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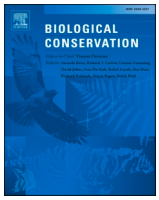

A systematic review of the effects of climate variability and change on black and brown bear ecology and interactions with humans

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ABSTRACT

Climate change poses a pervasive threat to humans and wildlife by altering resource availability, changing co-occurrences, and directly or indirectly influencing human-wildlife interactions. For many wildlife agencies in North America, managing bears (*Ursus* spp.) and human-bear interactions is a priority, yet the direct and indirect effects of climate change are exacerbating management challenges. Understanding the underlying ecological drivers of bear responses to climate variability and change, and the implications for conflict, will be critical for maintaining human-bear coexistence in North America. We synthesized 120 articles that identified direct and indirect mechanisms by which climate variability and change affect brown bears (*Ursus arctos*) and American black bears (*Ursus americanus*) in North America. The literature focused on examining climate impacts on bear diet, body size, habitat selection, space use, activity, denning chronology, and population demographics and dynamics. Across these categories, we summarized the documented and projected bear responses and resulting implications for human-bear interactions. Climate-driven changes in natural food availability were frequently implicated in influencing bear behavior and demography, and creating conditions under which interactions with humans are likely to increase. Bears in North America may face increased challenges as habitat and natural food availability continue to be altered by climate change. Our review provides a foundation upon which to identify climate drivers of bear ecology, conditions conducive to human-bear interactions, and adaptive management strategies. Given substantial evidence of climate impacts to bears, incorporating climate considerations into bear management can help managers strategically allocate resources and promote human-bear coexistence.

1. Introduction

Climate is a significant driver of ecological change, with direct and indirect effects on biodiversity from the species to community levels (Walther et al., 2002). As average global temperatures rise, shifts are occurring in growing season length, water availability, and snow regimes, along with an increased frequency and severity of wildfires, extreme weather events, and pest and pathogen outbreaks, among other impacts (Jay et al., 2018). These altered conditions are affecting plant and animal abundance, distributions, community assemblages, and phenology (Walther et al., 2002). As long-term climate change and acute climate events alter environmental conditions, the resulting changes in resource availability are also influencing the behavior, distributions, and demography of humans and wildlife (Abrahms et al., 2023).

Climate-driven changes in resource availability can increase co-occurrence and competition between humans and some wildlife species, leading to altered patterns of human-wildlife interactions (Abrahms, 2021; Abrahms et al., 2023). The term "human-wildlife interactions" refers to ways in which humans and wildlife come into contact or affect each other's lives, ranging from positive coexistence to

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conflict in shared environments (Peterson et al., 2010). We consider negative human-wildlife interactions to be instances when coexistence is challenged by conflicting objectives or activities that result in adverse effects for humans, wildlife, or both. Negative human-wildlife interactions are a primary cause of biodiversity loss, result in annual global losses of billions of dollars, devastate livelihoods and food security for humans, and can cause human and wildlife mortality (Nyhus, 2016). Although climate change is considered one of the most significant contemporary threats facing humans and wildlife, it is often an underrecognized driver of negative human-wildlife interactions (Abrahms et al., 2023). As a result, there are currently few studies evaluating how climate influences human-wildlife interactions, and the effectiveness of related management strategies (Nyhus, 2016; Abrahms et al., 2023).

Human-bear interactions are a common problem and management priority for many wildlife and land management agencies in North America (Spencer et al., 2007). Although bears hold important roles within their ecosystems and have cultural and economic value (Clark and Slocombe, 2009; Ripple et al., 2014; Penteriani et al., 2017), they are adaptable to human-modified landscapes and food sources, which creates ample opportunities for negative human interactions including property damage, livestock depredation, and human injury and mortality (Spencer et al., 2007; Can et al., 2014). Maintaining large carnivore populations is paramount to preserving the structure and function of ecosystems, but management challenges can arise because of their large home ranges and propensity for conflict with humans (Ripple et al., 2014).

Although the literature provides a broad view of how changes in climate and weather affect bears directly and indirectly, few studies have evaluated climate as an underlying driver of human-bear interactions. Recognizing the effects of climate impacts on bear behavior and demography, however, is imperative to understanding and mitigating negative human-bear interactions in North America as climate conditions change. Understanding the drivers of interactions and considering various manifestations of climate change will allow managers to more proactively and efficiently allocate resources (Zack et al., 2003).

We systematically reviewed literature on the direct and indirect mechanisms by which climate variability and change affect bears and human-bear interactions in North America. Our synthesis focused on two of North America's three bear species: American black bear (*Ursus americanus*) and brown bear (*Ursus arctos*; commonly referred to as grizzly bear in the interior of North America, so we use these names interchangeably and consistent with their regional use; Haroldson et al., 2021). Polar bears (*Ursus maritimus*) were excluded from this review because of their unique habitat requirements and conflict drivers compared with black and brown bears. Black bears are the most widely distributed bear species in North America and are frequently involved in human-bear interactions (Spencer et al., 2007). Brown bears, while much more limited in occupied range, are also implicated in human-bear interactions and share similar conflict drivers (Schwartz et al., 2003). Our objectives were to 1) compile and summarize the documented and projected effects of climate and weather on bear ecology, and 2) synthesize resulting implications for human-bear interactions.

2. Methods

2.1. Search

We systematically retrieved peer-reviewed literature using the citation databases Scopus and Web of Science Core Collection. In Scopus, we conducted searches based on the "Article title, Abstract, and Keywords" category, and all publication years (1788–2022). In Web of Science, we searched based on the "Topic" category, which included article titles, abstracts, author keywords, and "KeyWord Plus" (automatically generated terms found within the titles of citations). The timespan "all years (1985–2022)" was selected in Web of Science, as the authors' subscription did not enable access to articles published prior to 1985. All searches were conducted in English.

We used the Population, Exposure, Comparator, Outcome (PECO) framework to develop our search string and assess the relevance of retrieved literature (Richardson et al., 1995; Guyatt et al., 2011). Our framework was as follows: 1) Population: the study involved free-ranging *Ursus americanus* or *Ursus arctos* in North America; 2) Exposure: the study documented the exposure of black or brown bears to direct climate variables (e.g., temperature, precipitation) or their derivatives (e.g., winter severity, drought); 3) Comparator: the study made a comparison between at least two different time points; and 4) Outcome: the study documented a bear response to the exposure variables.

We developed search terms to identify literature within our PECO framework. In addition to the terms "climat*" and "global warming", we also included the term "weather", because climate is an aggregate of weather in a specific location and terminology can overlap in the literature (e.g., extreme climate events like heat waves can also be characterized as extreme weather events). We searched Scopus and Web of Science using the following Boolean search string: ("*Ursus americanus*" OR "*Ursus arctos*") AND ("climat*" OR "global warming" OR "weather" OR "precipitation" OR "temperature*" OR "snow*" OR "rain*" OR "heat" OR "freez*" OR "drought*" OR "flood*" OR "fire*" OR "extreme weather" OR "winter severity" OR "hurricane*" OR ("sea level" OR "sea-level") OR "inundation") AND NOT ("body temperature*"). We excluded "body temperature" as a search term to reduce irrelevant studies related to captive animal or immobilization techniques.

We used 15 articles of known relevance to check the retrieval performance of the search terms. Scopus retrieved 100% of the test articles and Web of Science retrieved 87%. To complement database searches, we implemented a backward snowballing technique, in which we reviewed the reference list of each article accepted during full-text review to identify relevant articles that were missed during our database searches (Jalali and Wohlin, 2012). Lastly, we reviewed opportunistically retrieved articles that we identified outside of the formal review process. Review articles do not describe empirical data and thus were not accepted for full-text review; however, primary sources within reviews were assessed during the snowballing process.

2.2. Screening

We screened the obtained literature for relevance using a two-stage approach: title and abstract screening, followed by full-text review. To minimize bias, title and abstract screening was conducted by two reviewers. At the onset of the title and abstract review process, we evaluated interrater reliability using Cohen's kappa statistic (Cohen, 1960). Each reviewer assessed the relevancy of the same 10% subset ($n = 69$) of literature identified from the citation databases. The chosen sample size exceeded that which is required to detect significant results with 90% power (Sim and Wright, 2005). The reviewers achieved 92.8% agreement with a kappa statistic of 0.74 (95% CI: 0.503–0.975), indicating sufficient agreement between reviewers (Landis and Koch, 1977). For the remainder of title and abstract screening, discrepancies between reviewers were discussed and we accepted any articles in which relevancy was unclear based on the title and abstract alone. Because we were interested in synthesizing responses to contemporary climate change, we restricted studies to those using post-Industrial Revolution data. Additionally, only literature available in English was accepted because of language restrictions of the authors. In the second stage, we conducted a full-text review of all literature accepted during the title and abstract screening. From each article, we extracted data on study location, species, empirically examined climate variables, bear responses to climate variables, implications for human-bear interactions, and relevant management strategies. We summarized the documented and projected bear responses for the most common response categories and resulting implications for human-bear interactions.

3. Results

3.1. Trends in the literature

We identified 852 unique articles: 688 were retrieved from Scopus and Web of Science, 150 were acquired during snowballing, and 14 were opportunistically retrieved (Fig. 1). A total of 154 articles remained after title and abstract screening and 120 articles remained after full-text review. Most studies focused solely on the responses of black bears (n = 67) or brown bears (n = 44), whereas a small number studied both species (n = 7), did not specify a species (n = 1), or were a corrigendum (n = 1). Bear populations across their ranges in North America were represented in the literature and some studies took place in multiple countries. Most of the retrieved literature examined or projected bear responses in the U.S. (n = 90), followed by Canada (n = 28), and Mexico (n = 6). The highest concentration of articles was in the northwestern portion of North America (Fig. 2).

A variety of climate variables and bear responses were examined in the literature. The most commonly measured exposure variables were temperature (n = 58), precipitation (n = 48), snow depth (n = 20), and drought (n = 13; Fig. 3). The outcomes most frequently studied were timing of den entry and exit (n = 18), impacts to habitat (n = 17), human-bear interactions (n = 17), survival (n = 15), recruitment (n = 11), and diet (n = 11). Human-bear interactions were represented in the literature by state-wide reports and incidents of property encroachment or damage, human food acquisition, livestock depredation, human attacks, and vehicular or train collisions. We synthesized bear responses to climate variability and change based on the responses most frequently examined in the literature: diet; body size; habitat selection, space use, and activity; denning chronology; and population demographics and dynamics. In subsequent sections, we describe select examples for clarity; Supplemental Table 1 includes a comprehensive list of references for each combination of climate variables and bear responses.

3.2. Diet

3.2.1. Food availability

Climate and weather can impact primary productivity, phenology, and plant and animal distributions, and therefore are important predictors of bear diets, influencing the quantity, quality, and accessibility of certain foods (Picton et al., 1986; McClelland et al., 2020; Rettler et al., 2021). For example, precipitation and temperature can impact the occurrence of plants that bears use for forage (e.g., Laskin et al., 2019; McClelland et al., 2020; Prevéy et al., 2020), variation in mast production (Rettler et al., 2021), and the nutritional content of plants (Coogan et al., 2012). Across systems, drought has been consistently implicated in natural food shortages for black and brown bears, reducing vegetation and mast availability (Moyer et al., 2007; Garshelis et al., 2017), limiting cutthroat trout (*Oncorhynchus clarkii bouvieri*; Teisberg et al., 2014), and reducing the availability of ungulate carrion (Picton et al., 1986). However, drought can also exacerbate wildfires, which can temporarily increase the availability of carrion (Blanchard and Knight, 1990).

Wildfire can have mixed effects on food resources for bears. Fires can reduce habitat quality in burned areas and cause loss of existing understory vegetation (Cunningham et al., 2003; Bard and Cain, 2020). However, after initial vegetation loss, early successional vegetation growth can include a high diversity of food for bears (Swanson et al., 2011; Bard and Cain, 2020). Large patches of early successional vegetation can also be created by other types of natural disturbances, but typically only by those that are most severe, such as hurricanes or extreme windstorms (White et al., 2011). Although early successional vegetation may be a beneficial outcome of some disturbance events, the early successional stage can be brief and burned areas can have fewer bear food plants years after the fire event, compared with unburned areas (Cunningham et al., 2003).

3.2.2. Dietary shifts

Bear foraging behaviors are also influenced by climate. In the Yellowstone region, grizzly bears foraged for earthworms, gophers, ants,

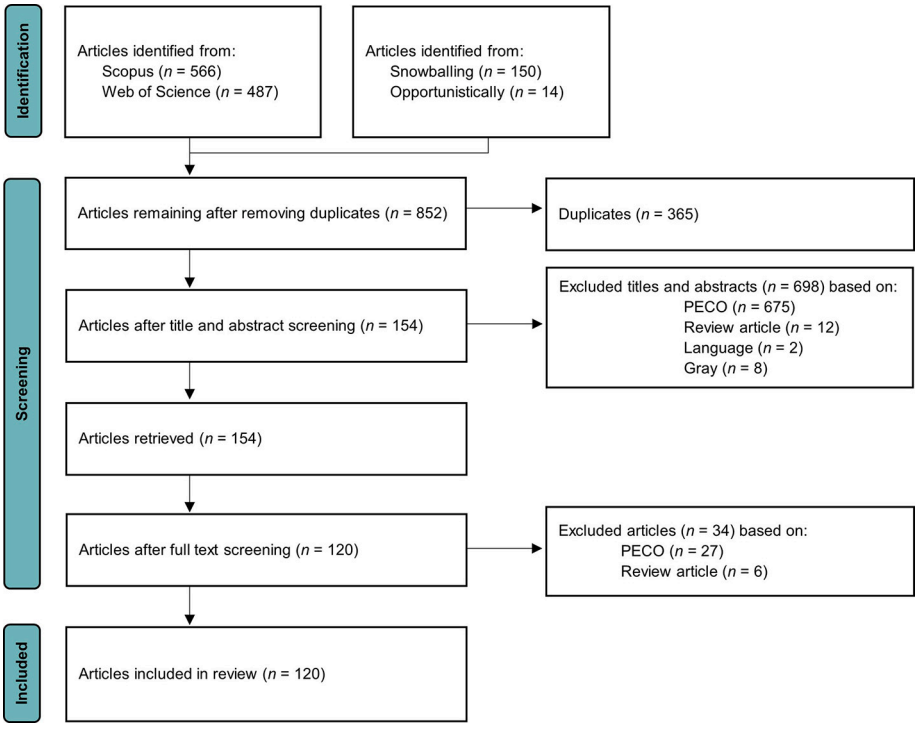

Fig. 1. The number of articles retained and excluded at each phase of the systematic literature review. Criteria were based on the Population, Exposure, Comparator, Outcome (PECO) framework.

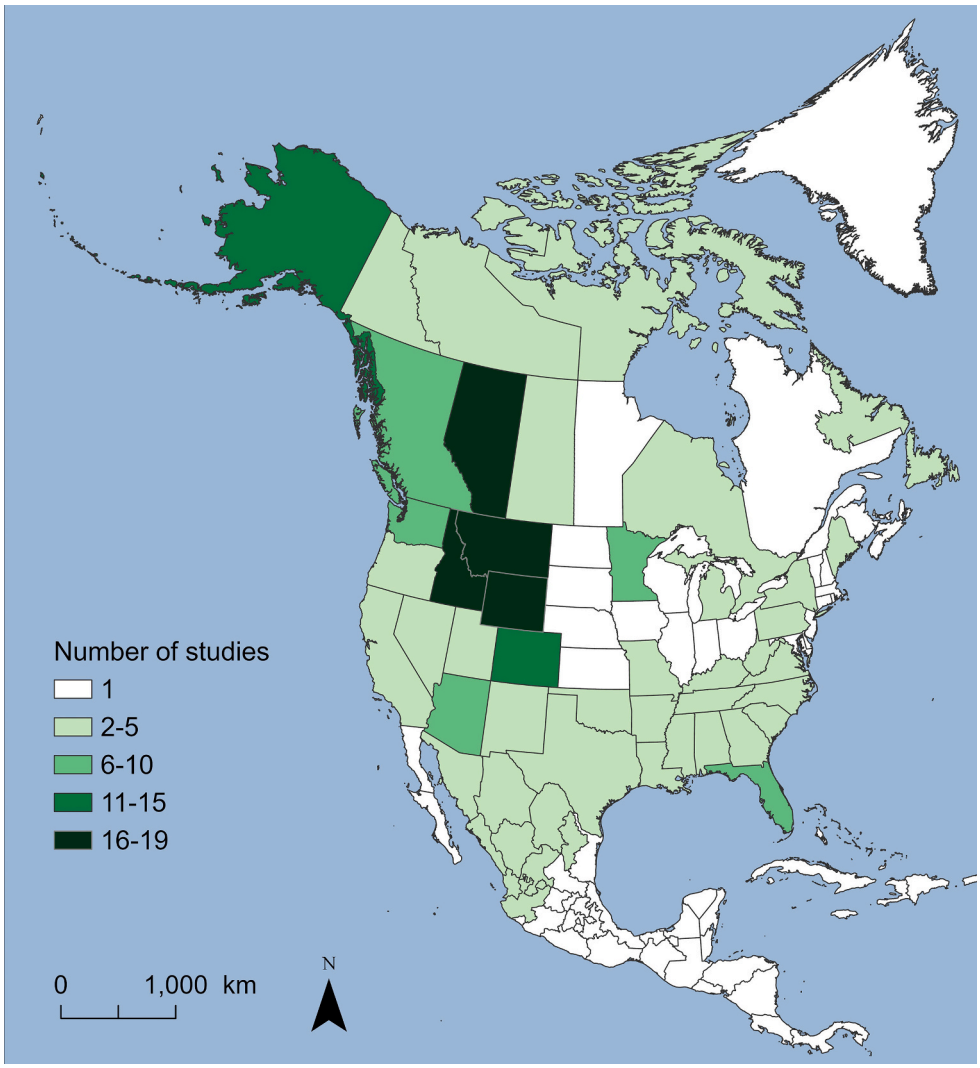

Fig. 2. Locations of studied American black bear (*Ursus americanus*) and brown bear (*Ursus arctos*) populations or habitats within literature reviewed during full-text screening. A continental-scale projection study was included, resulting in all states and provinces having at least one study. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and voles and vole food caches based on snowmelt, temperature, and precipitation conditions (Mattson, 2001; Mattson et al., 2002; Mattson, 2004a, 2004b). Climate and weather can also affect bear predation and scavenging behaviors (Lumpkin et al., 2012; Bastille-Rousseau et al., 2016; Allen et al., 2021). For example, black and grizzly bear predation on caribou (*Rangifer tarandus*) is correlated with environmental conditions such as the number of growing degree days, ambient temperature, spring and summer precipitation, and snowfall. These conditions are thought to influence caribou maternal body condition and thereby neonate vulnerability (Bastille-Rousseau et al., 2016, 2018). Additionally, when preferred foods are unavailable due to unfavorable climate conditions or other stressors, bears are known to readily switch to alternative food sources. For example, the diets of black and grizzly bears in the Greater Yellowstone Ecosystem were comprised of a greater percentage of ants (Hymenoptera: Formicidae) and biscuitroot (*Lomatium cous*) when preferred foods, such as whitebark pine (*Pinus albicaulis*) seeds and trout, were limited (Picton et al., 1986; Mattson, 2001; Fortin et al., 2013).

3.2.3. *Use of anthropogenic foods and human-bear interactions*

Bears often respond to climate-driven natural food shortages by visiting human development or areas near human development to find alternative sources of food (Teisberg et al., 2014; Johnson et al., 2020). Residential development and agricultural areas typically offer consistent, concentrated, and relatively accessible food and attractants in many forms (Can et al., 2014). Because of the accessibility of these alternate food sources, natural food shortages are a principal driver of human-bear interactions in North America (Can et al., 2014). Livestock depredation, attacks on humans, garbage scavenging, and home intrusions by bears have all been linked to natural food shortages (Artelle et al., 2016; Miller et al., 2016; Doan-Crider et al., 2017). For example, in British Columbia, grizzly bear attacks on humans increased approximately 20% for each 50% reduction in annual salmon biomass (*Oncorhynchus* spp.; Artelle et al., 2016). Most of these attacks, and bears killed due to negative human interactions, occurred after the approximate start of hyperphagia, a period of increased feeding activity prior to hibernation, further emphasizing the relationship between food acquisition and human interaction dynamics (Artelle et al., 2016). Similarly, in the Greater Yellowstone Ecosystem, Haroldson et al. (2006) found grizzly bear survival decreased during years of poor whitebark pine cone production. Most mortalities were of cubs during the hyperphagic season and occurred in association with human-bear interaction management directed at adult female bears (Schwartz et al., 2006b).

Drought is an important driver of natural food shortages and has been correlated with increased human-bear interactions. In the Lake Tahoe Basin, California–Nevada, a drought-caused natural food failure

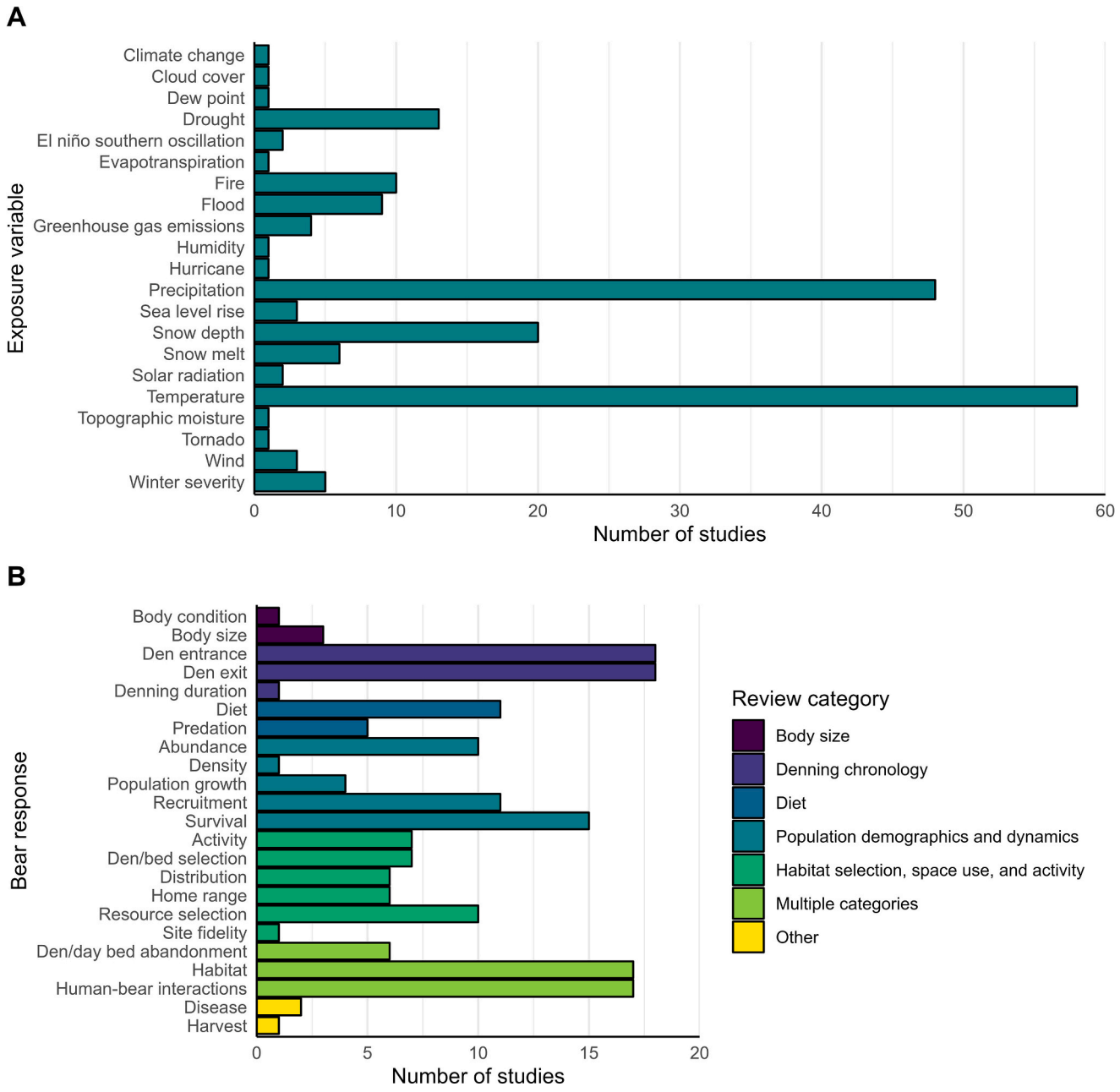

Fig. 3. A) Climate exposure variables examined in studies included for full-text review. B) American black bear (*Ursus americanus*) and brown bear (*Ursus arctos*) responses to exposure variables and corresponding review categories described in studies included for full-text review. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

was accompanied by a 16- to 17- fold increase in negative human-black bear interactions compared with the two years preceding and following drought conditions (Garshelis et al., 2017). Similarly, in Coahuila, Mexico, black bear predation on cattle dramatically increased during a natural food shortage amplified by a severe drought (Doan-Crider et al., 2017). The availability of attractants in human communities, such as garbage, can also increase interactions during periods of drought. For example, Miller et al. (2016) found that human-bear interactions in Utah occurred most frequently during a drought year and over half of the events involved accessible garbage or other attractants for black bears.

As drought and other climate changes lead to natural food shortages, bears are anticipated to adapt by increasing their reliance on lower-quality, natural foods (Picton et al., 1986; Mattson, 2001; Fortin et al., 2013) or by seeking human foods to meet energy requirements (Teisberg et al., 2014; Johnson et al., 2020). Reliance on human foods and behavioral changes resulting from low natural food availability can be reversed (Baruch-Mordo et al., 2014) but can also persist longer than the period of poor climatic conditions (Garshelis et al., 2020). Behavioral modification in bears that are heavily dependent on human foods and near human attractants can be challenging, and these behaviors may be passed on to offspring (Morehouse et al., 2016). This pattern could have mounting implications for human-bear interactions and coexistence.

3.2.4. *Projected climate impacts on food availability and diets*

Projected changes in climate suggest that bear diets will shift in response to changes in food availability, distribution, and phenology. Disturbance events that can impact natural food availability such as droughts, fires, and hurricanes may increase in frequency and severity in some regions (Jay et al., 2018; Ara Begum et al., 2022). These changes in climate may threaten the persistence of some high-calorie hard mast

foods (Fortin et al., 2013; Keane et al., 2017), alter the availability of carrion (Wilmers and Post, 2006), and impact suitable habitat for key berry and root-producing plants (McClelland et al., 2020; Prevéy et al., 2020). Additionally, shifts in plant phenology that result in florescence and fruiting occurring weeks earlier than normal, as is projected even under low emissions scenarios, could amplify potential instances of phenological mismatch (Laskin et al., 2019; Prevéy et al., 2020). Phenological mismatch occurs when there is deviation in the timing of life cycle events for interdependent species. This has already been documented during uncharacteristically warm years in Alaska: when two key foods of brown bears became synchronized, bears had an excess of preferred foods during one period, but neither food source was available in another period (Deacy et al., 2017).

Although shifts in phenology can result in a mismatch for bears, it can also have positive effects on bears if the availability of some food sources is extended by longer growing seasons (e.g., McClelland et al., 2020). In addition, although suitable habitat for important forage plants consumed by bears is expected to decrease across portions of the U.S. and Canada, it could expand at higher elevations and more northern latitudes (Roberts et al., 2014; Prevéy et al., 2020). For some forage species, the effects of climate change could be positive and negative. For example, if the climate becomes warmer and drier, increased fire could limit interspecies competition for whitebark pine and reduce the spread of white pine blister rust (*Cronartium ribicola*), but also increase the probability of mountain pine beetle (*Dendroctonus ponderosae*) infestations (Buermeyer et al., 2016). Although there is significant uncertainty, impacts to diet composition, food acquisition, and human-bear interactions are likely to continue as changes in climate impact food availability and distribution.

3.3. Body size

Several studies have shown that inter-annual variation in climate, and resulting changes in habitat quality, can influence bear body size. For example, Nielsen et al. (2013) found that in the Canadian Rocky Mountains, body mass and length of grizzly bears were greater in the most productive portions of their range, areas characterized by warmer average spring temperatures and less March snowfall. Furthermore, a "silver spoon" effect (i.e., when individuals raised in higher-quality natal environments have increased fitness as adults) was observed when above-average summer temperature and winter precipitation during the birth year resulted in greater adult grizzly bear body mass (Nielsen et al., 2013). Lower body mass and nutritional deficiencies of bears have also been associated with climate-induced reductions in natural food availability (DelGiudice et al., 1991; Johnson et al., 2020). Consequently, bears with lower body mass and nutritional deficiencies may increase their use of human-dominated areas to consume anthropogenic foods, which increases their body fat and mass (Ditmer et al., 2016; Johnson et al., 2020). Although bears may attempt to mitigate climate-induced nutritional deficiencies and smaller body sizes by seeking human resources, it often increases human-bear interactions (e.g., Johnson et al., 2020).

3.4. Habitat selection, space use, and activity

Bears typically seek productive habitats that allow them to thermoregulate, obtain adequate nutrition, and provide shelter (Pelton, 2003; Schwartz et al., 2003; Lara-Díaz et al., 2018). The literature demonstrates numerous ways in which climate variables, including temperature, precipitation, and extreme weather events, impact bear habitat and subsequently bear habitat selection, space use, and activity. Higher ambient temperatures create thermal constraints for bears (Rogers et al., 2021), and habitat can become less suitable for bears if food production is reduced by changing climate conditions (Teisberg et al., 2014; Laufenberg et al., 2018), sea level rise (Leonard et al., 2017; Davis et al., 2021), wildfire (Cunningham et al., 2003; Bard and Cain, 2020), or extreme weather (Waller et al., 2012). For example, fire can reduce cover (Cunningham et al., 2003; Bard and Cain, 2020) and flooding and tornados can inundate dens and damage habitats (Alt, 1984; Oli et al., 1997; Clark and Eastridge, 2006; Waller et al., 2012). Extreme weather can also lead to vegetation declines (e.g., downed trees are more susceptible to insect infestation and hurricanes can cause saltwater inundation and groundwater changes; Conner et al., 2005, Sheikh, 2008, Murrow and Clark, 2012).

3.4.1. Habitat selection: thermoregulation requirements

Thermoregulation requirements impact bear habitat selection at landscape and local spatial scales. For example, thermal constraints likely limit the southern range of black bears in Mexico (Lara-Díaz et al., 2018), as they preferentially select areas with annual mean temperatures <15°C and annual precipitation between 50 and 100 cm (Delfin-Alfonso et al., 2012). At more localized scales, grizzly bears in Canada have been observed selecting shaded sites to thermoregulate when temperatures increased (Pigeon et al., 2016a). Grizzly and black bears are also known to use water sources to thermoregulate (Sawaya et al., 2016; Rogers et al., 2021). This could lead to increased livestock depredation if bears increase their use of livestock watering areas (Doan-Crider et al., 2017). To thermoregulate during hibernation in cold climates, black and grizzly bears are known to select dens in areas with greater snowpack depth and cover. Warming global temperatures and subsequent impacts to snow regimes (Jay et al., 2018) may limit the availability of these sites, which offer protection from storms and disturbances (e.g., Baldwin and Bender, 2008; Crupi et al., 2020), support heat retention, and limit den abandonment (Immell et al., 2013).

3.4.2. Habitat selection: quality and nutritional requirements

Bears also select habitats that meet their cover and nutritional requirements, both of which can be affected by climate. For example, bears can use habitats affected by fire, but likely use burned habitat less frequently due to reduced vegetative cover (Cunningham et al., 2003, Bard and Cain, 2020). Bears also select areas where important plant-food species are available, which varies with precipitation (McClelland et al., 2020). As previously summarized, when bears are unable to meet their physiological needs in the area where they reside, they often search for resources elsewhere. In fact, a drought-induced mast failure was implicated in the migration and dispersal of nearly an entire Texas black bear population (Hellgren et al., 2005). Black and grizzly bears are also known to increase their home ranges during climate-induced food shortages (Blanchard and Knight, 1991; Cunningham and Ballard, 2004; Moyer et al., 2007). Bears may also seek resources near or in human-inhabited areas due to weather conditions, reduced habitat quality, and natural food failures (Picton et al., 1986; Baruch-Mordo et al., 2014; Berman et al., 2019). Although use of developed areas by bears may seem an effective strategy to mitigate low natural food availability, the potential for negative human-bear interactions increases and human development can serve as an ecological sink or trap rather than a refuge (e.g., Baruch-Mordo et al., 2014; Lamb et al., 2016; Laufenberg et al., 2018; Braunstein et al., 2020).

3.4.3. Timing and duration of daily activity

The timing and duration of activity can also be directly influenced by natural food availability, precipitation, and temperature (e.g., Baruch-Mordo et al., 2014; Lara-Díaz et al., 2018; Rogers et al., 2021). For example, black bears in Great Smoky Mountains National Park were less active during rain, snow, and when temperatures were <0°C or >25°C (Garshelis and Pelton, 1980). Additionally, grizzly bears in Yellowstone National Park were typically inactive during hours with increased likelihood of heat stress (Rogers et al., 2021). Rogers et al. (2021) suggested that the behavioral plasticity of grizzly bears enables them to occupy areas representing a wide range of climates, but that daily activity may be constrained in extreme thermal conditions, particularly for lactating females. In some areas, peak temperatures are mild enough

that daily bear activity remains consistent (Ayres et al., 1986). However, as global temperatures continue to rise, bear activity levels may decrease during the hottest periods of the day when upper critical temperature thresholds are more likely to be reached (Garshelis and Pelton, 1980; Rogers et al., 2021).

Increased limits on when bears can be active may also decrease foraging efficiency (McLellan and McLellan, 2015), particularly as open areas with limited cover or younger timber stands that offer abundant forage opportunities can be warmer than other stands (Pigeon et al., 2016a). Black and grizzly bears can use behavioral thermoregulation, such as submerging in water or digging daybeds down to mineral soil, to combat the effects of high temperatures (Sawaya et al., 2016; Rogers et al., 2021). Yet despite cooling strategies, bears may have fewer daily hours during which they can adequately thermoregulate due to the coupled effects of rising temperatures and reduced access to water for cooling (Sawaya et al., 2016; Rogers et al., 2021).

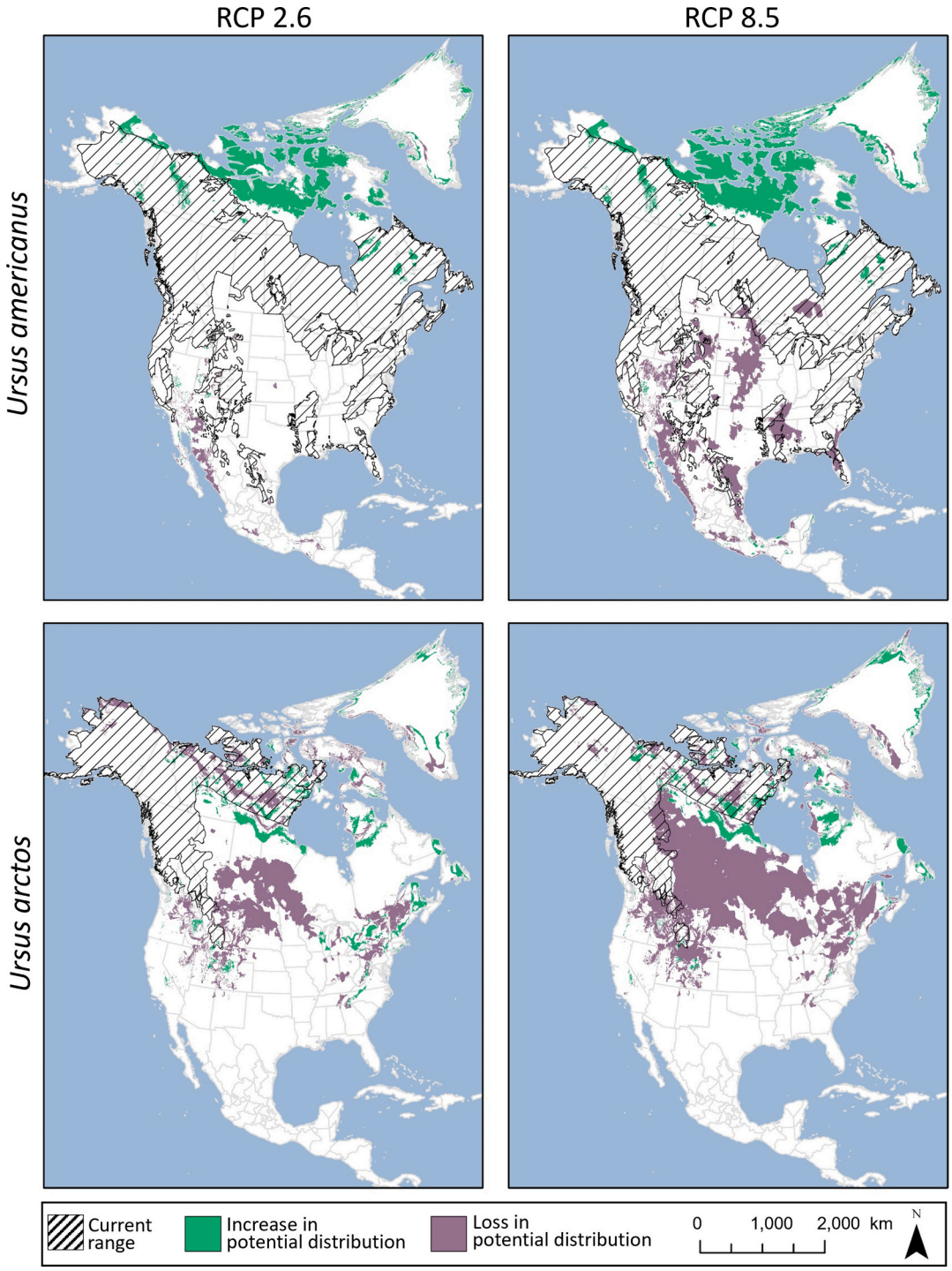

Fig. 4. Projected changes in distributions of the American black bear (*Ursus americanus*) and brown bear (*Ursus arctos*) across North America by 2070 under Representative Concentration Pathways (RCP) 2.6 and RCP 8.5. The RCP 2.6 scenario represents a low-greenhouse gas emissions trajectory while RCP 8.5 represents a high-emissions trajectory. Projected distributions provided by Pandey and Papeş (2018), current black bear range data from Scheick and McCown (2014), and current brown bear range data from Haroldson et al. (2021). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.4.4. Projected impacts on habitat selection, space use, and activity

Shifts in bear habitat availability and quality are projected to continue in the face of climate change. For example, as global temperatures increase, tree lines are expected to shift to higher elevations (Grace et al., 2002), reducing an important but already small and dispersed habitat for grizzly bears such as alpine ecotones (Fisher et al., 2014). In the southeastern U.S., Costanza et al. (2020) estimated that linkages between suitable areas of black bear habitat are projected to decrease 16% by mid-century based on an ensemble of climate projections under a high emissions scenario. Sea level rise has also been projected to fragment black bear habitat and populations (Leonard et al., 2017; Poor et al., 2020; Davis et al., 2021). For example, approximately 1% of black bear habitats in Florida could be inundated by 2100 under best-case scenarios (30-cm sea level rise projection) and 10% under worst-case scenarios (305-cm sea level rise projection; Poor et al., 2020). Additionally, disturbance events that are more common in southern regions (e.g., flooding of dens) may increase in frequency at higher latitudes (Rayl et al., 2014). These projected changes in habitat could modify resource selection and alter bear behavior and demographics.

The projected impacts of climate change on land cover and land use will likely affect species distributions. To investigate this effect, Pandey and Papeş (2018) modeled potential changes in the distribution of a suite of apex predators under four emissions scenarios (RCP2.6, RCP4.5, RCP6, and RCP8.5; Fig. 4). Brown bear distribution was predicted to decline under all scenarios, likely because much of their current range includes biomes undergoing rapid temperature increases (e.g., boreal forest and tundra), whereas black bears were the only species projected to experience increased distribution by 2050 and 2070, likely due to their generalist qualities and adaptability (Pandey and Papeş, 2018). By 2070, black bears were predicted to maintain much of their current range while also expanding into currently unoccupied areas such as portions of northern Canada (Pandey and Papeş, 2018). This indicates that future conditions could increase suitable habitat for black bears if they are able to track favorable climate conditions. However, temperature and precipitation changes are still anticipated to reduce black bear range in regions such as northwestern Mexico (Lara-Díaz et al., 2018; Pandey and Papeş, 2018). The ecological plasticity of bears will play an important role as they adapt their resource use and activity patterns, but their adaptive capacity may be challenged by more extreme and long-term perturbations in an increasingly human-dominated landscape.

3.5. Denning chronology

Hibernation is a life history strategy that helps bears mitigate effects of extreme weather conditions and conserve energy when food availability is low (Johnson and Pelton, 1980). Therefore, the timing and duration of hibernation are influenced by proximate environmental conditions (e.g., precipitation, temperature, extreme weather) and ultimate factors (e.g., food availability, energy intake; González-Bernardo et al., 2020). Bears that inhabit regions where winters are less severe and food is more consistently available experience shorter periods of hibernation or even forego hibernation altogether (Johnson and Pelton, 1980; Shoen et al., 1987).

3.5.1. Denning chronology: temperature

Warming temperatures are a key proximate environmental condition associated with changing denning chronology, resulting in delayed den entry in the autumn, earlier den emergence in the spring, and reductions in the duration of hibernation. Studies have shown an association between warmer autumn temperatures and delayed onset of hibernation (e.g., Johnson et al., 2018b; Supplemental Table 1) and even den abandonment in autumn during mild conditions (Shoen et al., 1987). There is also strong support for a relationship between warmer temperatures and earlier den emergence (e.g., Pigeon et al., 2016b; Supplemental Table 1). The effect of temperature on overall duration of hibernation follows similar trends. For example, Colorado black bears hibernated an average of 6 fewer days for each 1°C increase in winter minimum temperature (Johnson et al., 2018b).

3.5.2. Denning chronology: precipitation

In addition to temperature, researchers have examined the effects of precipitation on hibernation. Den entry has been shown to coincide with increases in precipitation (Immell et al., 2013), and the onset of severe weather (as indicated by lower barometric pressure; Johnson and Pelton, 1980), such as snowstorms (e.g., Servheen and Klaver, 1983; Supplementary Table 1). Den entry has also been observed to occur earlier during drier years, potentially due to reductions in food availability (Baldwin and Bender, 2010).

Precipitation, in particular snow conditions, is also associated with den emergence but it is important to recognize that spring temperatures and snow depth contribute to when snow melts (Schooley et al., 1994). Decreased precipitation, earlier snow melt, rapid snow melt, or inconsistent snow melt have all been associated with earlier den emergence (Pigeon et al., 2016b, Johnson et al., 2018b, Rickbeil et al., 2020; Supplementary Table 1). In one study, a 1.25-m increase in snow depth delayed grizzly bear spring activity dates by 7 days (Pigeon et al., 2016b). Delaying emergence until final snow melt is advantageous and enables bears to forage on newly available vegetation (Schooley et al., 1994). Increased precipitation has also been associated with delayed den emergence when habitats are flooded but dens are elevated, and den abandonment or early emergence when dens are inundated (e.g., Oli et al., 1997; Waller et al., 2012).

3.5.3. Denning chronology: food availability

Because the ultimate factor for the timing and duration of denning is related to energy, food availability can be a strong predictor of denning chronology. Studies indicate that low natural food availability and quality can result in earlier den entry (Pigeon et al., 2016b; Johnson et al., 2018b). For example, in Alberta, berry availability within grizzly bear home ranges explained 39% of observed den entry variation, and a 10-fold increase in preferred plant productivity delayed den entry by approximately 2 weeks (Pigeon et al., 2016b). The impact of food availability on denning chronology may be heightened for bears in poor body condition as they have been observed to den earlier than those in better physical condition (e.g., Johnson et al., 2018b).

3.5.4. Projected climate impacts on denning chronology

Changes in denning chronology have the potential to influence bears and their interactions with humans. More frequent den abandonment and early den emergence could lead to increased cub mortality (Gardner et al., 2014, Linnell et al., 2000). Emerging prior to sufficient food availability can increase maternal movement as bears seek suitable habitat, requiring increased cub energy expenditures and increasing exposure to infanticidal adult bears (Gardner et al., 2014). Later den entry and earlier den emergence could also increase how long bears are active and their vulnerability to harvest (Immell et al., 2013; Johnson et al., 2018b). Therefore, harvest season dates based on trends in bear behavior, environmental conditions, and food availability may ensure that harvest objectives are not exceeded (Miller et al., 2017). Similarly, changes in climate that result in shorter hibernation periods or more frequent den abandonment could lead to an increase in the frequency of human-bear interactions as bears are active on the landscape for longer periods. Additionally, early den emergence could lead to increased human-bear interactions if bears emerge when natural food is limited and turn to anthropogenic food sources. However, it is possible that vegetation availability and bear activity will remain synchronous in some areas (Rickbeil et al., 2020).

Warmer temperatures may be the most impactful environmental condition that affects the timing and duration of denning, delaying the onset of winter weather, lengthening vegetation availability, and expediting snow melt in the spring. As global temperatures are predicted to rise (Ara Begum et al., 2022), changes in denning chronology can be

expected. In Colorado, projected climate conditions are estimated to decrease the duration of black bear hibernation by 8–22 days by 2050 (Johnson et al., 2018c). Additionally, under projected future scenarios, climate shifts experienced in more northern latitudes may reflect the current climate of areas in southern latitudes (Fitzpatrick and Dunn, 2019). Thus, bear populations may adapt and exhibit similar denning chronology patterns to contemporary bear populations at lower latitudes.

3.6. Population demographics and dynamics

3.6.1. Direct climate impacts on population demographics and dynamics

Although the evidence of direct impacts of climate on population demographics and dynamics is limited, researchers have found effects on recruitment, survival, and population growth. For example, following a wildfire in Arizona, Cunningham and Ballard (2004) found that no cubs survived in the burned area and adult female and subadult numbers declined. However, despite potential negative effects on survival and population growth, bear populations can persist after widespread fire (Lindley, 2003). Several studies have also examined the effects of flooding on population dynamics. Flooding in Louisiana was not associated with lower recruitment, survival, or population growth, and a clear relationship between flooding and abundance was not identified (O'Connell-Goode et al., 2014; Clark et al., 2018). However, in Pennsylvania and Arkansas, many whole and partial litter losses have been attributed to flooding, particularly because of flooded dens (Alt, 1984; Clark and Eastridge, 2006).

3.6.2. Indirect climate impacts on population demographics and dynamics

The primary mechanisms by which climate affects bear population demographics and dynamics are indirect, via effects on habitat quality and food availability. Primarily, the effects on bear recruitment and survival have been examined. For example, black and grizzly bears typically breed every two to three years, respectively, but may forgo reproduction during years with food shortages (reviewed by Pelton, 2003, Schwartz et al., 2003). Researchers in the Greater Yellowstone Ecosystem, Colorado, Minnesota, and Ontario have found that grizzly and black bears have higher litter production and greater litter size with better habitat quality or food availability (Rogers, 1976; Picton et al., 1986; Schwartz et al., 2006a; Obbard and Howe, 2008; Johnson et al., 2020). More specifically, in Yellowstone National Park, grizzly bears had larger litters with higher cub survival when autumns and springs were warmer and drier, likely due to extended feeding opportunities, and when winters were warmer and had greater snowfall, likely due to reduced energy expenditures (Picton, 1978).

As further indication of the link between survival and nutrition, cubs and yearlings experience lower mortality when they are heavier and during years with more natural food availability (Rogers, 1976; Obbard and Howe, 2008). This relationship between survival and habitat quality experienced by cubs can continue into adulthood (Picton et al., 1986). The literature indicates that natural food shortages impact cub survival through both a lack of nutrition and increased use of human-development, whereas adult bear survival is primarily impacted by increased use of human-development alone (e.g., Baruch-Mordo et al., 2014; Johnson et al., 2020).

Recruitment and survival are primary determinants of population growth and abundance, and changes in these variables have important implications for population viability (Williams et al., 2002). Positive relationships between food availability and bear density, abundance, and population growth have been identified (e.g., Nielsen et al., 2017; Laufenberg et al., 2018). For example, models suggested that grizzly bears in Alberta doubled their local abundance for each 10-fold increase in buffaloberry (*Shepherdia canadensis*) and increased their local abundance by a factor of 59 for each 10-fold increase in ungulate carrion (Nielsen et al., 2017). However, bears can face ecological traps when they attempt to mitigate natural food shortages by searching for food in developed areas, leading to greater rates of human-caused mortality and population sinks (Lamb et al., 2016; Laufenberg et al., 2018; Johnson et al., 2020). For example, a late June freeze caused a natural food shortage in Colorado which led to increased use of human foods by bears (Johnson et al., 2020) and a subsequent 57% decline in female black bear abundance (Laufenberg et al., 2018). During the year of the food shortage, lethal conflict removals and harvest were double the annual average and bear-vehicle collisions were quadruple the five-year average (Laufenberg et al., 2018). As the climate changes, shifts in resource quality can be expected and may continue to increase these negative human-bear interactions with implications for bear population demographics.

3.6.3. Demographic impacts on human-bear interactions

Changes in climate that affect bear population growth and abundance also have the potential to impact the frequency of human-bear interactions; however, there is a lack of consensus in the literature on the role of population size in the occurrence of interactions. Garshelis et al. (2020) and Hristienko and McDonald Jr. (2007) concluded that expanding black bear populations were largely responsible for growing human-bear interactions in Minnesota and across North America, respectively. If this is the case, projected future increases in black bear range that may increasingly overlap with humans (Pandey and Papeş, 2018; Fig. 4) could lead to a geographic expansion in interactions. Results of other studies indicate that targeted bear reduction did not consistently reduce negative human-bear interactions (Obbard et al., 2014; Artelle et al., 2016; Northrup et al., 2023), even when correcting for population size (Treves et al., 2010). A direct, linear relationship between interactions and population size cannot be assumed because of the numerous potential drivers of interactions (e.g., changes in climate, natural food availability, human attractants, and bear behavior). Furthermore, metrics of interactions can be confounded by factors such as management actions, demographics of the complaint reporter, and public sentiment towards and tolerance of bears (Howe et al., 2010; McKinley et al., 2014; Wilbur et al., 2018).

4. Discussion

Collectively, the literature provides a broad view of how climate variability and change has already and will likely impact black and brown bears in North America. There is substantial evidence of direct impacts on bears, through flooding and wildfire events, and indirectly, through effects on habitat and food availability. We synthesized the effects of climate on bear diet; body size; habitat selection, space use, and activity; denning chronology; and population demographics and dynamics. Many of the examined effects have the potential to alter the frequency and severity of human-bear interactions, particularly those that result in reduced natural food availability or increase occupied range (Fig. 5). A primary indirect mechanism by which climate impacts bears is through natural food shortages (via drought, late freezes, and other causes of altered growing conditions), which was implicated in causing bear responses in every synthesized response category. Brown and black bears exhibit behavioral plasticity but will increasingly face challenges if their ability to adapt is outpaced by the rate of climate change and extreme climate events.

4.1. Data gaps

Much of the evidence shows relatively consistent trends across geographic location and species, but studies were unevenly distributed throughout North America. For example, only six studies assessed black bears in Mexico, which may have been due in part to our English-language selection criteria. Although the literature on denning chronology is abundant overall, we retrieved limited data regarding climate effects on denning in the northeastern U.S. Within the U.S. and Canada, only four studies examined the effects of climate on the body condition

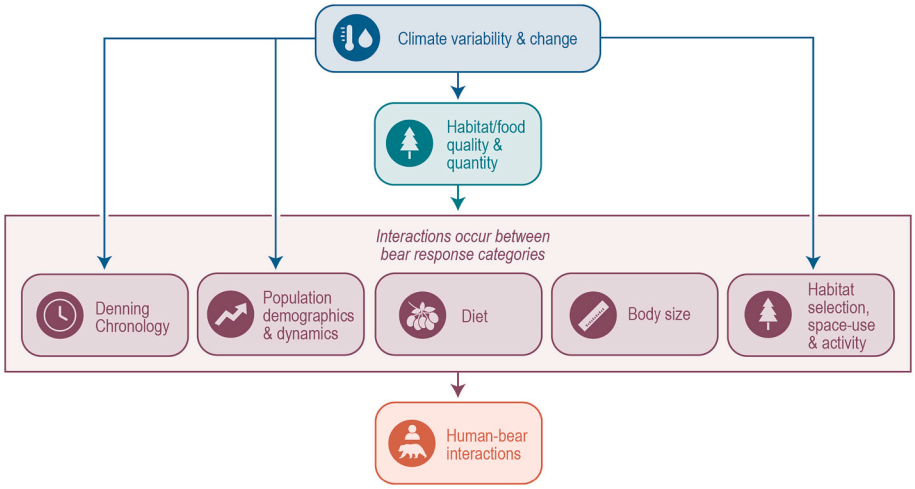

Fig. 5. A conceptual diagram illustrating the direct and indirect impacts of climate change and variability on American black bear (*Ursus americanus*) and brown bear (*Ursus arctos*) behavior and demography, resulting in implications for human-bear interactions. Anthropogenic drivers of interactions, which are also impacted by environmental drivers, are not represented in this figure.

of bears, and only two examined disease outcomes which limited our ability to review this topic. Geographic concentrations of literature were also present. For example, 87% of survival studies took place in the U.S. Den and daybed selection and abandonment studies showed a similar trend with 91% occurring in the U.S., half of which took place in Alaska. Future research is needed to fill identified gaps in bear responses and geographic gaps in data, especially as the behavior of bear populations can vary even at fine geographic scales (Van Daele et al., 1990).

4.2. Limitations

Several limitations should be considered when interpreting the results of this synthesis. First, sample size was limited in many studies (often ≤10 bears), likely associated with the difficulty and expense of studying bears and their relatively low densities on the landscape. Second, human-bear interactions were typically represented by incidents reported by the public to state management agencies. Such reports can be a biased measure of interaction frequency as public reporting can be influenced by numerous external social factors (e.g., personal experiences, tolerance for wildlife, gender, opinion of management decisions, and media reports; Howe et al., 2010, McKinley et al., 2014, Wilbur et al., 2018). Although an imperfect measure of the severity or frequency of human-bear interactions, public reporting represents the most commonly collected measure of interactions. Future work would benefit from accounting for biases in these data.

In addition, although our review focused on climate as a driver of human-bear interactions, we recognize the significance of anthropogenic drivers of interactions. Human development, human disturbance, and human population growth all significantly contribute to human-bear interactions in North America (Baruch-Mordo et al., 2014; Can et al., 2014; Smith and Herrero, 2018). Climate variability and change are likely compounding factors for bears already exposed to other non-climate interaction drivers and we aimed to highlight the growing importance of understanding the role of climate in exacerbating the frequency and severity of interactions.

4.3. Management implications

Given changing climate conditions and subsequent impacts to bear behavior and demography, it will become increasingly important for managers to incorporate climate considerations, particularly those impacting natural food availability, into bear management strategies. The literature suggests that the most effective strategy for managing human-bear interactions is to restrict bear access to anthropogenic foods, particularly during natural food shortages. Strategies likely to yield the greatest success include requiring and enforcing attractant management ordinances (e.g., use of bear-resistant trash cans; Barrett et al., 2014, Johnson et al., 2018a), use of effective deterrents such as electric fencing (Smith et al., 2018), and implementing livestock husbandry practices that reduce depredation risks (Khorozyan and Waltert, 2020).

When managing bears under changing climate conditions, it will also be imperative to use rigorous methods that can effectively track trends in bear populations and incorporate multiple data types and relevant covariates (e.g., weather and natural food conditions; Fieberg et al., 2010, Hatter et al., 2018). Combining data types can increase cost effectiveness, precision, and the ability to make inferences about population demographics across broader spatial and temporal scales (Chandler and Clark, 2014). As the climate continues to change, it is anticipated that bears will face increased non-harvest, human-caused mortality as their active season lengthens and bears seek out human food resources. Accounting for climate and subsequent changes in habitat when assessing management decisions (e.g., harvest limits) will allow for more effective and proactive management.

Proactive management also requires ensuring suitable habitat availability. Maintaining access to, and connections among, quality habitat areas is imperative to enhancing species resilience to climate change (Costanza and Terando, 2019). Management actions can improve habitat quality and connectivity when strategically planned and based on a thorough understanding of bear-habitat interactions and impacts of changing climate conditions. This could include considering increased space requirements needed to obtain resources during poor food years (e.g., Moyer et al., 2007) and modeling how the spatial and temporal availability of bear foods may shift under climate change scenarios (Roberts et al., 2014). Following identification of key habitats and corridors, maintaining or enhancing these areas will be imperative for genetic exchange and sustaining bear populations (Proctor et al., 2005; Murphy et al., 2017).

Given the influence of climate on different aspects of bear ecology, our literature review suggests that climate-influenced human-bear interactions are likely to increase in the future. Consequently, it is advantageous for managers to invest resources in strategies shown to be effective at reducing negative interactions and increasing opportunities for human-bear coexistence. To address current uncertainties and support management needs, future research directions include: 1) continued investigation of how climate variability and change impact

bear demography and behavior, particularly for responses and geographic areas yet to be fully understood (e.g., disease and bear responses at their most southern and northern range extents); 2) predicting future distributions and shifts of key natural foods of bears; 3) applying rigorous methods to efficiently monitor bear populations that explicitly consider the role of proximate environmental conditions and ultimate factors; and 4) developing decision frameworks to inform effective climate adaptation strategies in bear management.

4.4. Conclusion

Climate change is considered one of the most significant threats facing humans and wildlife today. As habitat generalists with a wide diet breadth, black and brown bears are less vulnerable to climate change than large mammals with more specific habitat requirements. In fact, black bear distributions may increase as the climate warms. However, the behavioral and physiological responses of bears to changes in climate can significantly affect their coexistence with humans, as bears make spatial adjustments in habitat use, search for alternative food sources, and reduce the length of their hibernation period. Understanding the underlying ecological drivers of bear responses to climate variability and change, and the implications for human-bear interactions, is critical for coexistence in an era of global change. Insights into the specific effects of climate on bear behavior and demography can help managers strategically allocate resources, guide decisions, support adaptation, and enhance human-bear coexistence.

CRediT authorship contribution statement

Katherine A. Kurth: Data curation, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Katherine C. Malpeli:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Visualization, Writing – review & editing. **Joseph D. Clark:** Methodology, Writing – review & editing. **Heather E. Johnson:** Methodology, Writing – review & editing. **Frank T. van Manen:** Methodology, Writing – review & editing.

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.

Data availability

No data was used for the research described in the article.

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Appendix A. Supplementary data

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