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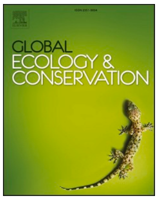

Wolverines (*Gulo gulo*) in a changing landscape and warming climate: A decadal synthesis of global conservation ecology research

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ABSTRACT

Wolverines are vulnerable to multiple, widespread, increasing forms of human activity so have become an indicator of conservation success or failure for northern ecosystems. Logistically difficult to research, the last two decades have seen marked changes in technology yielding new insights. We reviewed and synthesized this recent research and asked: what are the known drivers of wolverine populations and distribution, is there consensus on mechanisms for populations dynamics, and how can this knowledge inform wolverine conservation? From 156 peer-reviewed papers we observed wolverine research varies geographically in volume, and especially in focus. Most papers arose from Canada and the USA, whereas Scandinavia led Palearctic efforts; large gaps exist outside that region. DNA and telemetry are the most common modes of inquiry, with camera traps increasing recently. In Scandinavia coordinated long-term monitoring programs have yielded substantial information; the Nearctic relied on stand-alone research until the recent USA multi-state monitoring project, and Canada lacks such coordination. Globally, protected areas are important for wolverine conservation, but effective landscape and population

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management in the working land base is vital. The dual drivers of climate and landscape change manifest across wolverines' range, but past and current correlation between them remains a confound. Coordinated continental-scale analyses across gradients of development and climate change are needed to parse apart drivers of declines at macroecological scales, to inform effective conservation decisions.

1. Introduction

Wolverines (*Gulo gulo* L.) are an icon of wilderness and a source of popular fascination. A circumboreal species, much range in the Nearctic and Palearctic has been lost in recent centuries (Laliberte and Ripple, 2004), as wolverines are vulnerable to multiple forms of human activity. Consequently, wolverines have become a sentinel of biotic change and an indicator of conservation success or failure for northern ecosystems.

Nearctic wolverines once spanned Arctic, subarctic, boreal, coastal, and temperate biomes from the Arctic Ocean to the American southwest, and from the Pacific to Atlantic coasts; that range decreased markedly since European colonization (Laliberte and Ripple, 2004). Palearctic range and populations have also decreased in the recent past due to human pressures (Persson et al., 2015), but with some recent recoveries (Chapron et al., 2014).

Early wolverine research employed radio telemetry, snow-tracking, and den-site studies; these revealed rich details on wolverine movement, resource selection, and natality from focal locales (Banci, 1987; Copeland et al., 2007; Hornocker and Hash, 1981; Krebs et al., 2004; Lofroth and Krebs, 2007; Whitman et al., 1986) but spatially and temporally limited by logistics. Global Positioning Satellite (GPS) collars provided greater opportunities for behavioral study, and new technologies such as accelerometers are emerging to measure activity and energetics in the wild (Glass et al., 2020). Advances in DNA analysis allowed scientists to ask increasingly sophisticated questions about wolverine genetics (Kyle and Strobeck, 2001; Sawaya et al., 2019; Schwartz et al., 2009) and evolution (Krejsa et al., 2021; Rico et al., 2015). Working closely with wolverine hunters has permitted collection of biological samples from harvested populations, allowing greater understanding of aspects of their ecology (Kukka and Jung, 2015), evolution (Jung et al., 2016; Krejsa et al., 2021), health (Oakley et al., 2016; Robitaille et al., 2012; Sharma et al., 2021), and management (Kukka et al., 2018). The advent of remote camera trapping (Burton et al., 2015) advanced the ability to study wolverines and syntopic predators and competitors (Heim et al., 2017, 2019). Combining cameras and DNA hair trapping (Fisher and Bradbury, 2014; Magoun et al., 2011) with accompanying analytical advances (Royle et al., 2011) yields the ability to simultaneously ask questions about behavior, gene flow, distribution, density, and species interactions.

Consequently, a wellspring of new knowledge about wolverines emerged in the last two decades, compelled by significant conservation concerns. We conduct a review of wolverine research to: (1) identify where there is an abundance of knowledge and where information is lacking, and how this varies geographically; (2) identify wolverine responses to potential current and future threats across their range; and (3) synthesize research to inform future conservation strategies for this vulnerable species. Our central questions: what are the known drivers of wolverine populations and distribution, is there consensus on mechanisms for populations dynamics, and how can this knowledge inform wolverine conservation?

2. Methods

2.1. Exploring wolverine research geographically and topically

We adopt criteria for systematic literature reviews to avoid entraining unconscious bias (Haddaway et al., 2015; Xiao and Watson, 2019): we searched on defined search terms, followed set rules for exclusion, and co-authors checked for missing works. We searched Google Scholar and Web of Science for "*Gulo gulo*" OR "wolverine*" published between 2001 and 2021. We excluded only studies of captive wolverines and method development papers without wolverine-specific conclusions. We excluded gray literature and the obligatory value appraisals (Haddaway and Bayliss, 2015), and we were limited to English-language publications; hence we are subject to publication bias and western-science indexing bias.

From papers dated 2001–2021 we quantified the nation of study, sampling methods, measured response variables, and primary and secondary stressors (natural and anthropogenic mechanisms associated with the response) examined. We asked whether these parameters were similar among jurisdictions (allowing future meta-analysis) or if they differed – signaling different aspects of wolverine knowledge stems from different jurisdictions.

2.2. Synthesizing the last decade of wolverine research

Concision demanded we synthesize conclusions from the last decade of wolverine research (2011–2021). We include papers that contextualize current research (Westgate and Lindenmayer, 2017). Co-authors added details of ongoing research to illustrate future directions. We summarized the major foci and conclusions, with an eye to understanding wolverines' ecology to inform future conservation.

3. Recent history of wolverine research

In 2001–2021, 156 peer-reviewed papers referring to wolverines were published from nine countries that met our criteria (Supplementary Information). Few were transboundary, multinational endeavors, identified as *e.g.* Fennoscandia (Sweden, Norway, and Finland) or North America (Canada and the United States). Papers spanning the Nearctic and Palearctic were labeled 'global' studies (Fig. 1). In summary, Canada contributed most papers in the last two decades (52), followed by USA (43) and Sweden (20). Papers increased through time (though with a spike in 2010). Fewer wolverine papers were published from the Palearctic compared to the Nearctic (Fig. 1), likely lending a western bias to knowledge of wolverine ecology. Fennoscandia led transboundary efforts, with very little transboundary Nearctic work.

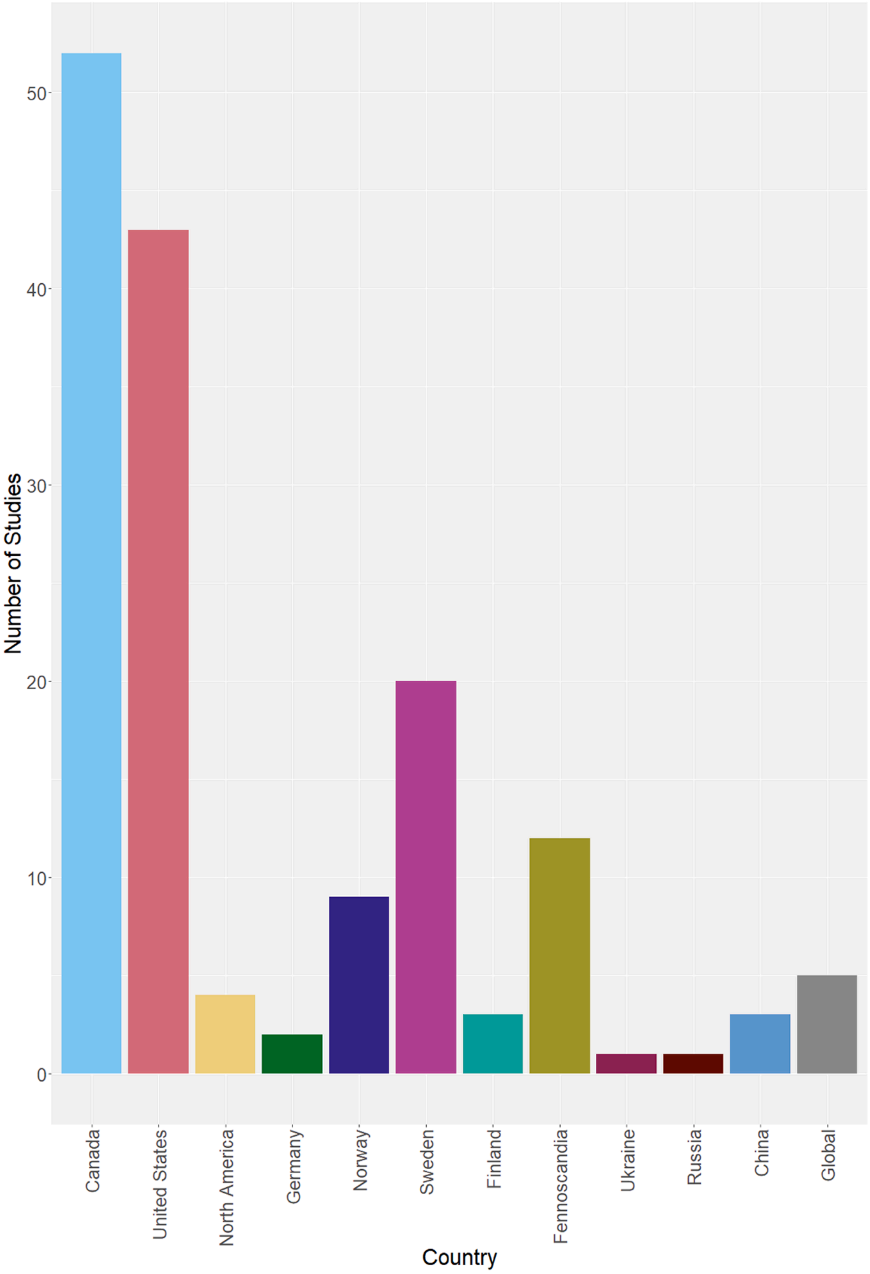

Fig. 1. The number of peer-reviewed studies of wolverines published between 2001 and 2021. Nearctic studies predominated, and Sweden led Palearctic efforts. Fennoscandia led transboundary efforts whereas very little trans-border research in North America, or global research, was conducted. Data provided in Supplementary Information.

3.1. Sampling methods

Research inferences are a product of the sampling methods used, so quantifying how wolverines have been studied is as important as what has been learned. In the last two decades wolverine research used nine generalized sampling methods, with many papers using multiple modes (Fig. 2; Supplementary Information). DNA analysis (hair, scat, tissue, blood; n = 69) and telemetry (VHF and GPS;

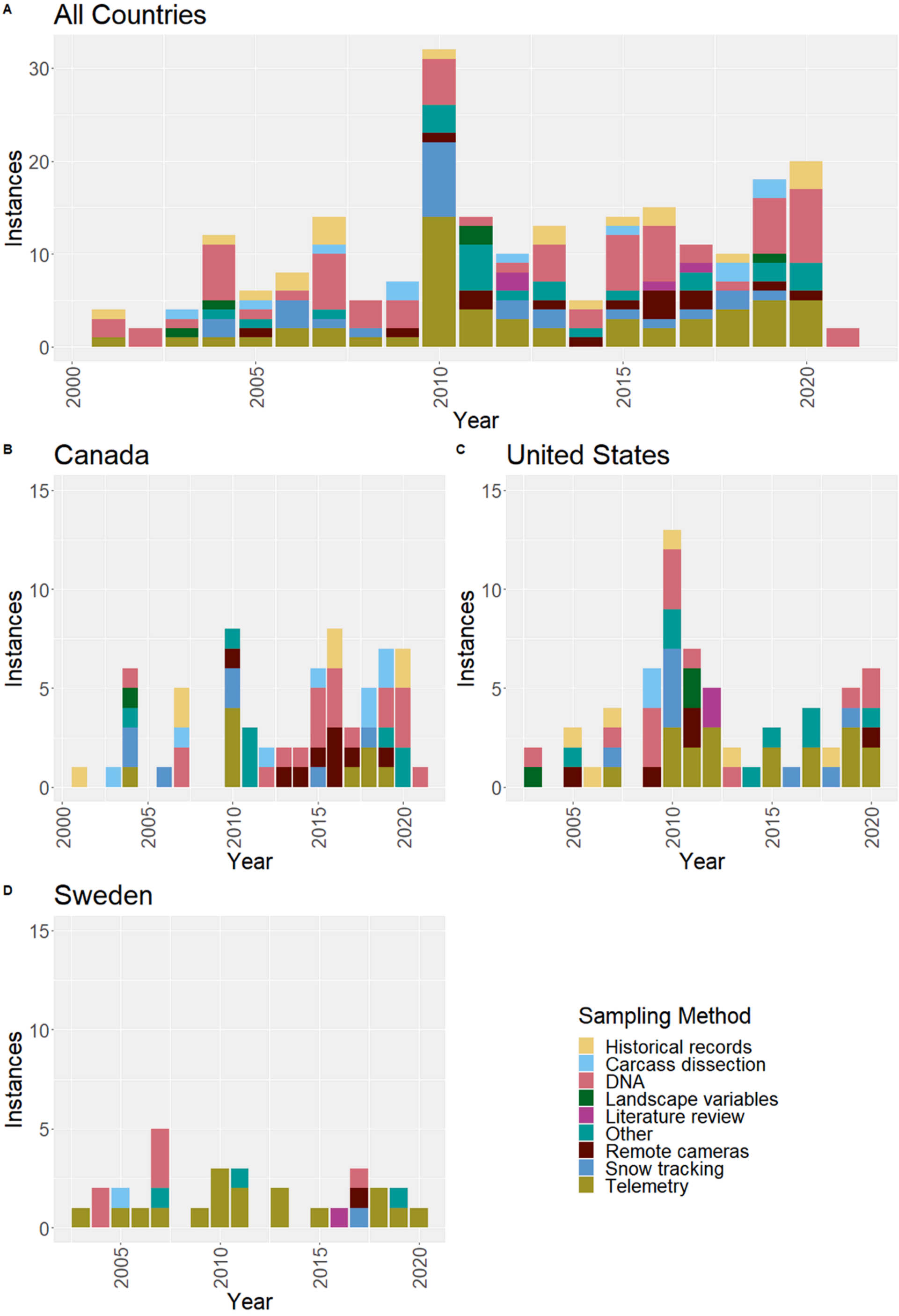

Fig. 2. The number of peer-reviewed studies using different sampling methods was published between 2001 and 2021 for all countries and the leading nations. (A) Except for a Nearctic peak in 2010, studies have generally increased through time. The sampling methods varied among Canada (B), USA (C), and Sweden (D), and changed through time in all jurisdictions. Data provided in Supplementary Information.

n = 55) were the most frequent modes (Fig. 2A). Telemetry studies on habitat use, movement patterns, home range requirements, and social structure of wolverines, have increased over two decades (Fig. 2).

Swedish research used telemetry data most frequently (Fig. 2C); this has generated much information about individuals' habitat use there, that is less available in the Nearctic. DNA research papers generate information about prehistoric and contemporary genetic diversity, gene flow, population structure, and connectivity; they vary nationally, with Canada leading and increasing after 2019

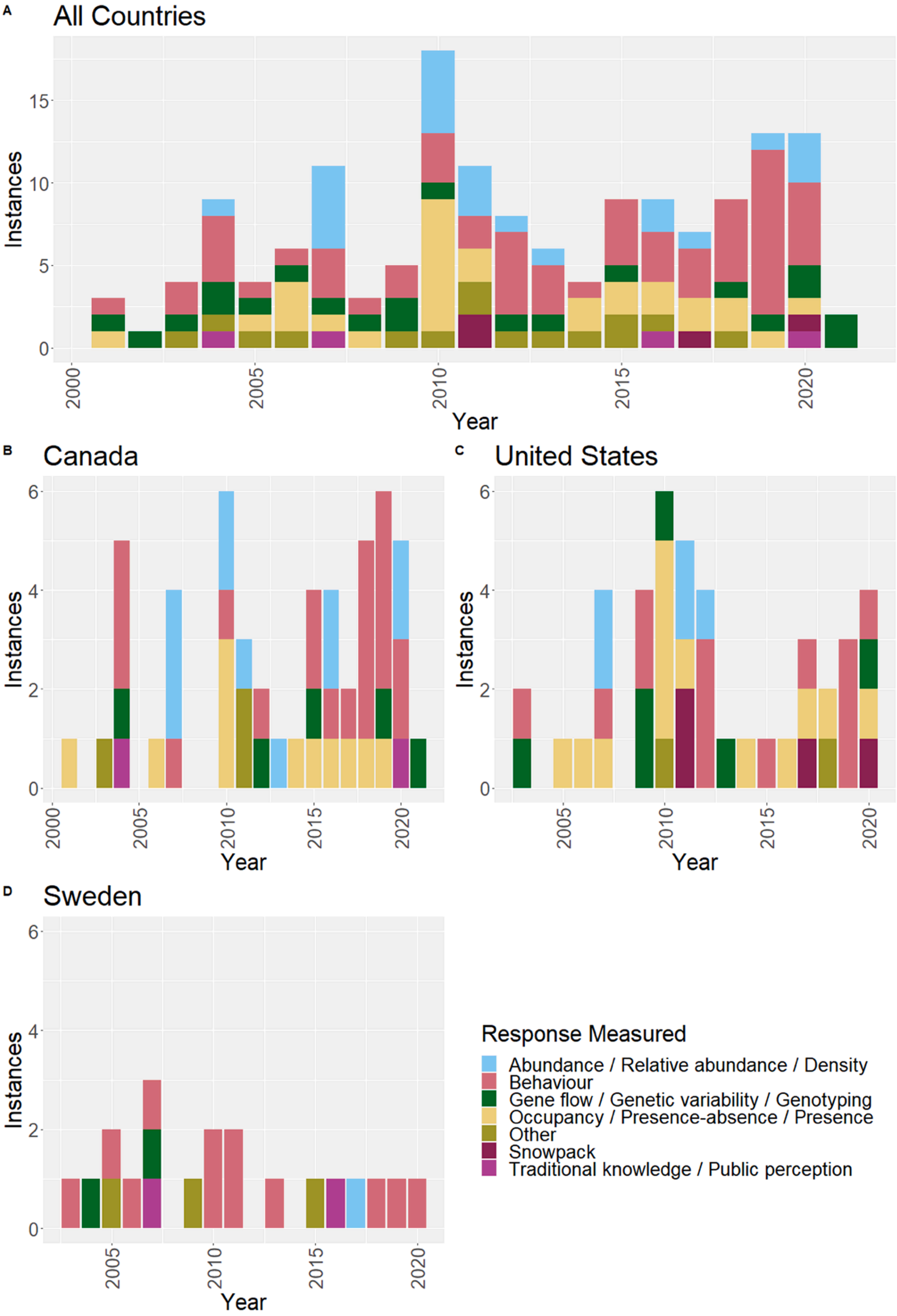

Fig. 3. The number of peer-reviewed studies examining different response variables for wild wolverines for all countries and the leading nations published between 2001 and 2021. (A) The sampling methods varied among Canada (B), USA (C), and Sweden (D) and changed through time more in the Nearctic. Data provided in Supplementary Information.

(Fig. 2B). Remote camera papers have increased since 2010, predominantly in Canada with one paper in 2000–2010 and eight in 2011–2021 (Fig. 2).

3.2. Response variables measured

Ecological inferences also depend on the response variables measured; quantifying how these vary geographically and temporally helps us direct future efforts. Fifteen generalized response variables were identified, spanning the ecological hierarchy from behavior through population and distribution (Fig. 3). Wolverine behavior – including dispersal (11), diet composition (9), and habitat selection (6) – is the most frequently measured response (Fig. 3A), reflecting widespread use of telemetry and snow-tracking.

Canada saw the greatest increase in behavior studies in the last two decades, from five (2000–2010) to 15 (2011–2021): half of all behavior studies (Fig. 3B). Those focused on biology (changes in temporal activity patterns, parasite load, injury), habitat selection, and movement. The USA primarily focused on habitat use, abundance, and occupancy (Fig. 3C). Sweden most consistently studied behavior with a greater focus on dispersal and interspecific interactions (Fig. 3D). Occupancy modeling of distribution increased in the last two decades from four (2000–2010) to nine (2011–2021) (Fig. 3A).

3.3. Wolverine stressors examined

We defined ‘stressors’ as challenges wolverines contend with: natural processes, climate change, landscape change, and human activity including industry, trapping, and recreation (Supplementary Information). We binned papers as *natural processes* if they examined geographic connectivity; gene flow, genetic connectivity, and genetic lineage; natural landscape heterogeneity; autecology, including predation, foraging, diet, fat storage, space-use, territoriality, denning, and reproduction; and intra- and interspecific interactions (Supplementary Information) though recognize these can be affected by anthropogenic factors too.

Natural processes were most frequently examined in Canada (25) and the USA (25) (Fig. 4). The second-most frequent stressor

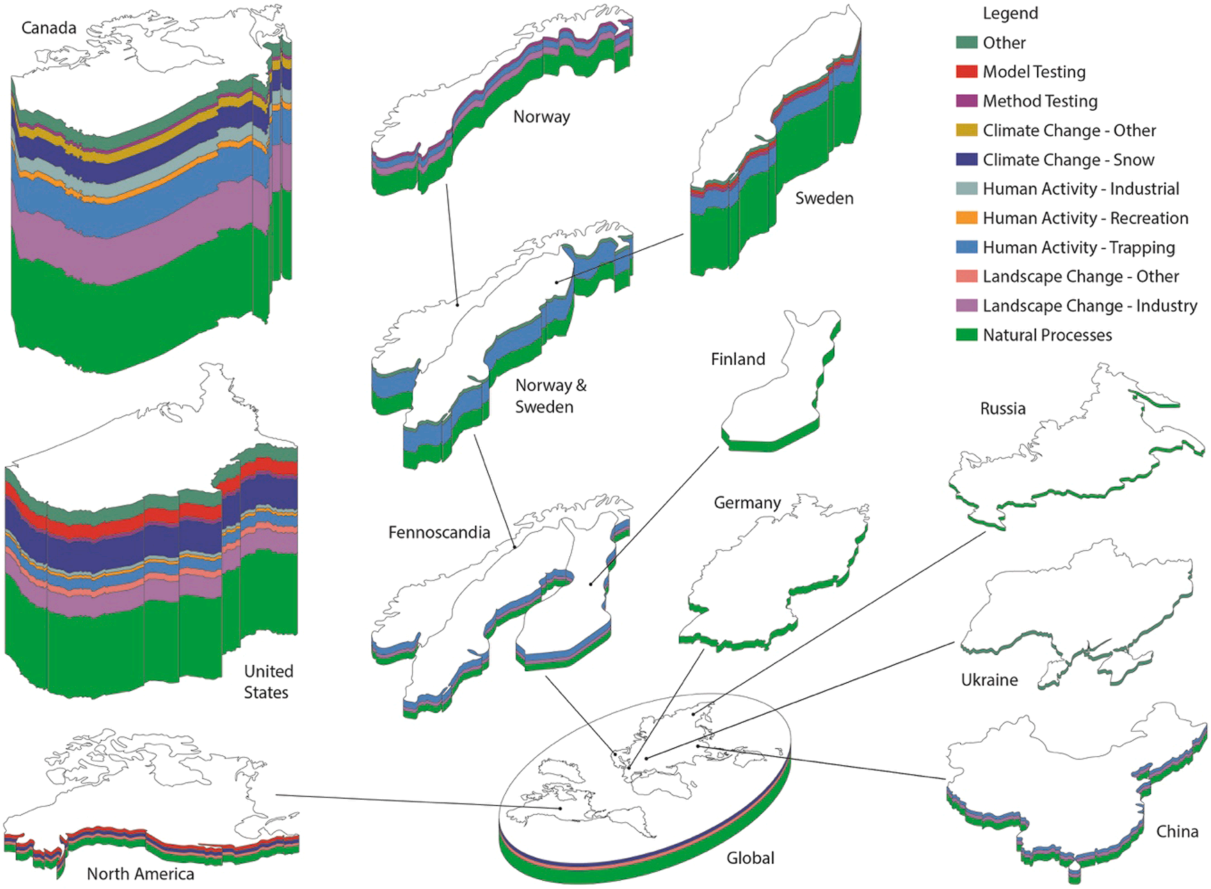

Fig. 4. The relative frequency of research papers published 2001–2021 examining stressors on wolverines, ranging from natural processes (most frequent, in green) to climate change, landscape change, and human activity. Few transboundary studies occurred, and these mostly in Norway and Sweden. Little information arose from Eurasia outside Fennoscandia. Most research arose from Canada and then the USA, with different stressors reflecting different regional priorities. Data provided in Supplementary Information.

examined varies by country: industry-driven landscape change in Canada (14); climate change and snow in the USA (9); and trapping, predator harvest, and management in Sweden (5).

4. Synthetic review

4.1. Evolutionary, historic, and current distribution

Extant wolverines spans the Holarctic but *Gulo*'s evolutionary origin is debated. Mitogenomic analysis suggests *Gulo* separated from close relatives *Pekania* and *Martes* in the late Miocene, 8MYA (Li et al., 2014). However, a recent USA fossil predates other *Gulo* records by a million years (Samuels et al., 2018) suggesting *Gulo* arose in the Nearctic and spread to the Palearctic during the Pliocene era. Genetic analysis from Russian specimens suggests *Gulo gulo* arose during the middle Pleistocene 181,000 – 234,000 years ago (Malyarchuk et al., 2015); they were widespread during the later Pleistocene, with fossil specimens described from that period in the Ukraine (Marciszak and Kovalchuk, 2011) and beyond (Samuels et al., 2018). Mitochondrial analysis from the full Holarctic distribution suggests dispersal across the Beringia land bridge during the last glaciation, followed by a westerly colonization during the Holocene (Zigouris et al., 2013). Nuclear microsatellite and mitochondrial DNA analyses suggest Beringian occupation followed by stable gene flow thereafter (Krejsa et al., 2021). The apparent Pleistocenic origins of *Gulo gulo* suggest a species adapted to a cold snowy climate, and this is likely a driver of some ecological challenges it faces today.

In the Nearctic, wolverine distribution has decreased since the Pleistocene glaciations (Samuels et al., 2018), and again substantially following European colonization (Laliberte and Ripple, 2004). Wolverines span the Arctic, boreal forest, and mountains of western Canada and USA. Wolverines have been extirpated from large swathes of North America. The extirpated Vancouver Island wolverine was deemed a separate subspecies based on cranial morphology, but genetic analysis shows they were indistinct from mainland wolverines (Hessels et al., 2021). Wolverines occur in nearby coast mainland ranges (Regehr and Lacroix, 2016). Wolverines are extirpated from eastern Canada; historical fur-trapping records show wolverines occurred throughout the mainland Atlantic provinces in 1700–1800 s (Forbes and McAlpine, 2020). A central Canada population remains southwest of Hudson Bay; a large-scale systematic survey of Ontario's boreal forest showed wolverine occupancy increased north and west and was more likely in subarctic ecozones (Ray et al., 2018). Genetic analysis suggests these were eastern wolverines, genetically isolated from wolverines in western Canada (Zigouris et al., 2012) despite current contiguity with Arctic populations. In the North American Arctic, gene flow appears uninterrupted across northern Alaska, Yukon, and Northwest Territories (Krejsa et al., 2021) with phylogeographic studies of wolverine parasites suggesting regional structuring of past populations (Sharma et al., 2021, 2020). Studies on wolverine population trends across the Canadian Arctic remain unpublished, but wolverines are actively harvested there.

Wolverine range in the contiguous USA is restricted to mountain regions in the west (Aubry et al., 2007). Mitochondrial DNA analysis of museum and contemporary specimens suggest wolverines were extirpated from the lower 48 states by the early 20th century, as remnant populations are more genetically similar to wolverines from Canada and Alaska, suggesting 20th-century recolonization (Mckelvey et al., 2014). Wolverines occur throughout Alaska, varying with natural topography (Poley et al., 2018). Genetic analysis suggests the Kenai peninsula population may be distinct from other populations (Krejsa et al., 2021).

Recent palearctic research on distribution is rare outside Fennoscandia, where wolverine range spans 247,500 km^2 in two populations – one spanning some alpine regions of Norway and Sweden, and a separate, geographically isolated population in Finland (Chapron et al., 2014). Little was found about papers from Russia save phylogenetic analysis (Malyarchuk et al., 2015). Mongolian wolverine research has not yet been published. In China wolverines are an endangered species (Zhu et al., 2016); a four-year survey of the Great Khingan Mountains yielded an estimate of only 200 individuals spanning 80,000 km^2 (Zhang et al., 2007). For three decades no wolverine signs have been observed in the Altai Mountains (Sinkiang, northwestern China) likely due to habitat loss, food limitation, and poaching (Zhang et al., 2007). The paucity of Russian and Asian research in this review could be an English-language, western-science indexing bias (Konno et al., 2020; Trisos et al., 2021), or reflect real differences in researchers' interests, national conservation priorities, and available funding for research.

4.2. Human perception of wolverines

In the Nearctic wolverines are often viewed as mischievous, cunning, intelligent, and fierce by people living in Arctic regions, and are largely misunderstood by the majority of people not living with wolverines (Bonamy et al., 2020a, 2020b; Cardinal, 2004). In the Palearctic wolverines are sometimes viewed with fear (Johansson et al., 2016) and Indigenous Sámi peoples hunt wolverines as predators of domesticated reindeer (Hobbs et al., 2012). Recent programs to financially incentivize protection of wolverines have met with success (Persson et al., 2015) but globally, social attitudes towards wolverines – especially how social attitudes can enhance conservation – remain understudied.

4.3. Wolverine biology

4.3.1. Diet

Wolverines search vast expanses of cold rugged environments for food, so their energetic requirements are considerable. Fat accumulation and storage is vital, and a measure of body condition (Robitaille et al., 2012). Modeling by Young et al. (2012) suggest males require 5096 kJ/day (2925–7462 kJ), and females 3645 kJ/day, and they meet this need with a generalist diet.

Palearctic wolverines are predators and facultative scavengers, whose diet predominantly consists of semi-domesticated reindeer

(*Rangifer tarandus*) in Sweden (84%) and Finland (66%), as well as moose (*Alces alces*), sheep (*Ovis spp.*), hares (*Lepus spp.*), ptarmigans (*Lagopus spp.*), rodents, and birds (Koskela et al., 2013a; Mattisson et al., 2016). Wolverines hunt reindeer and other mammals in the summer, switching largely to scavenging in the winter (Mattisson et al., 2016). Diet varies with sex; human- and wolf (*Canis lupus*)-killed carrion is important for breeding females in areas of low ungulate density (Koskela et al., 2013b).

In the Nearctic, arctic wolverines eat a diverse diet including ungulates and cricetid rodents (69%), snowshoe hare (*Lepus americanus*, 9%), fox (*Vulpes spp*. 6%), and squirrels, birds, and beaver (*Castor canadensis*) (Dorendorf et al., 2019). Wolverines pursue caribou (*Rangifer tarandus)* over long distances (4–62 km) ending in predation when the caribou becomes exhausted (Magoun et al., 2019). Nearctic wolverines also seasonally prey-switch, foraging for caribou in the summer and scavenging in winter (Inman and Packila, 2015). Porcupines (*Erethizon dorsatum*) are predated, yielding risk of injury (Kukka and Jung, 2015).

Boreal and montane wolverines also eat a diverse diet of large and small prey (Lofroth et al., 2007). In the northern boreal, telemetry analysis revealed predation behavior varied seasonally; wolverines spent more time at large-prey kills in winter than in summer, suggesting importance of large-prey events then (Scrafford and Boyce, 2018). In mountain environments small rodents such as hoary marmots (*Marmota caligata*) are important prey especially for reproductive females, and may be impacted by climate change (Lofroth et al., 2007). Wolverine diet appears to adapt to available resources; in Canadian coastal systems, isotopic analysis reveals wolverines eat ocean-run salmon (*Oncorhynchus spp*) (Shardlow, 2013).

4.3.2. Denning

Research and conservation focussed on denning habitat is critical for wolverines, with naturally low reproductive rates. Early telemetry research showed wolverines use complex snow tunnels as dens, or fallen trees and boulders covered with 1-m of snow (Magoun and Copeland, 1998), leading to the hypothesis that snow dens provide thermal cover and predation refuge for cubs. Copeland et al. (2010)'s global analysis showed most recorded wolverine dens were found in areas of persistent spring snow. May et al. (2012) found all Norwegian dens studied were in snow: steep, rugged terrain at higher elevations, away from human activity. In USA mountain landscapes, wolverine den sites occur under downed trees, boulders, and in rock caves accessed through deep snow (Yates et al., 2017). Magoun et al. (2017) advocate aerial methods to map persistent spring snow at the spatial scale of den sites to inform management and conservation.

Mechanisms behind the association between den sites and snow is debated. Many of the den sites used in Copeland et al. (2010) were from Sweden and heavily relied on snow-tracking to find dens, a sampling bias exaggerating the inferred reliance on spring snow (Aronsson and Persson, 2017). Moreover lactating females are recolonizing Sweden's boreal, outside of the range of persistent spring snow (Aronsson and Persson, 2017, 2018). Fur harvest data and trapper questionnaires suggest Alberta boreal wolverines – including reproductive females (Webb et al., 2016) – occur in areas with little persistent spring snow (Webb et al., 2019). In the Nearctic boreal forest, a few wolverines have been observed denned under hollows without persistent (lasting until April) spring snow (Jokinen et al., 2019). Copeland et al. (2010) acknowledge that areas classified as snow-free *via* satellite imagery may contain enough drifted snow for dens. Few dens have been described from the Arctic, where winter can be quite dry. The role of snow in wolverine denning may be debated (even among co-authors) yet this research is essential to understand the mechanisms behind wolverines' denning requirements.

4.3.3. Dispersal

Large home range size and high intrasexual territoriality are likely driven by patchy resources: wolverines can travel long distances (Vangen et al., 2001). One male traveled straight-line distances of 516 km then 826 km from Wyoming (USA) to Colorado and North Dakota, then was killed (Packila et al., 2017). Wolverine females also disperse (Aronsson and Persson, 2018) but generally females display high home-range fidelity; in Sweden, 86% (of 47) females maintained residency while 6% annexed a neighboring territory; only 8% dispersed (Aronsson and Persson, 2018). In the Canadian Rockies, genetic isolation for females but not males across a major highway bisecting the national park led Sawaya et al. (2019) to infer philopatry and behavioral avoidance of the road, generating sex-biased dispersal and demographic fragmentation (Sawaya et al., 2019). Dispersal among local populations is key to maintaining gene flow, given fragmentation by existing private lands and increasing human activity in the contiguous USA (Carroll et al., 2020). In the southern range periphery especially, snow-associated places are increasingly limited under climate change, reducing dispersal opportunities (Inman et al., 2012b) so dispersal remains a key focus for wolverine research.

4.3.4. Interspecific interactions

As facultative scavengers, multiple carnivores – several larger than a wolverine – compete for limited resources, particularly winter-killed ungulates.

Wolverines may be dependent on heterospecific predators to provide scavenging opportunities, especially in winter. In the Palearctic wolverines are facilitated by Eurasian lynx (*Lynx lynx*)-killed reindeer, with scavenged carcasses eclipsing wolverine kills (Mattisson et al., 2011): a conclusion supported by harvest data (Khalil et al., 2014). Analysis of telemetered syntopic wolverines and Eurasian lynx show they select similar habitats with high spatial overlap (Rauset et al., 2013). In the Nearctic, evidence for dependence on predators to provide winter scavenging opportunities is scant. Certainly, death from starvation occurred at a higher rate than predation-related mortalities in North America (Krebs et al., 2004), suggesting food is difficult to procure. The Canadian Rocky Mountains provides the only test of facilitation, and no spatial signal of facilitation was observed facilitation by North American lynx (*Lynx canadensis*) – which is smaller than Eurasian lynx and a snowshoe hare specialist (Chow-Fraser et al., 2022). Though wolves (*Canis lupus*) and arctic wolverines have been anecdotally noted feeding on the same carcass (Wallace et al., 2021), no evidence for facilitation by wolves – measured as spatial co-occurrence – was observed in the Canadian Rockies (Chow-Fraser et al., 2022).

Meta-analysis of Nearctic wolverine mortalities shows frequent intraguild predation (Krebs et al., 2004), and in the boreal mortalities from wolves were observed (Scrafford et al., 2017). Exploitation competition from smaller more numerous carnivores may also pose a problem: in the Canadian Rockies, the relative abundance of coyotes (*Canis latrans*) and red fox (*Vulpes vulpes*) were negatively correlated with wolverine abundance (Heim et al., 2017, 2019), and an expanding footprint of linear features exploited by anthrophilic coyotes brings these competing species into close proximity (Boonstra et al., 2018; Chow-Fraser, 2018).

4.3.5. Physiology, pathogens, and pollutants

Disease-induced mortality could conceivably contribute to population declines but this remains understudied south of the Arctic. Carcass collections offer insights on wolverine health emerging only recently: Robitaille et al. (2012) examined fat stores, and Oakley et al. (2016) documented prevalence of renal anomalies. Arctic wolverines – especially older wolverines –have high prevalence of *Toxoplasma gondii* exposure (Sharma et al., 2018, 2019a). One instance of *Trichinella pseudospiralis* represented a novel geographic occurrence; how widespread this may be is unknown (Sharma et al., 2019b). A new species *Trichinella chanchalensis*, recently discovered, occurs only in wolverines (14 of 42 animals) (Sharma et al., 2020). How infection translates to mortality or even sub-lethal effects is unknown. Physiology of free-ranging wolverines is also understudied. In a novel work, Thiel et al. (2019) implanted free-ranging wolverines with biologgers and showed temperature varied with reproductive status. Finally, as a facultative scavenger of long-lived, large mammals, wolverine may bioaccumulate contaminants, but this remains unstudied.

5. Wolverine monitoring

5.1. Palearctic

Scandinavian wolverine researchers have implemented widespread long-term snow-tracking and DNA monitoring programs, exceeding Nearctic efforts. Snow-tracking seeks to count reproductively successful den sites (May et al., 2012) and underpins the successful conservation program whereby each certified wolverine reproduction results in monetary compensation (Aronsson and Persson, 2017). The reliance on snow tracking may underestimate southern boreal areas with less consistent snow, where remote camera research reveals recolonization and expansion (Aronsson and Persson, 2017).

Scandinavia's considerable genetic sampling program has yielded impressive insights, such as genetic diversity. From 10 wolverines Ekblom et al. (2018)'s 2.42 Gb draft genomic sequence (>85% of the genome) showed genome-wide nucleotide diversity of 0.05% – among the lowest detected genetic diversity in a population of concern. Demographic analysis suggested a decrease in effective population size from 10,000 to < 500, with significant spatial structure signaling disconnectivity (Ekblom et al., 2018). Genetic data also inform space-use: in Sweden, male home ranges are double female home ranges, and male ranges overlap several females' home ranges, but not other males' (Bischof et al., 2016). In a novel analysis, genetic data informed open-population (multi-year) spatial capture-recapture (SCR) models to estimate density, mortality, and population growth rates (Bischof et al., 2020). Wolverines were primarily impacted by human-caused mortality, especially culling. Where direct mortalities have been reduced, populations have recovered or stabilized (Bischof et al., 2020), demonstrating wolverines' susceptibility to harvest and direct mortality. In sum, coordinated and consistent transnational wolverine monitoring reveals insights not available from single research projects.

5.2. Nearctic

Until recently, Nearctic wolverine research has been conducted on a project-by-project basis, without any (published) coordination among political jurisdictions to produce long-term population trends (Fig. 4). Regional programs adopted different techniques, such as snow-tracking in Canadian Rocky Mountain national parks (Whittington et al., 2015). Snow tracking relies on ephemeral environmental conditions and is hard to replicate, leading to recent adoption of more replicable techniques, such as camera-trapping (Steenweg et al., 2016). In a large Nearctic sampling effort, western Canadian researchers combined remote camera and DNA *sensu* Fisher and Bradbury (2014) – an extension of Mulders et al. (2007) original Arctic design. Over five years (2011–2016) and $> 50,000$ km^2 a common systematic design of 10×10 km^2 or 12×12 km^2 grid cells were sampled at 1–2 points (Mowat et al., 2020). SCR analysis estimated 2.0 wolverines / 1000 km^2, increasing with spring snow and decreasing with road density (Mowat et al., 2020). Monitoring programs relying on carcass submissions by wolverine hunters are underway in northern Canada and Alaska (Kukka et al., 2018).

Establishing a monitoring program capable of detecting change in population or distribution over time requires substantial coordination (Carroll et al., 2021), sampling effort (Ellis et al., 2014), and analytical tools (Emmet et al., 2021). In 2015 the USA states of Washington, Idaho, Montana, and Wyoming, began coordinated long-term monitoring program (Lukacs et al., 2020) using a combination of remote cameras and DNA sampling: 185, 15×15 km^2 grid cells deployed in a stratified design. Occupancy analysis estimated a 0.33 probability of wolverine occupancy in a cell, with variation weakly explained by habitat, snow cover, and human disturbance (Lukacs et al., 2020). Recognizing that attractants markedly increase detection rates (Fisher and Bradbury, 2014) but are difficult to maintain in sampling extremely remote and mountainous areas, researchers at Woodland Park Zoo (Seattle, Washington), Microsoft Research, and collaborators developed an automated scent dispenser now deployed by the USA monitoring initiative. Monitoring will expand into California, Colorado, Oregon, and Utah in 2021–22, and will play an important role in guiding wolverine conservation research and management in the contiguous USA.

6. Stressors to wolverine populations

6.1. Climate change: snow

As Nearctic wolverines are restricted to mountain, boreal, and arctic environments, they are inferred to require snow. Copeland et al. (2010) found 98% of 562 dens globally distributed occurred where snow cover (measured *via* satellite imagery) persisted into mid-May. Concurrently, Brodie and Post (2010) correlated declining 20th-century fur returns with diminishing snowpack, and suggested wolverines are at risk of future climate change. This work was widely contentious, as fur harvest returns fluctuated with trapper effort and fur pelt prices – which also declined – potentially leading to a spurious correlation (DeVink et al., 2011; McKelvey et al., 2011b). The debate on this relationship remains (Brodie and Post, 2011).

Modeling suggests snow in wolverine range in the USA and southern British Columbia will diminish markedly in the coming century (McKelvey et al., 2011a). Projection models based on climate-change scenarios suggest a marked reduction of persistent spring snow in the lower half of inferred denning elevation bands (Barsugli et al., 2020) and across all elevations in currently occupied states (Peacock, 2011) for the USA population. In the Greater Yellowstone Ecosystem (USA), GPS telemetry showed wolverines strongly selected for high-elevation alpine meadows, forests, and boulder fields, implicating snow cover as important because these high-elevation areas occur where snow persists to the end of the denning period (Inman et al., 2012a, 2012b). Genetic analysis in the southwestern corner of USA range suggests snow cover was the most important feature explaining contemporary genetic structure, with substantial contribution of topography and development (Balkenhol et al., 2020). At smaller spatial scales ($<$ 230 km) environmental variability explained wolverine genetic structuring, whereas at larger spatial scales ($>$ 420 km) landscape development (housing density) and terrain ruggedness explained the most variability (Balkenhol et al., 2020). Further north in Alaska, snow depth and snow compaction were important predictors of wolverine occurrence, as measured by snow-track transect surveys (Pozzanghera et al., 2016).

Few USA studies weighed evidence of snow in explaining wolverine distribution against other processes, such as landscape change: extant wolverine range is largely located on National Forests and Parks, with limited development. In Canada, extant wolverine range still spans gradients of landscape disturbance and highly variable snow regimes. In the Canadian Rocky Mountains on the southeastern range edge, Heim et al. (2017) found persistent spring snow pack was positively related to wolverine occurrence, but was eclipsed by natural landcover and industrial development. Kortello et al. (2019) examined wolverine distribution in the mountains of southeastern British Columbia and found food and human disturbance drivers outweighed climate and snow. Strong correlations between road densities and persistent spring snow did not allow the relative contributions of these two factors to be resolved with clarity. In the Ontario boreal forest, Ray et al. (2018) suggested both road density and climate warming (thawing degree days) had a negative effect on probability of wolverine occupancy.

The effect of snow, or climate change more broadly, on wolverines has not been a major focus of research in the Palearctic (Fig. 4). Wolverines have recolonized former ranges in the boreal forests of southern Sweden, outside of the climatic envelope of Copeland et al. (2010), suggesting less dependence on persistent spring snow than was previously hypothesized (Aronsson and Persson, 2017).

The mechanisms for how (and to what degree) snow drives wolverine persistence are debated; they are likely multi-modal and influencing several life-history requirements. Copeland et al. (2010) suggest snow is needed for denning; Inman et al. (2012a) suggest that as food-caching scatter hoarders, cold caches are needed to refrigerate food and prevent decomposition. In Scandinavia wolverines transport food up to 1-km away (mean 0.5 km) to cache it – less if the item is an ungulate killed by another carnivore (van der Veen et al., 2020). It is unclear whether refrigeration or antitheft or both is the driver of wolverines' scatter-hoarding, and the implications for climate change effects on wolverine are quite different. Of course wolverines may be snow-reliant for other reasons not examined: for example wolverine morphology allows traveling on snow which may provide a competitive advantage over other species less snow-adapted – an advantage lost without snow.

Finally, snowy regions – the mountains, boreal, and arctic – are also the least agriculturally productive, and thus were not settled by Europeans in the last centuries. This raises the question: are wolverines snow-dependent, or are these refugia from widespread landscape change, hunting, and trapping? An examination of these additional stressors (q.v.) in areas of current wolverine range – where snow co-occurs with recent landscape disturbance, and of variable hunting pressure – will help elucidate these mechanisms.

6.2. Landscape change

It is too late to discern whether historic extirpations of Nearctic wolverines were a function of intensive trapping, wholesale agricultural conversion, forestry, urbanization, or climate change – or synergistic effects thereof. Historic records suggest USA wolverine ranges followed the mountains in the west and stretched to south of the Great Lakes in the east (Aubry et al., 2007; Laliberte and Ripple, 2004). The effect of development in prairie, Great Lakes, and New England portions of historic range cannot be known. Currently wolverines are restricted to the mountains at their southern range periphery (Inman et al., 2012c), without the landscape development gradients necessary for analysis.

In the boreal and mountain Nearctic range of Canada, landscape change is more recent but proceeding rapidly (Pickell et al., 2013, 2015). Aerial surveys in central Canada suggested wolverine occurrence declines with road density (Bowman et al., 2010), a result corroborated by research at larger scales (Ray et al., 2018). DNA research in the Alberta Rocky Mountains showed wolverine distribution and density decreased with density of anthropogenic linear features, including roads and petroleum-exploration 'seismic' lines (Fisher et al., 2013). To the south – spanning national parks and adjacent developed landscapes –wolverine occurrence declined with density of anthropogenic landscape features, including roads, seismic lines, harvest cutblocks, and other industrial footprint (Heim et al., 2017) – with linear features the most pervasive feature driving wolverine occurrence. The explanatory power of industrial disturbance eclipsed spring snow by 7-fold, and effect size exceeded snow by 3-fold. In adjacent British Columbia two studies of over 40 radio-collared wolverines showed both sexes responded negatively to roads and motorized recreation (Lofroth and Krebs, 2007). Kortello et al. (2019)'s multi-scale analysis suggested wolverine presence at hair-trap stations during the winter denning period were best explained positively by food and negatively by human disturbance.

Wolverines' negative relationship to linear features is partly a result of mortality. In boreal Alberta, wolverines selected seismic lines and borrow pits along roads, contributing to observed wolverine mortality (Scrafford et al., 2017). Analysis of wolverine movement showed wolverines traveled faster on roads than other areas; this effect was greater with increasing traffic volume (Scrafford et al., 2018). Wolverines were also attracted to newly-logged areas, where males selected cutblock edges during summer and females selected cutblock edges during winter, but both avoided cutblock interiors (Scrafford et al., 2017). In landscapes with extensive anthropogenic land use activities, wolverine exhibit heightened vigilance – a subtler stress response (Stewart et al., 2016). Landscape change in arctic environments is currently much less pronounced but development pressure from mining and transportation continues, but these effects are understudied. Similar conclusions stem from Palearctic research, where anthropogenic landscape change was more important for home range location than was habitat, as habitat selectivity was greater in undeveloped habitats than in developed habitats (May et al., 2006).

6.3. Diminishing connectivity

Connectivity among suitable habitats is vital to wolverine persistence, especially in landscapes where extensive development has occurred. Genetic data has offered much insights into connectivity (Cegelski et al., 2003, 2006); as DNA databases grow through hair-sampling monitoring and specimens obtained from fur trappers, more insights on genetic connectivity await.

Wolverine ranges in the USA are restricted to mountain environments and are fragmented by developed private lands in valley bottoms. As snowpack decreases through the 21st century wolverine populations are expected to become more fragmented and isolated, especially in the USA (McKelvey et al., 2011a). A connectivity analysis in the Yellowstone system based on GPS collar data showed wolverines selected multiple topographical, environmental, and anthropogenic features; wolverines were less selective during dispersal movements, and less sensitive to habitat quality, during dispersal than within-home range movement and selection (Carroll et al., 2020). While not surprising, the increased flexibility in wolverine selection during dispersal movements is important for metapopulation connectivity in this highly fragmented system. Unfortunately, there is some threshold at which wolverine dispersal movements are constrained that requires further investigation.

Likewise, major transportation corridors provide a potentially substantive barrier to female wolverine movement, and a source of wolverine mortality (Clevenger, 2013). In the Canadian Rocky Mountains the Trans-Canada Highway bisects prime wolverine habitat. A large DNA survey (2586 samples in 2011–2013) across an 8000 km^2 area employed population and individual-based genetic analyses to examine genetic structure across the highway (Sawaya et al., 2019). From 49 individuals (29 M, 20 F), there was strong genetic differentiation in females across the highway, and weak population structure in males. Sex-biased dispersal across transportation barriers can fragment and genetically isolate wolverine populations which require demographic connectivity (i.e. female movement) to maintain metapopulation processes such as recolonization, marking cross-road connectivity as a prime stressor for wolverines (Sawaya et al., 2019). Some connectivity can be restored with highway crossing structures (Clevenger, 2013).

6.4. Fur harvest and predator control

Predator control varies significantly across Fennoscandia (Andrén et al., 2011; Hobbs et al., 2012). In Sweden the predator compensation program has led to population recovery (Persson et al., 2015), yet heavy predator control in connected Norway is likely leading to a source-sink scenario (Bischof et al., 2020). Overexploitation remains a significant stressor for Fennoscandic wolverines, but remains unknown across Eurasia.

In the Nearctic, extensive unregulated fur harvest occurred through the 17th-20th centuries. Wolverines are still harvested in Alaska, and in Arctic and western Canada. Meta-analysis of Nearctic wolverine mortalities showed 45% were human-caused within trapped populations – likely additive to natural mortality rates (Krebs et al., 2004). Modeling suggesting trapped populations would decline without immigration from untrapped areas (Krebs et al., 2004). In British Columbia several fur management areas are overharvested, based on harvest data and population models (Lofroth and Krebs, 2007; Lofroth and Ott, 2007). Mowat et al. (2020) estimated low wolverine densities (mean $= 2\ /1000\ \text{km}^2$) where provincial harvest records reveal trapping mortality of $> 8.4\%$ per year; models indicate wolverines are overharvested by *ca.* 50%. Exploitation was inferred as a major driver of declines; halving the current trapping mortality was recommended (Mowat et al., 2020) and regionally adopted – one of the very few recent wolverine conservation actions in Canada. Alberta's harvest quota of one per trapline (plus one incidental) has never been investigated; very low occupancy and densities (Fisher et al., 2013; Heim et al., 2017; Mowat et al., 2020) suggest it is unsustainable in some areas.

Few harvest sustainability analyses are published from the Arctic. Demographic analysis of harvested Yukon wolverines showed a bias towards young males; this varied seasonally as more adults were harvested in late winter, including near- and post-partum females (Kukka et al., 2018). Given the vulnerability of wolverine populations to harvest (Krebs et al., 2004), especially of breeding females, the authors suggested a shift to early-winter trapping season, and this has since been adopted – another rare wolverine conservation decision. Harvest records from wildlife management agencies are currently underutilized and can provide information to help inform wolverine harvest management (Jung et al., 2020).

7. Wolverine conservation: protected areas

Globally, biodiversity conservation rests heavily on protected areas (PAs) with only partial success (Jones et al., 2018; Le Saout et al., 2013; Rodrigues et al., 2004). Palearctic wolverine conservation areas prioritize paying Sami reindeer herders and other livestock ranchers to conserve dens (Hobbs et al., 2012; Persson et al., 2015). In the Nearctic, wolverine conservation focusses on managing fur harvest, and protecting habitat from industrial disturbance – usually through PAs. Two studies spanning Canada's Rocky Mountain PAs and adjacent heavily-developed landscapes showed a marked decrease in wolverine occurrence outside PAs (Fisher et al., 2013; Heim et al., 2017). PAs in British Columbia – which have difficult access in winter and see little human use – were also positively associated with wolverine occurrence (Kortello et al., 2019). One could conclude that mountainous PAs – offering cold, snowy, undisturbed habitat – are important to wolverines; that a refuge from trapping allows wolverine population persistence; and/or that these rugged landscapes were areas where humans could not historically overharvest wolverines – another ghost of exploitation past.

Though current wolverines are associated with PAs, extensive DNA-and-camera data spanning Canada's Rocky Mountain national parks estimated 3.0 – 3.3 wolverines per 1000 km^2 – less than expected for a largely unharvested population in high-quality habitat (Barrueto et al., 2020). Densities decreased toward Park boundaries (Barrueto et al., 2020), suggesting an intrusive edge effect from surrounding harvest pressure and/or landscape development. Wolverine behavior changed markedly at bait stations inside *vs.* outside national parks (Stewart et al., 2016): within national parks staying-time was variable, but outside these – in provincial protected areas allowing more landscape disturbance – wolverines evidenced risk-avoidance by spending less time at the bait (Stewart et al., 2016). Within Canada's Banff National Park, the TransCanada Highway bisects wolverine range and hinders female dispersal, key to maintaining wolverine populations (Sawaya et al., 2019). Wolverine road mortalities do occur in protected areas, and highway over- and under-passes may help to facilitate safe wildlife movements (Clevenger and Waltho, 2000); evidence suggests that females may be using them to traverse the Trans-Canada Highway (Sawaya et al., 2019).

In the mountain regions of the USA wolverines' close association to snow interacts with backcountry winter recreation. Using simultaneous GPS monitoring of mountain wolverines and winter recreationists, Heinemeyer et al. (2019) showed wolverines avoided otherwise high-quality habitats in areas with higher recreation levels. The strength of avoidance increased with increased recreation, was greater for dispersed off-trail activities, and was greater for motorized than non-motorized recreation (Heinemeyer et al., 2019). As human pressures for recreational space mount, increasing effects on wolverines are expected in protected areas as last bastions of habitat, adding to the list of stressors for future wolverines.

8. Conclusions: the future of wolverines

Wolverines face significant conservation challenges globally. Data from China, Fennoscandia, USA, and Canada all suggest declining populations in at least some parts of their range. In the Palearctic, only in Sweden has population-scale recovery been observed, where the predator conservation program has successfully increased wolverine numbers and geographical range (Persson et al., 2015); but even here recolonization of southern Sweden is likely to face challenges due to the greater human activity there. Conservation efforts in Sweden are hampered by extensive exploitation in neighboring Norway, leading to compensatory immigration and a source-sink population dynamic (Gervasi et al., 2015). Other measures have shown limited or no success. The European Endangered Species Program has been captive breeding wolverines in zoos since 1994, with limited achievement (Loberg et al., 2020). Translocations have been more successful; these have added to the genetic signature of the recent genetic bottlenecks in the extant Finnish populations (Lansink et al., 2020), but do require viable source populations. Both translocations and captive breeding may be useless if the mechanisms for decline are not mitigated.

In the Nearctic wolverines face different challenges in mountain, boreal, and arctic populations. The challenges facing them are only expected to increase – warming climates, developed landscapes, and increasing pressure from human activity inside and outside protected areas (including harvest in Canada). Mountain range edges are especially at risk due to their patchy remnant habitats and high human pressures. Increased warming and changing precipitation patterns will undoubtedly reduce late spring snowpack in the southern mountains of both Canada and the United States, reducing high-quality habitat. Both boreal and mountain wolverines are under increasing stress from industrial landscape development. The dual drivers of climate and landscape change have been, and will be, manifested across much of wolverines' range. The Arctic, still cold and mostly undeveloped, likely retains stable populations based on carcass collection and harvest reporting, but much research on population trends remain unpublished. However in the longer term of arctic warming induces changes to mammal communities, altering food-webs (Lawler et al., 2009); declines in Arctic wolverines may follow, so research is much needed.

In Canada, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) lists wolverines as Special Concern across a panmictic range, but by design this designation does not consider regionally specific or context-dependent threats. Mountain wolverines face different and perhaps more acute challenges than boreal and arctic wolverines, and should be managed more intensively, though arguably through a coordinated federal plan that acknowledges these regional threats.

In the contiguous USA wolverines face some significant challenges. Fortunately, approximately 92% of contemporary wolverine range is held in the USA public land system with some degree of protection from development (Carroll et al., 2020, 2021). Thus, while exurban and urban development remains a hurdle for wolverine dispersal in the contiguous USA, development within high-quality wolverine habitat is not the most pressing threat to species persistence in this region. Climate change is projected to eliminate spring snow pack from lower elevations, and much of wolverines' contemporary range within mountain habitats is already fragmented by valley bottom development. Barring adequate protection at state and federal levels (such as protections under the *Endangered*

Species Act, ESA) wolverine conservation remains precarious. A recent petition to list wolverines under the ESA was denied due to controversy over the scientific assessment of the threats to wolverine persistence.

It worth noting that research on Nearctic wolverines started centuries after their range had collapsed by half (Laliberte and Ripple, 2004), so the ghost of exploitation past encumbers ecological inferences, which are necessarily derived from wolverines' current range. As North American colonization was most intense in the flat, temperate east and south – the north and west being climatically and topographically less favorable for agriculture and development – wolverines are now constrained to these colder, higher landscapes (Aubry et al., 2007; Copeland et al., 2010). Furthermore, the correlation between anthropogenic landscape change and snow cover remains a confound across the Nearctic range south of the Arctic. Coordinated continental-scale analyses across gradients of development and climate change – especially snow – are needed to parse apart drivers of declines at macroecological scales, to inform effective conservation decisions.

The last twenty years have seen a steady increase in wolverine research, and foci are geographically disparate, reflecting regional stressors: human-caused mortality in Sweden, landscape change and harvest management in Canada, and climate, snow, and connectivity in the USA (Fig. 5). The Scandinavian DNA and snow-tracking monitoring programs and associated research have yielded substantial knowledge about wolverines, which has subsequently informed effective conservation. An abundance of stand-alone projects in the Nearctic has shed light on wolverine distribution, density, health, and genetics, and continues to parse apart the main drivers of wolverine declines: cumulative effects of multiple stressors is a common conclusion. Despite this growing body of knowledge, the few recent conservation decisions remain limited to regional (but important) adjustments to trapping.

A review of sampling efforts has shown a reliance on snow tracking for den site research. GPS telemetry continues to yield important insights into behavior but studies are limited in spatial scope, and effective translation of small-scale telemetry research into jurisdiction-wide conservation has not yet been apparent. Aerial surveys are also providing useful information on abundance, and

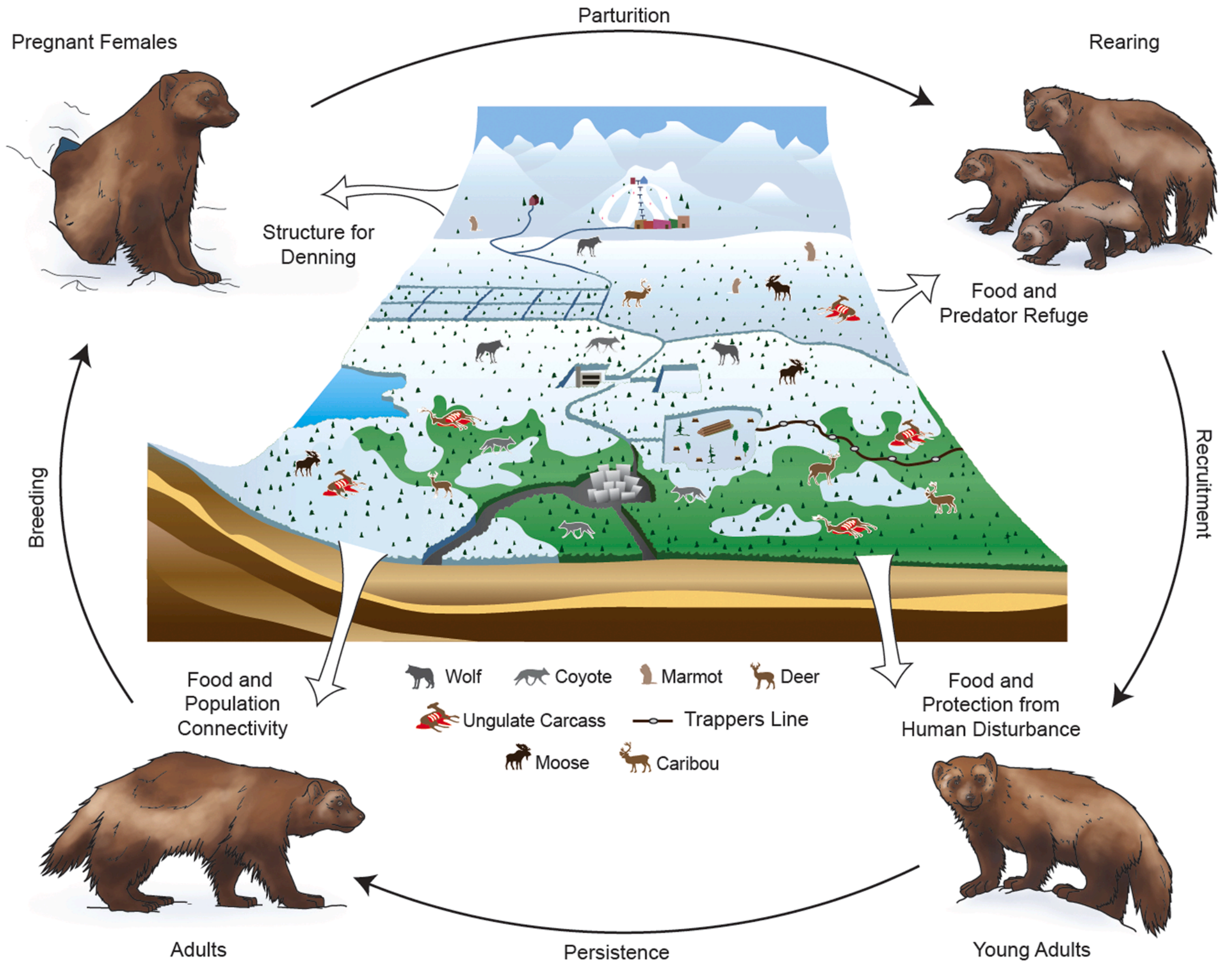

Fig. 5. Wolverines are subject to multiple anthropogenic stressors throughout their life cycle, including mountain recreation such as ski hills (upper center), industrial linear features (center left), forest harvesting and urbanization (lower center), roads (throughout), changes to prey availability (including small marmot prey and larger ungulate hunting and scavenging opportunities), overharvesting, diminishing landscape connectivity, and climate change.

hopefully trend, in remote areas where ground surveys are difficult. Camera traps and noninvasive genetic tagging have yielded critical insights over large areas, but their past application in short projects, rather than long-term monitoring, has not allowed for the longitudinal analyses needed for measuring wolverine conservation effectiveness. We recommend that long-term monitoring agnostic to environmental conditions – such as DNA and camera-traps – is needed. The nascent monitoring program in the USA is a good start and a similarly coordinated program could be adopted over wolverines' Nearctic range; DNA monitoring and the use of contemporary UAV technology in the Palearctic could expand to support den-identification efforts. Current research foci need not remain static, nor siloed; coordinated research among jurisdictions that explicitly weighs evidence for different competing drivers of wolverine abundance and distribution will aid in understanding global wolverine ecology, and inform effective responses to wolverine stressors. In particular, comparative studies demonstrating differences in the human or ecological factors limiting wolverines will be critical.

Because regional context for wolverine conservation differs within and between countries, there remains a need for focussed research and monitoring aimed at resolving regional issues. However global wolverine conservation will require a coordinated approach transcending political boundaries. Norway and Sweden's conflicting management plans confound conservation efforts. The USA's small isolated wolverine populations could be heavily dependent on immigration from Canadian source populations (Balkenhol et al., 2020; Kyle and Strobeck, 2001). However in Canada, differences in the ecology and threats to wolverine among boreal, mountain, and arctic environments makes coordinated management difficult; and currently wolverine population management differs among jurisdictions with little federal coordination. Local conservation strategies should adopt foci that address regional stressors, such as preventing overharvest. However transboundary conservation strategies are needed to protect this wide-ranging low-density species, especially in mountain biomes.

Throughout wolverines' range conservation strategies should encompass landscape protection from intensive development and human activity, restoring and maintaining connectivity of high-quality habitat, and climate change mitigation. These stressors are not limited to wolverines but are archetypal of stressors to biodiversity globally (Maxwell et al., 2016). Wolverines are more sensitive to these stressors, and as such are sentinels for change; conservation decisions for wolverines are likely the same to conserve vertebrate diversity across the northern Holarctic.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02019.

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