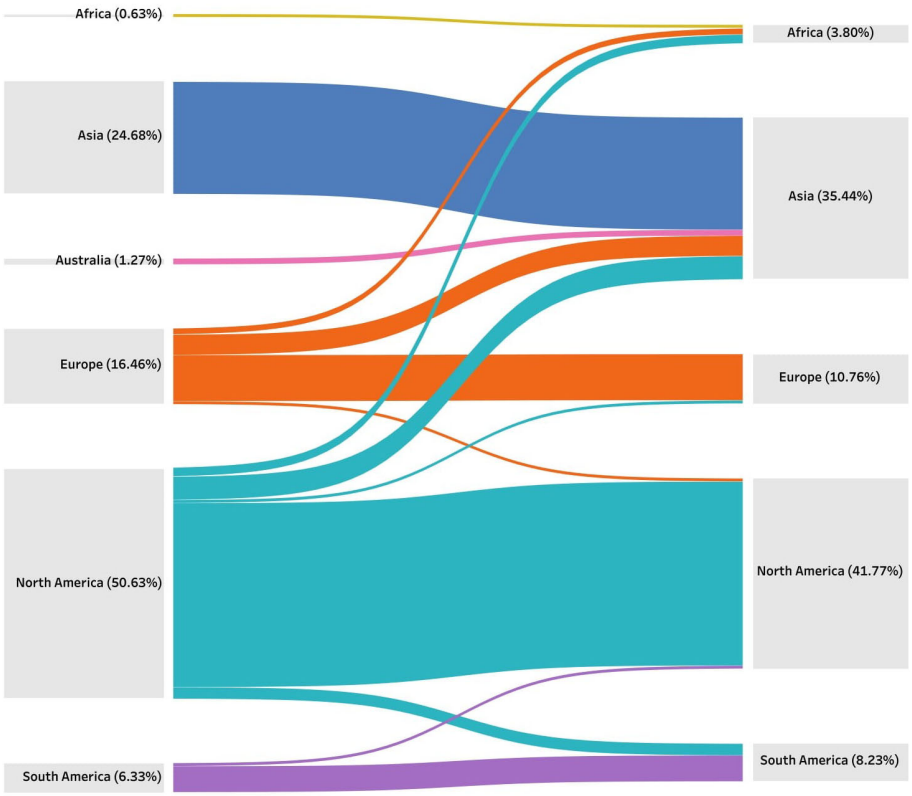

FIGURE 6
Connections between the location of the lead author's institutional affiliation and study sites/countries at a continental scale. The percentage value shows the proportion of studies for each continent where the lead author's affiliated institution was located (left) and where the study was conducted (right), and the width of the links is proportional to the number of studies.

more on measuring the use of existing corridors, indicating a shift towards assessing corridor effectiveness, which aligns with the emphasis on corridors as a tool to mitigate the threats of habitat fragmentation and climate change across entire landscapes and land use tenures.

Patterns in corridor identification and their use by large carnivores

Although wildlife corridor and connectivity research attracted attention in the 1990s, research focusing on large carnivores gained momentum only in the last decade. This recent trend is comparable to that reported by Ayram et al. (2016) in their review of habitat connectivity studies which indicated increased research focus on large carnivore corridors across their range. The recent increase in the number of publications on this topic (Figure 2) is most likely triggered by the global plight of large carnivores and their habitats (Ripple et al., 2014; Wolf and Ripple, 2017), as well as the increasing role of large carnivores as conservation flagship species (Thornton et al., 2016; Macdonald et al., 2017). Advances in the methodological approaches used for connectivity research (e.g., circuit theory, step-selection functions, etc.) and the consideration of climate change threats (Heller and Zavaleta, 2009) provide opportunities for better evaluation of corridor effectiveness (Ayram et al., 2016; Naidoo et al., 2018; Smith et al., 2019; Ghoddousi et al., 2020). The shift in momentum for corridor research over the last decade is also fueled by the application of systematic and spatial planning in linking habitat connectivity with reserve selection and increased scientific understanding and concerns related to the effects of habitat fragmentation and unchecked human population growth, especially in more biodiverse countries (Ayram et al., 2016; Naidoo et al., 2018). Furthermore, increased availability of inexpensive and improved technologies for species monitoring, such as smaller and better-performing camera traps, GPS tracking devices (Wilmers et al., 2015), and access to species presence records and spatial data may have enabled more research on the topic (Kool et al., 2013; Wade et al., 2015).

While early studies focused on identifying corridors for large carnivores, there has been an increase in the number of studies evaluating the use of corridors by large carnivores in recent years. This is likely to be a natural research progression as the growth in publications focusing on the identification and proposing the establishment of corridors may have prompted researchers to measure the use of existing and proposed corridors, as well as the permeability of modified landscapes (Smith et al., 2019). However, most of the studies reviewed here assessed the use of the corridors by large carnivores by reporting the species' presence or movement but did not quantify the connectivity provided by the corridors.

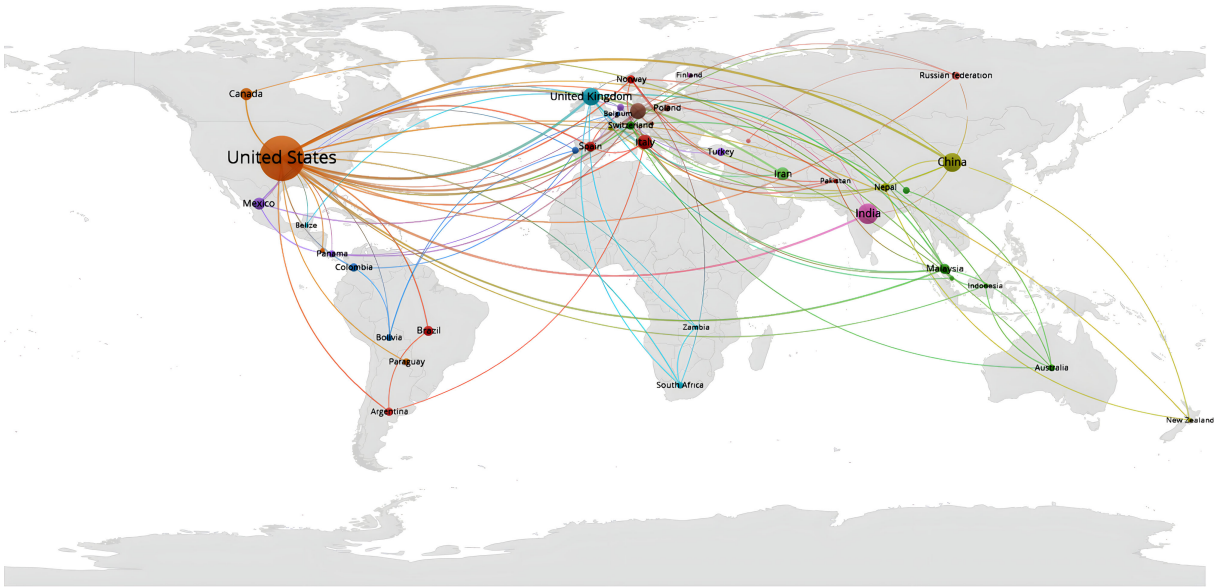

FIGURE 7
Global research collaboration (co-authorship) for large carnivore corridor research, including studies on both the identification and the use of the corridors. From: VOSviewer doi: 10.3389/fcosc.2023.1094443.

While the presence of species within corridor habitats is a useful indicator of the use of corridors, it does not necessarily measure the effectiveness of the corridors. It is therefore considered a weak predictor of connectivity (Gregory and Beier, 2014). The effectiveness of the corridor can be better assessed by tracking the movement of several dispersing individuals in the landscape (see Smith et al., 2019), and developing quantitative metrics related to the genetic, demographic, ecological as well as economic, and social impacts of the corridors during the early phases of corridor planning so that future studies can use the baseline data and metrics to evaluate and compare the effectiveness of the corridors over time and across landscapes.

The spatial extent of connectivity studies

One of the benefits of selecting large carnivores as focal species for connectivity planning is that it facilitates analyses at a landscape level simply because of the greater mobility and large area requirements of these species (Dalerum et al., 2008). It allows practitioners to develop and implement a single, comprehensive, and consistent connectivity conservation plan for a landscape that can provide connectivity for a wide range of species rather than developing and implementing multiple conservation plans within a single landscape. Therefore, it is not surprising that we have found more studies focusing on connectivity across large spatial extents (> 1000 km^2), and these frequently incorporate multiple protected areas. However, one of the issues with large-scale studies is that they frequently generalize environmental conditions and threats, ignoring the fine-scale variability present in the landscape (Lawler et al., 2013; McGarigal et al., 2016), which can lead to misinterpretation or inaccurate prediction of conservation needs (Huber et al., 2010; Newman et al., 2019). Given the fine-grained spatial scale at which a species interacts with its immediate environment, we suggest that there is scope for future corridor research to explore these aspects in greater detail to fully appreciate the nature and level of threats to connectivity for large carnivores.

Because all or most of the populations of the selected focal species for this review are predominantly found within protected areas (Watson et al., 2014; Rich et al., 2017), the finding that the majority of the studies focused on corridors either originating from or connecting to protected areas is not unexpected. Nevertheless, this finding further emphasizes the importance of maintaining a connected network of protected areas sufficient to support a viable population of large carnivores as a critical requirement for the long-term survival of the species that will also benefit a range of other species and ecosystem services (Watson et al., 2014; Rich et al., 2017). Furthermore, a connected network of protected areas will provide species with a greater buffer to support any adaptation to the potential range shifts resulting from climate change.

Importantly, few studies focused on corridors leading to non-protected habitats highlighting the importance of conserving and restoring habitat outside protected area networks for large carnivores and other species. Furthermore, there is evidence of the recovery of large carnivores, and limited space available within protected areas may not be sufficient to accommodate this increase in carnivore populations (Chapron et al., 2014; Lamichhane et al., 2018). Identifying and connecting potential habitats outside protected areas through large carnivore corridors may become vital for the future survival of many large carnivores.

Despite the increase mentioned above in research assessing the use of corridors by large carnivores, we identified four key research gaps and expand on each to guide future research and planning. These include i) the taxonomic bias in the selection of focal species, ii) gaps in the geographical coverage of studies, iii) adequate inclusion of key conservation issues, and threats (e.g., infrastructure development, human-wildlife conflict, climate change) facing large carnivores potentially using corridors, and iv) cross-sector collaboration among researchers for large carnivore corridor research.

Selection of focal species

Several frameworks have outlined species' attributes, such as their umbrella value, role in ecosystem functioning, home range size, extinction risk due to habitat loss and fragmentation, etc., as a guide for selecting appropriate focal species for connectivity conservation studies (Beier et al., 2008; Krosby et al., 2015; Meurant et al., 2018). While almost all large carnivores are threatened by habitat loss and fragmentation, they are not necessarily ideal focal species for connectivity research and planning (Beier et al., 2008) because of variations related to their life histories, biology, behavior, and threats. For example, for some species, such as brown hyena, human persecution and retaliatory killing are a more significant threat compared to the loss of connectivity (Wiesel, 2015), whereas other species that have adapted to using human-modified landscapes, such as leopards (Athreya et al., 2013; Van Cleave et al., 2018) and striped hyena (AbiSaid and Dloniak, 2015), are less sensitive to loss of connectivity. Furthermore, the variation among large carnivores in terms of their value as an umbrella, flagship, or keystone species, home range size, role in ecosystem functioning, and sensitivity towards habitat loss and fragmentation may also explain the taxonomic bias observed in focal species used for the corridor research studies reviewed here. For example, although the jaguar and the mountain lion share similar habitat, Coppolillo et al. (2004) concluded that the jaguar is a better focal species than the mountain lion for site-based conservation based on heterogeneous habitat and area required, their role in ecosystem function, and the wide range of threats that can be addressed by its conservation which will also benefit several other species.

While most large carnivore species included in our review were selected as focal species for at least one connectivity research study (n=22 studies, 81%), only five were regularly used. Therefore, our review showed a distinct preference toward larger charismatic species and apex predators (e.g., tiger, jaguar, mountain lion, brown bear). The selection of these large charismatic and apex predators is justified because they not only regulate the populations of prey species but also populations of sympatric carnivores through intraguild competition, thus exerting a greater influence on the ecosystem structure and function through trophic cascades (Steinmetz et al., 2013; Tshabalala et al., 2021). Similarly, charismatic species have the potential to garner greater public engagement, support for conservation, and direct conservation efforts (Macdonald et al., 2015; Li and Pimm, 2016; Albert et al., 2018), while also being used as symbols to secure the necessary funding for conservation projects (e.g., giant panda, Kontoleon and Swanson, 2003; Verissimo et al., 2011). Some of the selected focal species also have greater social, cultural, and religious significance for the local people, which may have led to a greater emphasis on their conservation. For example, the tiger and leopard are considered sacred animals and the protector of forests by Hindus and Muslims in the Sundarbans region of India and Bangladesh, and therefore these species receive greater support for conservation compared to other carnivores (Dhee et al., 2019; Akash and Zakir, 2020). Other species, particularly large canids (e.g., dhole, Ethiopian wolf), were not represented in corridor research, likely because of their poor charismatic appeal compared to co-inhabiting felids. The higher aesthetic appeal of wild felids has been reported as a major factor influencing their greater use for conservation research and planning (Macdonald et al., 2015; Albert et al., 2018). In general, felids received greater research attention than canids, with the grey wolf being the exception, which aligns with previous reviews (Tensen, 2018). Nonetheless, research on the use of existing corridors by under-represented species, such as canids, can be important to ensure that their connectivity needs are also met. One approach for incorporating these less-studied species is to use them as secondary species in corridor research, with other large, charismatic species serving as primary focal species.

Regarding the focus of the research, we identified a disconnect between research published in scientific journals and grey literature. While it may be natural for researchers to focus on a single large carnivore species based on the argument that their umbrella value will address the connectivity needs of other species, this may not apply in all cases (Cushman and Landguth, 2012; Penjor et al., 2021). Such over-reliance on the umbrella species for connectivity research may lead to gaps in understanding the needs of less-studied species and, consequently, in the planning and implementation of appropriate measures to meet their connectivity needs. Therefore, multi-species corridors are often considered a more effective tool for landscape connectivity planning (Beier et al., 2008; Meurant et al., 2018). For example, Wang et al. (2018) noted that corridors identified for giant pandas poorly represented the connectivity requirements of other sympatric deer species. While the giant panda may not be a typical representative within the 'carnivore' guild, the issue being highlighted here remains. One of the major drawbacks of single-species corridor research is that this may lead to establishing and managing multiple corridors within a single landscape. This approach may not be feasible or financially viable and is highly likely to confound the problem of prioritization and management of the most efficient corridors. As such, most of the grey literature reviewed already focused on the identification or use of corridors by multiple species to address this problem, whereas research published in scientific journals investigating multi-species corridors has only increased since 2015. This suggests that there is an encouraging, yet gradual, shift towards assessing multi-species approaches to corridor research. However, further advances in academic research in this area could better support conservation practitioners with effective corridor planning and implementation on the ground.

Geographical coverage of the studies

Geographical bias in ecological research from the Americas (North and Central) and European countries has been reported by several previous ecological reviews related to animal biodiversity, habitat fragmentation, tropical conservation research, etc. (Ayram et al., 2016; Wilson et al., 2016a; Fardila et al., 2017; Reboredo Segovia et al., 2020), and this pattern was largely consistent with our review for large carnivore corridor research, with some research gaps in eastern Europe and Scandinavia. While the USA has been at the forefront of conservation research, publications from China and India have increased recently (Di Marco et al., 2017; Lozano et al., 2019). The preponderance of studies conducted in these countries could be explained by greater access to research funding, demand for connectivity research to support development, better research facilities, capacity, and access to publications (Campos-Arceiz et al., 2018; Melles et al., 2019).

The major geographical gaps we identified in corridor research for large carnivores were found in eastern Europe, Scandinavia, Southeast Asia, Africa and the Middle East, and nexus countries between South and Central America. These regions were also among those experiencing declines in carnivore populations due to fragmentation, persecution, depletion of prey, and contraction of their range (Ripple et al., 2014; Wolf and Ripple, 2017). For example, habitat fragmentation and isolation have been identified as a major threat to the Amur tiger and leopard populations in Russia (Kerley et al., 2002; Carroll and Miquelle, 2006; Tian et al., 2011; Tian et al., 2014); however, there were few studies published from the region on the identification and use of corridors by these large carnivores. The relatively fewer studies from these regions are likely due to limited financial capacity, trained human resources for research, or language barriers leading to difficulty publishing in English-based journals (Griffiths and Dos Santos, 2012; Christie et al., 2021). Similarly, despite a high level of habitat fragmentation across Europe (Haddad et al., 2015; Ibisch et al., 2016), there was comparatively little published research on large carnivore corridors in the region. This is likely due to the historical low population densities of large carnivores in the region and they not being suitable flagship or umbrella species for connectivity conservation needs of the landscape. However, as the population of large carnivores is gradually recovering across many parts of Europe (Chapron et al., 2014; Boitani and Linnell, 2015), the research focusing on the identification and use of corridors to facilitate their movement will likely become an important topic. Compared to Europe, the habitat in Scandinavia is less fragmented, particularly in northern and central Scandinavia (Jaeger et al., 2016; Svensson et al., 2020). While forest fragmentation is considered an issue for the dispersal and movement of some species, such as butterflies (Modin and Öckinger, 2020), fungi (Nordén et al., 2013) and forest grouse (Lindén et al., 2000), it is not considered as a major conservation issue for large carnivores or their prey, which may explain the relatively low attention given to large carnivore corridor research. For example, Kopatz et al. (2012) reported the gene flow and bi-directional migration among the sub-populations of brown bears from Karelia and Pinega that were nearly 600 km apart. Moreover, the negative perceptions of local people towards large carnivores (Krange et al., 2017) coupled with their broad tolerance to modified habitats (Torres et al., 2012; Boitani and Linnell, 2015) may have contributed to the lack of their use as focal species for corridor research in Scandinavia. The research gap across eastern Europe and Scandinavia may also be due to the diversity of languages across the region and the publication of research in native language journals. Conversely, the research gap observed for Australia and Oceania is most likely due to the low representation of carnivores and other threats to biodiversity present in the region that may be more dominant than the loss of connectivity. Similarly, the absence of studies in Greenland, another exception, may be due to relatively stable landcover, low human population, and presence of predominantly marine carnivores.

Although few studies from these regions have been published, there are several examples of ecological corridors being implemented in the region, including the Biodiversity Conservation Corridor Initiatives (BCI) across Vietnam, Cambodia, and Laos, Thailand's ecological network of protected areas, and conservation of the Albertine Rift landscape across six African countries, which has improved connectivity for threatened species including large carnivores (Hilty et al., 2020). As such, geographic bias in corridor research does not necessarily mean bias in implementing the conservation efforts on the ground or undermining the conservation efforts aimed at protecting viable populations of large carnivores. However, we emphasize that the results and lessons from such conservation interventions need to be published and disseminated. This will contribute to advancing knowledge on wildlife connectivity and allow replication of similar success elsewhere. Most of the grey literature in our review is from North America, which may be due to our selection of studies published in the English language only. Synthesis of grey literature and publications in academic journals available in languages other than English may help to overcome such a language barrier and provide better insights into the geographical gaps that exist within the research literature. Identifying such geographical gaps can help prioritize future research in those regions to improve our understanding of connectivity status.

Variables considered in corridor research

Although variables selected for corridor research often tend to be species or locale-specific, one of the major omissions in corridor research relates to the human-wildlife interactions frequently associated with large carnivore corridors. Few studies considered human-wildlife interaction e.g., conflict, persecution, retaliatory killings, etc., as a variable in their research, which is concerning because large carnivores are among those most frequently linked to human-wildlife conflict because of their diet and movement requirements (Inskip and Zimmermann, 2009). Increased movement of large carnivores along the corridor inevitably increases the risk of potential human-wildlife conflict. Such risks should be identified in the early stages of corridor planning to allow appropriate mitigation measures to be identified and implemented

to prevent or reduce human-wildlife conflicts. However, the current research pattern indicates that there is a greater focus on measuring the conflicts within and around the existing corridors (Ravenelle and Nyhus, 2017; Krafte Holland et al., 2018) rather than incorporating human-wildlife conflicts in research to identify safe corridors. Any increase in conflict along the corridors may lead to significant economic loss, negative sentiments among local communities towards corridor conservation, and large carnivores, thereby offsetting the ecological benefits of such corridors. Including human-wildlife conflict scenarios in corridor research can help identify safer corridors for both humans and wildlife while also guiding practitioners on implementing appropriate mitigation measures to prevent potential human-wildlife conflict in corridors used by large carnivores.

An additional gap from our review highlighted the limited integration of climate change impacts. While improving landscape connectivity is one of the frequently recommended strategies for climate change adaptation (Heller and Zavaleta, 2009), few studies assessed the connectivity achieved by corridors under future climate change scenarios for large carnivores. It is important to incorporate climate change scenarios and their potential impact on thermal tolerance and range shift for species as a factor in corridor identification, which may significantly impact the present use and future viability of the corridor networks.

Research collaboration

Research collaboration among different sectors is important as it ensures that the research needs of each sector are addressed while producing actionable knowledge that resolves the problems existing within each sector (Cooke et al., 2021). The involvement of individuals representing 'knowledge user' groups for research collaboration through shared authorship can contribute to capacity building through the exchange of knowledge, ownership of the shared knowledge, and influence the endorsement of recommendations presented in the publication (Carmen et al., 2015; Norström et al., 2020; Cooke et al., 2021). Furthermore, exchanging ideas and perspectives among researchers representing different institutions can help understand and resolve any conflicts between science and practice and lead to developing the consensus knowledge that is pertinent, practical, and easier to implement (Nesshöver et al., 2016).

Given that our review focused predominantly on peer-reviewed literature, we expected a greater representation from academia in our results. Our review confirmed this expectation, as nearly 77% of studies on corridor identification and use were published by authors affiliated with academic institutions. However, there was also some wider collaboration across multiple sectors in the field, which suggests that there is scope to transfer research findings to improve conservation outcomes for these species. Collaboration between academics and practitioners can therefore facilitate research studies that are needs-based and that have a practical application (Young et al., 2014) as academics fill in knowledge gaps while practitioners bring *in situ* perspectives to improve implementation and address challenges. There is already notable collaboration between authors from academia, government, and non-governmental institutions for large carnivore connectivity research. However, large carnivore corridor research is missing involvement from the private sector, which is a key stakeholder in determining the successful implementation of connectivity conservation plans (Keeley et al., 2018; Keeley et al., 2019). The joint authorship of the publications may not capture all the collaborations happening among these institutions, for example, some of the papers authored only by academics may have reached practitioners, whereas some co-authored by practitioners and academics may not have reached the crucial practitioners. Nevertheless, the review provides valuable information on patterns of research publication involving multiple institutions.

Despite the evidence of some degree of collaboration between researchers and end users in corridor research shown here, there is still limited apparent involvement from the private sector. Mainstreaming the private sector in conservation has been identified as an effective and sustainable solution to the biodiversity problem (Barbier et al., 2018; Rose et al., 2018). For example, the partnership between government, non-government, and industry sectors for palm oil production has reduced deforestation rates in Indonesia (Carlson et al., 2018). While collaboration among the private sector and other institutions may exist for conservation actions, similar collaborations are necessary for carnivore corridor research and practice to prevent further habitat fragmentation and improve connectivity.

Limitations of the review

The review focuses on assessing specific literature on the identification and use of corridors by large carnivores within the broader connectivity research context. The specific scope of this review may limit its interpretation for corridor research on other topics and taxonomic groups. We recommend a similar synthesis of the literature covering those topics and broader taxonomic groups to guide future connectivity research. Our review also excludes literature not documented in the databases used for this review and published in non-English languages. Considering similar synthesis of patterns, priorities, and gaps within the corridor research literature using a systematic review process covering multiple databases and languages would be useful for guiding future connectivity conservation efforts. While we acknowledge some limitations of the method used and the potential risk of bias, the review comprehensively assesses the patterns observed in the large carnivore corridor literature.

Synthesis and recommendations

The taxonomic bias and geographical gaps in large carnivore corridor research may undermine the conservation efforts to protect these species' viable populations. The research on the identification and use of conservation corridors for large carnivores is primarily informed by single-species studies focusing on solitary apex species and lacks evidence for the effectiveness of such corridors for other species sharing the landscape, future human interactions, or climate change scenarios. The current conservation challenges facing large

carnivores require a broader multi-species approach to the connectivity problems to provide insights into how corridors effectively meet the needs of a suite of species. Furthermore, quantitative research using well-defined and consistent metrics on the use of corridors by large carnivores, such as movement or presence data collected at regular intervals for target species, records of human interactions within corridors, genetic flow between connected populations, etc., is needed to measure the effectiveness of such corridors as well as adaptive management of the corridor habitats in the future.

The early identification and mitigation of potential human-wildlife conflicts resulting from large carnivore corridors are critical for managing safe and functional corridors and maintaining local support for conservation. Corridor identification research should include specific recommendations to mitigate the potential human-wildlife conflict that can be implemented in practice. Land use and land cover, together with human disturbance, remain important variables for research on the identification and use of large carnivore corridors. Road and railway networks were identified as a major threat to the connectivity of these corridors. Researchers have a consensus that the adverse effects of roads need to be minimized to realize the full potential of the corridors. Establishing road crossing structures at key pinch points, reducing vehicular traffic on roads passing through corridors, and habitat restoration along the roads have been shown to minimize the effects of linear infrastructure on connectivity (Denneboom et al., 2021; Hill et al., 2021). In addition, researchers have also advised setting up mechanisms to oversee the future development of such linear infrastructure through corridors to ensure that any future development activities carried out within corridors do not affect the connectivity potential of the corridors.

Although corridor research had considerable collaboration among academia, and governmental and non-governmental institutions, there is an apparent need for greater involvement of the private sector in corridor research to identify practical and sustainable solutions for connectivity conservation problems and their endorsement. The involvement of the private sector, which includes businesses and commercial entities but also rural communities or community groups, is also critical given the increasing need for conservation efforts that extend beyond protected area networks to accommodate non-protected habitats. Actions are required to enhance and support the capacity building of researchers in high biodiversity regions to fill the research gap.

The identification of corridors by researchers and their use by large carnivores directly influence where and how large carnivores persist in, and interact with, their habitat. Additional research on large carnivore movement and dispersal in corridors is needed to fill the research gap in measuring corridor use and effectiveness. We suggest scaling up the lessons from studies conducted at smaller spatial extents to larger landscapes to demonstrate the benefits of large carnivore corridors. Such studies will help validate the corridors' functional value and justify the considerable funding required to maintain these corridors.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

All authors contributed to the conceptualization and design of the study; TRB led the search for relevant literature, data extraction, and analysis, with support from all co-authors. TRB wrote the first draft of the manuscript, and all authors contributed to the manuscript's review, editing, and revisions.

Conflict of interest

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

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2023.1094443/full#supplementary-material

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