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Perspective

Applied winter biology: threats, conservation and management of biological resources during winter in cold climate regions

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Winter at high latitudes is characterized by low temperatures, dampened light levels and short photoperiods which shape ecological and evolutionary outcomes from cells to populations to ecosystems. Advances in our understanding of winter biological processes (spanning physiology, behaviour and ecology) highlight that biodiversity threats (e.g. climate change driven shifts in reproductive windows) may interact with winter conditions, leading to greater ecological impacts. As such, conservation and management strategies that consider winter processes and their consequences on biological mechanisms may lead to greater resilience of high altitude and latitude ecosystems. Here, we use well-established threat and action taxonomies produced by the International Union of Conservation of Nature—Conservation Measures Partnership (IUCN-CMP) to synthesize current threats to biota that emerge during, or as the result of, winter processes then discuss targeted management approaches for winter-based conservation. We demonstrate the importance of considering winter when identifying threats to biodiversity and deciding on appropriate management strategies across species and ecosystems. We confirm our expectation that threats are prevalent during the winter and are especially important considering the physiologically challenging conditions that winter presents. Moreover, our findings emphasize that climate change and winter-related constraints on organisms will intersect with other stressors to potentially magnify threats and further complicate management. Though conservation and management practices are less commonly considered during the winter season, we identified several potential or already realized applications relevant to winter that could be beneficial. Many of the examples are quite recent, suggesting a potential turning point for applied winter biology. This growing body of literature is promising but we submit

that more research is needed to identify and address threats to wintering biota for targeted and proactive conservation. We suggest that management decisions consider the importance of winter and incorporate winter specific strategies for holistic and mechanistic conservation and resource management.

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Introduction

Winter at latitudes spanning temperate to polar regions is a cold, challenging season for plants, animals and researchers alike. Historically, winter has been an understudied season in biological research for a number of reasons. Conducting research during winter involves sampling challenges, safety concerns and logistical considerations that commonly result in insufficient data collection (Marchand, 2013; Hampton *et al.*, 2015; Fernandes and McMeans, 2019). For example, prolonged exposure to cold temperatures can damage equipment, shorten battery life, freeze sensitive samples and prevent or hinder many traditional approaches for data collection in warmer, ice-free seasons (Block *et al.*, 2019; Marsden *et al.*, 2021). Moreover, many biologists have viewed winter as a season in which life is dormant and migratory animals are gone, limiting previous motivation for winter research (Studd *et al.*, 2021). Consequently, data used to inform conservation and management decisions are predominantly collected during warmer seasons. This pattern has motivated urgent calls for research focused on improving our understanding of ecological processes in winter, especially given the disproportionate impact of climate change on this season (Barnett *et al.*, 2005; Campbell *et al.*, 2005; Studd *et al.*, 2021).

Fortunately, identifying winter as a gap in biological research and advancements in technology has invigorated a broader motivation for winter research. Winter is now increasingly recognized as a critical mediator of organismal biology and ecological processes through its impacts on fitness (underpinned by physiological tolerances), population-level processes and ecosystem structure and function (Sinclair *et al.*, 2003; Campbell *et al.*, 2005; Farmer *et al.*, 2015; McMeans *et al.*, 2020; Ozersky *et al.*, 2021). A focus on winter ecology has identified threats to biota that were historically under-appreciated or unknown. In addition, recent work has used novel methods to aid in the pursuit of conservation and management that considers winter processes more centrally. The challenge remains to incorporate emerging knowledge into conservation and management actions to mitigate damage caused by global change threats that occur in winter.

In this synthesis, we highlight the importance of winter conservation and management practices for the maintenance of biodiversity and healthy natural populations. To do so, we use the International Union of Conservation of Nature—Conservation Measures Partnership (IUCN-CMP) *Unified Classification of Direct Threats* and *Unified Classification of Conservation Actions Needed* working documents as our framework to categorize threats to biodiversity in cold climate regions that emerge during winter and suggest possible avenues for improved conservation and management efforts. Our definition of winter considers the nine maxims proposed by Studd *et al.* (2021) and is influenced by the concepts of astronomical and frigid winter (Contosta *et al.*, 2020). We define winter as the longest of either: (a) the period spanning from winter solstice to vernal equinox in regions that experience daily minimum air temperature below 0°C for a minimum of 28 days, cumulatively, or (b) the period between threshold start and end dates related to the number of freezing days within a seven day period (see Glossary for more details). This definition was produced to recognize differences in day length and winter severity between regions, and to recognize the impact of climate change-induced temperature variation on the winter season (e.g. weather whiplash; Casson *et al.*, 2019). We consider various biological mechanisms that span physiology, behaviour and ecology and operate in diverse ways and across various levels of biological organization (as per Cooke *et al.*, 2023). We wish to make it clear that this article is not a robust systematic review but rather a synthesis of existing literature that we use to outline important concepts and highlight relevant examples. That said, we attempt to be taxonomically inclusive in our examples and focus on threats that occur, or will be present, during winter in cold climate regions (including temperate, boreal, polar and high altitude regions) around the globe. Members of the authorship team work in cold-climate regions on a wide range of systems and taxa in academia and governments. Although the majority of authors reside in North America, team members work in cold-climate regions around the world, including Antarctica, Europe, Asia and North America.

Relevance of Winter to Biodiversity Threats

The IUCN-CMP *Unified Classification of Direct Threats* working document (Version 3.2; IUCN, 2022b) is a hierarchical structure representing the drivers of species decline. The IUCN defines direct threats as proximate human activities or processes that have impacted, are impacting, or may impact the status of a species or group of species (IUCN, 2022b). Here, using this scheme which classifies threats into 11 categories (e.g. Residential and commercial development, Agriculture and aquaculture, Biological resource use, etc.), we discuss threats to biodiversity that manifest in winter months. For each category, we briefly outline the threat(s) and emphasize how each threat impacts natural systems in winter, drawing from a broad set of examples (for more details on the threat categories, see Table 1). We follow the threats classification scheme which has explicit instructions regarding which threats are considered under each classified threat type. Where specific threats could be perceived to overlap (which is an inherent reality of any threat classification scheme), we make note of this and point to the associated section where more information can be found.

1. Residential & commercial development

Habitat loss resulting from anthropogenic land development is the primary cause for species decline globally (Haddad *et al.*, 2015; Horvath *et al.*, 2019). Such developments reduce habitat quality and quantity for wildlife; however, there is a general lack of knowledge surrounding species-specific winter habitat requirements. Therefore, our ability to anticipate how land development may impact overwintering species is poor and critical wintering habitat for many terrestrial and aquatic species is likely at risk. Anthropogenic land developments can limit overwintering habitat availability and impede key migratory routes both directly (habitat destruction) and indirectly (avoidance of developed habitat) (Polfus *et al.*, 2011; Wyckoff *et al.*, 2018). In addition to impacting animal movement, increased development in key winter ranges is associated with reduced recruitment in some ungulates, though the distinct mechanism driving this pattern is unclear (Johnson *et al.*, 2016; Wyckoff *et al.*, 2018). Similarly, ectothermic organisms (e.g. fish, reptiles, amphibians) may be particularly sensitive to wintertime development as their ability to perceive and respond to disturbance may be impaired in the cold (Crawshaw, 1984, Temple and Johnston 1998, Szabo *et al.*, 2008). For example, development near breeding pools poses a greater mortality risk to wood frogs (*Rana sylvatica*) during the winter when compared to other seasons, presumably due to an inability to avoid these disturbances during their dormancy (Regosin *et al.*, 2003). Construction near waterways can also result in increased sediment loading which damages critical winter habitat, reduces habitat complexity, water depth and available oxygen and may result in reduced overwinter survival of fish and other aquatic fauna (Cunjak, 1996). Thus, protecting overwintering habitat from both direct and indirect effects of development is critical to the maintenance of resilient urban ecosystems.

In addition to introducing spatial barriers and damaging overwintering habitat, urbanization and fragmentation associated with development can alter winter microclimates. For example, fragmented forests experience colder winter temperatures due to greater heat loss from increased forest edges which may impact growth patterns and survival in some species (Latimer and Zuckerberg, 2016). Conversely, urban environments are often warmer than their surrounding areas (largely due to anthropogenic heat production from burning fossil fuels; Hinkel *et al.*, 2003; Varentsov *et al.*, 2018), which can act as a refuge for non-native species (Varentsov *et al.*, 2018; Sachanowicz *et al.*, 2018; see *9. Pollution* and *8. Invasive & other problematic species & diseases* for more details). Residential and commercial developments are also associated (to varying degrees) with an increased likelihood for human intrusions (see *6. Human intrusions & disturbance)* and increased pollution (e.g. anthropogenic litter, wastewater, thermal pollution; see *9. Pollution*), which can have negative consequences on wintering biota.

2. Agriculture & aquaculture

Agricultural activities can affect both habitat suitability and food availability for overwintering organisms. Interactions between agriculture and winter may be particularly strong in temperate regions, which have undergone extensive land use transformations as a result of converting forests and grasslands to cropland and rangeland. Moreover, at temperate latitudes, snow, ice and freezing temperatures typically play a strong role in constraining the survival of overwintering organisms (Kreyling, 2010). For organisms that overwinter in soil, agricultural practices that alter ground cover via crop residues, cover crops, or grazing can directly affect the thermal environment. For example, ground cover can increase near-surface soil temperatures during winter (Yang *et al.*, 2021), while on a larger scale, cover cropping can increase positive radiative forcing during winter and accentuate recent patterns of winter warming (Lombardozzi *et al.*, 2018). Nevertheless, the bulk of research on winter soil temperatures in croplands has been restricted to the overwinter survival of resident insect pests and weeds (e.g. Shimoda and Hirota, 2018); it remains largely unknown to what extent the overwintering of other organisms that reside in agricultural fields may be affected. However, agricultural activities also introduce sediment into adjacent waterways, which negatively impacts critical winter habitat for aquatic organisms (Cunjak, 1996; similar to the impacts of construction; see *1. Residential & commercial development*, for more details).

Table 1: Summary of the IUCN-CMP Unified Classification of Direct Threats (Version 3.2) detailing which threats should be included in each section

IUCN-CMP Unified Classification of Direct Threats Exposition	
1. Residential & commercial development	Threats from human settlements or other non-agricultural land uses with a substantial footprint. These are threats tied to a defined and relatively compact area, which distinguishes them from those in *4. Transportation & service Corridors*, which have a long narrow footprint, and *6. Human Intrusions & disturbance* which do not have an explicit footprint.
2. Agriculture & aquaculture	Threats from farming and ranching due to agricultural expansion and intensification, including silviculture, mariculture and aquaculture. Threats resulting from agrochemicals, rather than the direct conversion of agricultural use, should be included in *9. Pollution*. Likewise, in cases where conversion to agriculture caused increased run-off and hence sedimentation of rivers and lakes, that is also best treated under *9. Pollution*. Domesticated livestock that have become feral should be treated under *8. Invasive & other problematic species & diseases*.
3. Energy Production & mining	Threats from production of non-biological resources. Various forms of water use (for example, dams for hydro power) could also be put in this class, but these threats seemed more related to other threats that involve alterations to hydrologic regimes. As a result, they should go in *7. Natural system modifications*. Oil spills that occur at the drill site should be placed here; those resulting from oil tankers or pipelines should go in *9. Pollution*. Threats from sediment or toxic chemical runoff from mining should be placed in *9. Pollution*.
4. Transportation & service corridors	Threats from long narrow transport corridors and the vehicles that use them including associated wildlife mortality. This class includes transportation corridors outside of human settlements and industrial developments. These corridors create specific stresses to biodiversity including especially fragmentation of habitats and lead to other threats including farms, invasive species and poachers. Off-road vehicles are treated in the appropriate category in *6. Human intrusions & disturbance*.
5. Biological resource Use	Threats from consumptive use of "wild" biological resources including both deliberate and unintentional harvesting effects; also, persecution or control of specific species. Consumptive use means that the resource is removed from the system or destroyed - multiple people cannot use the same resource, as they could under *6. Human Intrusions & Disturbance*. Threats in the class can affect both target species (harvest of desired trees or fish species) as well as "collateral damage" to non-target species (trees damaged by felling or fisheries bycatch) and habitats (coral reefs destroyed by trawling). Persecution/control involves harming or killing species because they are considered undesirable.
6. Human intrusions & disturbance	Threats from human activities that alter, destroy and disturb habitats and species associated with non-consumptive uses of biological resources. Non-consumptive use means that the resource is not removed - multiple people can use the same resource (for example, birdwatching). These threats typically do not permanently destroy habitat except perhaps in extremely severe manifestations. The development of permanent recreation or tourist facilities should be included under section *1. Residential & commercial development*.
7. Natural system modifications	Threats from actions that convert or degrade habitat in service of "managing" natural or semi-natural systems, often to improve human welfare. This category deals primarily with changes to natural processes such as fire, hydrology and sedimentation, rather than land use. Thus, it does not include threats relating to agriculture (which should be under *2. Agriculture & aquaculture*), or infrastructure (*1. Residential & Commercial development* and *4. Transportation & service corridors*).
8. Invasive & other problematic species & diseases	Threats from non-native and native plants, animals, pathogens/microbes, or genetic materials that have or are predicted to have harmful effects on biodiversity following their introduction, spread and/or increase in abundance.
9. Pollution	Threats from introduction of exotic and/or excess materials or energy from point and nonpoint sources. This class deals with exotic or excess materials introduced to the environment.
10. Geological Events	Threats from catastrophic geological events. This section includes events such as volcanic eruptions, earthquakes, tsunamis, avalanches and landslides. All other severe weather events belong in *11. Climate change & severe weather*.
11. Climate change & severe weather	Threats from long-term climatic changes which may be linked to global warming and other severe climatic/weather events that are outside of the natural range of variation, or potentially can wipe out a vulnerable species or habitat. Strictly speaking climatic events may be part of natural disturbance regimes in many ecosystems. But they are a threat if a species or habitat is damaged from other threats and has lost its resilience and is thus vulnerable to the disturbance. Many climatic events may also be increasing in frequency or intensity outside their natural range of variation due to human causes.

3. Energy production & mining

The activities inherent to energy production and mining (i.e. oil and gas drilling, mining, quarrying and renewable energy) are associated (to varying degrees) with the production of pollutants including noise, artificial light, excess heat and chemical contaminants, which we address below in *9. Pollution*. Here, we consider other potential effects of energy production and mining on winter habitats and animal physiology.

Direct physical disturbance or disruption of hibernacula by mining activities during winter can cause mortality to dormant wildlife. Additionally, winter mining activities can alter environmental conditions that enable successful overwintering. For example, repeated flooding and drainage of an actively mined peat bog can interfere with the aerobic, flood- and frost-free "life zone" required by overwintering Massasauga rattlesnakes (*Sistrurus catenatus;* Yagi *et al.*, 2020). The effects of strip-mining and quarrying can also carry over into the winter even when activity is limited to summer months, as with the destruction of overwintering habitat of timber rattlesnakes (*Crotalus horridus*) caused by ridge-top mining (Maigret *et al.*, 2019). Mining activity can also alter animal movement and habitat use (sage grouse *Centrocercus urophasianus*: Pratt and Beck, 2019; mule deer *Odocoileus hemionus*: Northrup *et al.*, 2021), evidenced by the active avoidance of areas with mining disturbance during wintering periods. These effects are likely driven by noise and light pollution (see *9. Pollution* for more details) rather than the other impacts of energy production. Animal movements may also be influenced by industrial linear features produced from gas and oil extraction activities (e.g. seismic lines used in oil and gas exploration). Wolf movements, for example, have been shown to be influenced by these features but the use of these features differed by season and line type and may be less important in the winter (Latham *et al.*, 2011). The demographic effects of these disturbances and their specific relevance to winter ecology are not well understood.

Burning fossil fuels for energy production has contributed greatly to current patterns in global warming and climate change (Pedersen *et al.*, 2021), disproportionately impacting winter conditions at temperate and Arctic latitudes (see *11. Climate change & severe weather* for more details). In response to global concerns surrounding fossil fuel emissions and worsening future climate scenarios, many nations have pledged to reduce their fossil fuel use by transitioning to renewable energy sources (United Nations, 2015). Though renewable energies offer effective alternatives to fossil fuels, the infrastructure necessary for their production may still pose unique threats to biodiversity. For example, hydroelectric dams alter flow regimes, warming temperatures in their upstream headpond, changing the formation and type of ice cover and inhibiting habitat connectivity (Cunjak, 1996; Heggenes *et al.*, 2021). These alterations thereby impact the winter conditions available to riverine aquatic organisms (the impacts of hydroelectric dams are discussed in more detail in *7. Natural system modifications*). Further, solar and wind energy developments occupy large physical footprints, fragmenting landscapes and reducing the available overwintering habitat for some species (Larson and Guillemette, 2007; Lovich and Ennen, 2011; Smith *et al.*, 2020). Nuclear power plants, although non-renewable, offer high efficiency, zero-carbon-emission energy production. However, warm water thermal effluent from nuclear facilities can alter seasonal mixing regimes and decrease ice cover, potentially altering phytoplankton species assemblages and abundance with consequences for higher trophic levels (Shatwell *et al.*, 2008; Kirillin *et al.*, 2013). Additionally, warmed winter waters can have seasonal carryover effects on reproduction in some fish species (Farmer *et al.*, 2015; Firkus *et al.*, 2018; see *9. Pollution* for more details on thermal pollution). Ultimately, more winter oriented research is needed to better understand the potential impacts of these energy sources.

4. Transportation & service corridors

Winter is a critical period for the transportation of resources in Arctic regions due to the construction of temporary winter and ice roads. Little permanent infrastructure exists in these regions, and overland travel via temporary winter roads is less environmentally damaging and more cost-efficient than travel by air or sea (Gädeke *et al.*, 2021). Unfortunately, safe transport across ice roads requires thick ice and snow to sustain the weight of vehicles, and increasingly mild conditions are shortening the season for these temporary roads, reducing the potential for winter road construction and use (Woolway *et al.*, 2022). Moreover, thawing of permafrost is predicted to damage existing infrastructure in these regions, resulting in increased construction of all-season roads and bridges and expensive repairs (Schindler and Smol, 2006; Shiklomanov *et al.*, 2016; Gädeke *et al.*, 2021). This increased construction will cause increased fragmentation and pollution, which will negatively impact sensitive Arctic biota (see *1. Residential & commercial development* and *9. Pollution* for more information on the impacts of fragmentation and pollution, respectively).

Conversely, shipping transportation in northern regions is expected to increase in response to shorter and milder winters. Ice is the largest obstruction to shipping, so climate change-induced reductions in ice cover duration and thickness will result in increased navigable area, vessel safety and shipping season length (Stephenson *et al.*, 2011; Mudryk *et al.*, 2021). As a result, global interest in the Arctic's increased potential for resource exploration and intercontinental shipping is growing and future year-round shipping is being considered for areas such as the Great Lakes of North America (Millerd, 2011; Stephenson *et al.*, 2011). Very little information exists on the projected impacts of increased winter shipping, but increased shipping is likely to result in increased pollution and more opportunities for invasive species transport (Millerd, 2011). Moreover, although mid-winter shipping still seems unlikely in Arctic regions, the shoulder seasons could become more viable via ice-breaking especially if winter ice thickness is reduced. Increased ice breaking could negatively impact species such as beluga (*Delphinapterus leucas*) or narwhal (*Monodon monoceros*) that are sensitive to loud noise (Erbe and Farmer, 2000). More research is needed to directly assess the ecological impacts of increased wintertime shipping.

5. Biological resource use

In boreal and Arctic human settlements, winter provides opportunities to access key resources such as mammals (e.g. seals, bears, ungulates), birds (e.g. grouse, duck) and fishes (e.g. salmonids), supporting cultural and economic health and food security. For instance, ice fishing supports subsistence communities (Mustonen, 2014) and northern commercial fisheries (Miller, 2018), and attracts economic stimulation from local and international tourists (Sundmark and Gigliotti, 2019; Lawrence *et al.*, 2022). However, many aquatic species aggregate during winter months, increasing their potential susceptibility to harvest. Indeed, strong exploitation pressure during winter can shape fish populations, causing reduced productivity and lower average body sizes in target species (e.g. Isermann *et al.*, 2005; Johnston *et al.*, 2011; Sendek and Bogdanov, 2019). Moreover, catch-and-release ice-angling can cause stress and tissue damage to fish, especially while exposed to sub-zero winter air (Lawrence *et al.*, 2022). The potential for winter climate change to interact with human activities in ways that lead to resource depletion underscores the need to consider winter climate change in management and conservation planning (See *11. Climate change & severe weather*).

Winter climate change may also restrict physical access to resources for both humans and wildlife. As intermittent winter ice cover becomes increasingly prevalent across north-temperate lakes and coastal systems, access to safe ice is expected to decrease substantially (Sharma *et al.*, 2019). A shorter period of navigable snow and ice cover will reduce the contribution of subsistence, recreational and commercial fisheries and hunting grounds, impeding access to historical foraging activities that have cultural significance (Pearce *et al.*, 2010; Tam *et al.*, 2013). In addition to impacting human travel and access to traditional harvest sites, these winter changes are altering migration timing and paths of species that are key to northern food security, making resource availability less predictable from year-to-year (Downing and Cuerrier, 2011; Leblond *et al.*, 2016). Thus, recreational and commercial hunting and fishing pressure will likely be amplified during a shorter window of viable ice cover if the season of ice cover continues to narrow. However, winter climate change is likely to have divergent/asymmetrical impacts across ecosystems/biomes. For example, increased weather variability has decreased the predictability of fish and shellfish distributions and thus reduced fishing success by some subsistence communities (Moerlein and Carothers, 2012). In contrast, at high latitudes where ice fishing is only possible during the shoulder seasons, reduced ice thickness may increase its feasibility during winter (Stewart, 2005). Understanding the net consequences of shifts in this resource for polar communities and ecosystems is necessary to appropriately manage these changing landscapes.

6. Human intrusions & disturbance

Potential conflict zones between humans and overwintering flora and fauna have been expanding in accordance with the contemporary diversification of winter recreational activities (Braunisch *et al.*, 2011; Olson *et al.*, 2017; Lesmerises *et al.*, 2018; Heinemeyer *et al.*, 2019). Broadly, human winter recreation can be organized into motorized (e.g. snowmobiling) and non-motorized (e.g. skiing and snowshoeing) activities, both of which can negatively influence winter patterns of movement and habitat use (Braunisch *et al.*, 2011; Lesmerises *et al.*, 2018; Heinemeyer *et al.*, 2019; Squires *et al.*, 2019), energy expenditure (Arlettaz *et al.*, 2015) and fitness (Goodrich and Berger, 1994). Motorized winter activities can expose biota to acute high-decibel noise in both terrestrial and frozen aquatic habitats (e.g. if snowmobiling over frozen water bodies). Intensive snowmobiling can result in the displacement of caribou (*Rangifer tarandus*) from areas of suitable winter habitat (Seip *et al.*, 2007). Conversely, heli-skiing activity appears to have little effect on their winter habitat selection and behaviour (Huebel, 2012). Further investigation is needed to determine the impacts of these activities to effectively manage their impacts. In addition, shared reliance on critical, yet declining, winter habitat features (e.g. snowpack) between recreationists and wildlife is likely to increase the risk of human-wildlife conflict during winter following continued climate change (Arlettaz *et al.*, 2015; Brambilla *et al.*, 2016). Due to the potentially wide-ranging impacts of winter recreation, these activities should be carefully monitored and considered in conservation management plans, especially in protected areas that must balance human activity with conservation goals (Sato *et al.*, 2013; Lesmerises *et al.*, 2018; Ordiz *et al.*, 2021). Zonation in protected areas is one common mechanism of restricting human activity to specific areas or periods that results in the least disruption to animal life in winter (Geneletti and van Duren, 2008).

7. Natural system modifications

The modification of waterways and their shorelines for hydroelectric power generation, flooding and erosion management, and water abstraction poses conservation challenges to over 60% of the Earth's large rivers (Grill *et al.*, 2019) and nearly one-third of the Earth's large lakes (Mammides, 2020). These modifications have explicit consequences for biota during winter that must be considered when identifying ecological risk factors. For example, regulated reservoirs often employ winter drawdowns where the water levels are commonly maintained several meters lower than the maximum reservoir water level observed in the summer and fall (Carmignani and Roy, 2017). This practice minimizes the likelihood of flooding from snow melt but also reduces critical overwintering and foraging habitat for freshwater fish and invertebrates, promoting conflict (Eloranta *et al.*, 2017; Kytökorpi, 2019; Trottier *et al.*, 2019; Bunt *et al.*, 2021). This reduction of winter habitat can cause a reduction in dissolved oxygen concentrations which increases the likelihood for winterkill (Carmignani and Roy, 2017). Additionally, the winter discharge of freshwater through these hydroelectric dams can lead to a freshening of surface waters in nearshore marine systems, with significant implications for wildlife that depend on polynyas, flaw leads and other open water marine features in winter (Eastwood *et al.*, 2020). Pre-emptive ice blasting is also conducted in some areas to reduce the likelihood of flooding, such as along the Rideau River in Ottawa, Canada (Lane, 2011). Little research exists on the effects of ice blasting on overwintering fish species; however, one observational study found that considerable numbers of fish are killed annually from this practice (Schaap *et al.*, 1998). Similarly, traditional lentic and lotic shoreline modifications alter flow regimes and littoral habitats, reducing the availability of suitable overwintering areas for aquatic invertebrates and fishes (Oswood *et al.*, 1991; Cunjak, 1996). In addition to their structural characteristics, ideal overwintering areas for many freshwater organisms contain sites of groundwater upwelling (French *et al.*, 2014; Westhoff *et al.*, 2016). However, these areas may be at severe risk of depletion following water abstraction, the creation of impervious surfaces (i.e. pavement) and reductions in water table depth. Thus, it will be critical to consider how threats from modifications to aquatic systems manifest in every season to properly manage these ecosystems.

Human caused forest fires are extremely destructive causing roughly 8000 km^2 of damage each year in the United States (Balch *et al.*, 2017). Unfortunately, warming winters and reductions in snow cover are projected to worsen the prevalence and severity of boreal forest fires (Randerson *et al.*, 2006). Though anticipated changes to wintertime precipitation and humidity are geographically variable (Reinhard *et al.*, 2005; Kilpeläinen *et al*., 2010), an increased incidence of rain relative to snowfall, increased minimum winter temperatures and earlier spring warming are all projected to substantially reduce winter snow cover and drive positive radiative forcing (Kuang and Yung, 2000; Reinhard *et al.*, 2005; Randerson *et al.*, 2006). Positive feedbacks involving reductions in winter snow cover, warmer summer temperatures and increased drought frequencies will result in increases in forest fire occurrences and a broadening of the fire season (Stocks *et al.*, 1998, Kilpeläinen *et al*., 2010). Human ignited forest fires are contributing to the lengthening of the forest fire season and, in contrast to natural ignitions, human-ignited forest fires are more evenly distributed throughout the year (Balch *et al.*, 2017). In fact, approximately 20% of human-ignited forest fires occur in the winter (Balch *et al.*, 2017). The likelihood of forest fires overwintering (i.e. remnants of fires that persist by smouldering in the organic soil layer) has also increased in the past 20 years (Scholten *et al.*, 2021). These increases in fire frequency, duration and magnitude will have drastic consequences on overwintering biota that are currently somewhat unclear. However, one can expect that slower regrowth of certain high-value vegetation and/or differential impacts of fire on overwintering habitat types will likely drive disparity in the impact of forest fires on boreal and Arctic communities. For example, lichens, the preferred for age of North American caribou representing up to 83% of their winter diet (Jandt *et al.*, 2003), were slow to recover from fires and were largely replaced by vascular plant species post-burn (Jandt *et al.*, 2008). Conversely, overwinter forage for small mammals appears less affected by summer fires, and in some cases increases post-burn (Zwolak and Foresman, 2008; Ecke *et al.*, 2019). As a result, changes to forest communities resulting from increased fires may be driven by ecological consequences that manifest during winter months. Targeted and intensive fire prevention and suppression in small, high-value habitats (as suggested by Stocks *et al.*, 1998), such as lichen-dominated caribou overwintering areas (Russell and Johnson, 2019), combined with adaptive forestry management (see *4. Harvest and Trade Management* for more details on adaptive management) that enhances fire resistance and surface albedo via the establishment of broad-leaved tree species, may increase the resilience of boreal forest ecosystems (Bright *et al.*, 2017; Astrup *et al.*, 2018).

8. Invasive & other problematic species & diseases

Winter represents a key constraint on the geographic ranges of many species. Cold temperatures typically preclude the migrations of species poleward or up elevation gradients as they lack sufficient physiological or behavioural adaptations to such conditions in their current ranges. Due to the effects of climate warming, many species are now expanding their range poleward. Species are moving to higher latitudes at a median rate of 16.9 km per decade (Chen *et al.*, 2011). Mitigating these poleward migrations will pose significant challenges for land and fisheries managers. Further, the decision to actively combat the poleward migration of non-native species is debated widely. Some argue that these species are refugees of climate change and that preventing these shifts may be futile, causing range collapses or extinctions at broader scales (Urban, 2020). Moreover, poleward migrations of species will also inevitably introduce novel pathogens and aid in the spread of disease vectors such as mosquitoes (Osland *et al.*, 2021) and ticks (Lindgren *et al.*, 2000). Unfortunately, warmer winters are already expected to increase free living bacteria, parasites and insect-borne pathogens whose survival and development are limited by temperature (Bradley *et al.*, 2005). In both invasive and native pest species, harsh winter conditions play a pivotal role in determining population and invasion dynamics (Neuvonen *et al.*, 1999). Due to warming winters, the current mountain pine beetle (*Dendroctonus ponderosae*) outbreak has spread both further east and north than previously recorded (Sambaraju and Goodsman, 2021). The jackpine trees (*Pinus banksiana*) of the newly invaded range are comparatively naive, which will likely have significant consequences for forest structure and function

(Cullingham *et al.,* 2011). Similarly, the northern spread of hemlock wooly adelgid (*Adelges tsugae*) in the north-eastern United States and south-eastern Canada is limited by cold winter temperatures (Skinner *et al.,* 2003). However, with the combination of warming winters and potentially greater cold tolerance of the insect, stands of eastern hemlock trees could be affected by this pest throughout its entire range (Albani *et al.,* 2010; Ellison *et al.,* 2018). Changing winters will also have a significant impact on the performance and geographic range of terrestrial plants (Kreyling, 2010; Williams *et al.,* 2015), promoting the spread of invasive species (e.g. Bañuelos *et al.,* 2004; Boyte *et al.,* 2016). Building a decision framework combining the challenges of climate change on climate-tracking species and the conservation of local species is necessary when prioritizing conservation actions at larger scales.

9. Pollution

Road salts play a significant role in the transportation sector during the winter months to de-ice roadways, entering adjacent habitats via run-off in the spring. This contributes to the salinization of freshwater ecosystems, the effects of which often persist into the summer months in large urban centres (Dugan *et al.,* 2017; Lawson and Jackson, 2020). Salinization can physically and chemically alter freshwater ecosystems, impacting local biodiversity (Hintz and Relyea, 2019). For example, a $\geq 50\%$ reduction in cladoceran abundance was observed in aquatic systems that approached or reached the established Canadian, United States and European threshold levels for Cl^- in recent years, with similar trends being observed for copepod and rotifer zooplankton (Hintz *et al.,* 2022). Such declines can have dramatic effects on lake food webs, altering nutrient cycling and water clarity, causing eutrophication and triggering declines in fish and other aquatic macroorganisms (Hintz *et al.,* 2022). In fact, most freshwater aquatic macroorganisms exhibit direct negative effects when exposed to concentrations of road salts. Among other things, studies have shown that fish digestion, growth and development rates are impaired (Boeuf and Payan, 2001; Hintz and Relyea, 2017), amphibian development and behaviour are disrupted (Denoël *et al.,* 2010; Hopkins *et al.,* 2013), and freshwater bivalve reproductive success is significantly reduced when exposed to concentrations of road salts (Todd and Kaltenecker, 2012; Nogueira *et al.,* 2015). If concentrations are high enough road salt-induced mortality is also a risk for some species (e.g. Kostecki and Jones, 1983; Kszos *et al.,* 1990). Although important for safe transportation during winter months, the subsequent increased salinization of freshwater ecosystems greatly threatens biodiversity year-round. Alternative de-icing agents have been developed due to the urgent demand motivated by recent road-salt research; however, these also exhibit detrimental levels of ecotoxicity (Schuler *et al.,* 2017; Gillis *et al.,* 2021). Currently the best method to reduce road salt use may be through optimizing their use. For instance, a 20-year program in Finland was able to reduce road salt use by 35% by improving de-icing devices and practices, meteorological online data services and education, as well as a reward program for private contractors responsible for de-icing (Salminen *et al.,* 2011).

Climate change is altering precipitation regimes and freeze/thaw cycles, modifying runoff and delivery of sediments and pollutants to aquatic systems (see *11. Climate change & severe weather*; Creed *et al.,* 2018). The delivery of contaminants into freshwater systems (e.g. mining effluent) can alter the freezing points of freshwater systems and change the timing and duration of ice cover, while increased sedimentation can elevate total suspended solids, turbidity and coloured dissolved organic matter through the process of brownification (Blanchet *et al.,* 2022). Brownification reduces underwater light penetration and selectively filters short wavelengths (blue/green light), reducing resource quality, success of visual predators and potentially alters food webs (Hedström *et al.,* 2017; Creed *et al.,* 2018). Increased browning of northern freshwaters combined with glacier melt is also darkening adjacent coastal systems, with similar and widespread consequences for oceanic and coastal food webs (Mustaffa *et al.,* 2020). Though observed in all seasons, closely monitoring and responding to the consequences of pollutants introduced during winter may be critical to maintaining the function of northern aquatic ecosystems.

Additionally, terrestrial wildlife wintering in or near urban or developed areas may be exposed to a greater volume and wider array of pollutants. Overwintering organisms in urban areas suffer from increased waste (e.g. discarded plastic, byproducts of food production), light, noise and thermal pollution (Kyba *et al.,* 2011; Kim and Brown, 2021; Murphy and King, 2022). Though these urban pollutants are present year-round, light and noise pollution may be more damaging to some organisms during the winter due to the physiological cost of arousal from dormant periods (Thomas *et al.,* 1990; Karpovich *et al.,* 2009). Light pollution is amplified by winter conditions as the reflection of artificial light at night increases substantially with snow cover (Jechow and Hölker, 2019). For example, light pollution may negatively affect bat abundance and diversity by compromising their hibernation and overwinter survival; however, the effects of light pollution on roosting bats are still debated and more research is needed (Kalnay and Cai, 2003; Longcore and Rich, 2004). Likewise, the effects of noise pollution on overwintering organisms are poorly studied, but negative effects have been demonstrated in some cases. Winter noise pollution can alter the diversity of bird communities, and some bats may avoid noisy areas when selecting overwintering roost sites (Thomas, 1995; Luo *et al.,* 2014; Ciach and Fröhlich, 2017). When not avoided, some bat species can acclimate to urban noise and are rarely disturbed during their torpid or hibernating periods (Luo *et al.,* 2014).

Urban areas are typically warmer than their surrounding areas and are known as 'urban heat islands'. This thermal phenomenon can reduce local snow cover (and therefore subnivean habitat) and create phenological mismatches in abiotic cues (e.g. misalignment of temperature and photoperiod) that affect fitness (Walker *et al.,* 2019). Some species may benefit from excess anthropogenic heat; for example, ravens (*Corvus corax*) which roost near heat sources during the winter (Peebles and Conover, 2017), presumably to reduce energetic costs of thermogenesis. However, such cases appear to be an exception. Thermal pollution can also occur in aquatic environments due to wastewater effluent from industries or power plants. The addition of warmed water during the winter alters the spawning phenology of some fish species (Firkus *et al.,* 2018) and can create ecological traps (i.e. warmer waters are selected by overwintering fishes, but this subjects overwintering individuals to elevated levels of contaminants, predation and competition; Mehdi *et al.,* 2021). The distribution of some pollutants can also vary seasonally, with increased exposure risk for wildlife during the winter. For example, organisms active in urban areas during the winter experience increased air pollution in the form of smog, which reaches higher concentrations in winter due to increased burning of fossil fuels for heat and transportation (Hauck *et al.,* 2016). Future research, management and policy must consider the interactive and additive biological effects of thermal, light and chemical pollution on wintering organisms.

10. Geological events

Though geological mass movements (e.g. landslides, avalanches, rock falls) occur infrequently, they are important disturbance events that shape ecosystems (Cooke *et al.,* 2022). For example, forested communities impacted by mass movements often show altered structure following disturbance, typically characterized by smaller, shorter trees, shade intolerant species, lower stem densities and greater structural diversity compared to unaffected subalpine forests (Bebi *et al.,* 2009; Restrepo *et al.,* 2009; Hilton *et al.,* 2011). These disturbed communities can provide unique habitats for various animal and plant species that contribute to higher overall alpha and beta biodiversity (Bebi *et al.,* 2009). Additionally, paths carved out by mass movements are valuable foraging areas for large predators. For example, post-denning grizzly bears (*Ursus arctos*) often seek out these areas to scavenge carrion killed over the winter (Butler, 2012).

Climate change is altering these disturbance regimes. Notably, winter landslides are predicted to increase in frequency because of increased winter precipitation, increased freeze/thaw cycles and permafrost thawing (Patton *et al.,* 2019; Sobie, 2020). Predicted changes in avalanche frequency and intensity are less clear due to uncertain trends in snow fall, extreme weather conditions and differences in regional characteristics (Reardon *et al.,* 2007). However, there will likely be an increase in the ratio of wet to dry avalanches in alpine forested areas, with decreased avalanche frequency in lower elevation forests where rising temperatures will reduce the number of possible heavy snowfall events (Bebi *et al.,* 2009). Efforts should be made to identify areas at risk of avalanche or landslide events to best manage the species in these areas and to predict how they may respond in the future. If species-at-risk are located in such areas, species translocations to more stable regions may be beneficial.

11. Climate change & severe weather

The disproportionate warming of winter months in cold-climate regions has changed central tenets of the winter landscape that continue to drive broad ecological consequences. Gradual reductions in winter snowpack, driven by an increased incidence of rain relative to snow and increased extreme warming events during winter, have led to more frequent weather whiplash (rapid high-amplitude fluctuations in weather conditions; Casson *et al.,* 2019). Many terrestrial organisms rely on sufficient snow depth for surviving winter months; snow cover improves hunting success/top-down control of large and small herbivores (Gese and Grothe, 1995; Ylönen *et al.,* 2019), can act as a barrier to overwinter herbivory/predation (Merritt *et al.,* 2001; Simons *et al.,* 2010; Guiden *et al.,* 2019; Ylönen *et al.,* 2019), and can function as critical thermal refugia (Penczykowski *et al.,* 2017). A lack of sufficient snow cover can also lead to a greater depth, duration and severity of soil freezing and occurrence of soil freeze/thaw cycles. This can result in a cascade of negative impacts on northern hardwood forests such as reduced arthropod abundance and diversity (Templer *et al*., 2012), and increased root mortality and damage leading to impaired vegetation growth (Comerford *et al*., 2013; Campbell *et al.,* 2014; Reinmann *et al*., 2019). Weather whiplash also causes severe weather events such as rainstorms followed by freezing that encases ground-level vegetation in ice, reducing the already limited resources available for herbivores during winter (Hansen *et al.,* 2010; Korslund and Steen, 2006). Such events have been linked to reduced survival, reproduction and range shifts in ungulates and small mammals (Aanes *et al.,* 2000; Stien *et al.,* 2010). Severe or uncharacteristic cold snaps are responsible for decreased survival and condition of organisms, and in extreme cases cause mass mortality events (Anthony and Willis, 2009; Schwemmer *et al.,* 2014).

Warming winters and the loss of snow and ice also pose unique conditions for aquatic life. Notably, as most aquatic organisms are ectothermic, warmer winter water temperatures will increase overwintering metabolism. It is likely that fish species with dissimilar temperature optima (e.g. cold-water adapted and warm-water adapted fish, see Coker *et al.,* 2001) will be differentially impacted by this warming, altering communities and potentially resulting in biodiversity loss (Shuter *et al.,* 2012; Kao *et al.,* 2015). For example, warm-water species may benefit from elevated water temperatures provided that energy consumed exceeds overwintering metabolic costs, benefitting growth, reproduction and survival. Conversely, cold-water species may suffer if sufficient resources cannot be acquired to sustain overwintering metabolic costs, negatively impacting growth, reproduction and survival. Some species are already displaying negative reproductive success in response to warmer, shorter winters.

For instance, following warm, short winters, yellow perch *(Perca flavescens*) egg size, egg energetic and lipid content and hatching success are reduced; although it is unclear whether such reductions result from metabolic or maternal endocrine disruptions (Farmer *et al.*, 2015). More research is needed to determine how aquatic species and communities will respond to increasing overwintering energetic demands and altered seasonal abiotic cues (Fernandes *et al.*, 2022).

In marine environments, reductions in sea-ice appear to be increasing primary production due to earlier ice breakup and warmer spring temperatures which may result in increased zooplankton and fish production (Loeng *et al.*, 2005; Hamilton *et al.*, 2013). However, earlier ice breakup may negatively impact food webs by shifting the phenology of spring blooms, creating a mismatch in timing between primary and secondary producers (Leu *et al.*, 2011). Moreover, warming will result in the colonization of novel species (see *8. Invasive & other problematic species & diseases*) and favour disturbance-tolerant species, leading to changes in phytoplankton species composition (Moran *et al.*, 2010). Similar changes are expected in freshwater systems (Shuter *et al.*, 2012). These changes may alter food webs and ecosystem carbon flow (O'Connor *et al*., 2009). Additionally, clear ice can pass up to 95% of the photosynthetically available radiation (Bolsenga and Vanderploeg, 1992), providing a vast, seasonally available habitat on which phytoplankton can grow. These ice-associated algae are significant contributors to winter food webs and support a multitrophic range of consumers (Melnik *et al.*, 2008). In some areas, under-ice primary production frequently exceeds that of the ice-free period such as in Lake Baikal and Lake Haruna (Maeda and Ichimura, 1973; Hampton *et al.*, 2008). Unfortunately, little research exists on these unique ice-algae communities, especially in freshwater environments (Hampton *et al.*, 2015). As in many cold-climate systems, an improved understanding of the winter biology of these environments is needed to anticipate the directionality and severity of the consequences brought on by warming and reductions in ice cover.

Warmer and shorter winters are also altering ecologically important phenologies. Many biologically important events are intimately tied to the recession of winter and onset of spring. Organisms often use environmental cues to accurately time important life history events (e.g. arousal from dormancy, reproduction) to match with a window of optimal environmental conditions. Many plant and animal phenologies are advancing as a result of warming winters (Bernard, 2014; Forrest, 2016; Ettinger *et al.*, 2020). However, organismal phenologies are shifting at different rates due to species-specific mechanisms and therefore, unbalanced shifts in phenologies can result in detrimental mismatches. For example, Kudo and Ida (2013) reported that the flowering of *Cordyalis ambigua* often occurred before first pollinator detection (bumble bees; *Bombus spp.*) following early snowmelt, resulting in lower seed production. Such mismatches can have severe consequences and may result in biodiversity loss (Visser and Both, 2005). However, changes to phenology are not necessarily negative and in some instances could be adaptive (e.g. the change in phenology maintains or improves organismal performance or fitness) (Visser *et al.*, 2012; Visser and Gienapp, 2019). However, most shifts in phenology lead to mismatches with organisms on which the target species depend (see review by Visser and Both, 2005).

Relevance of Winter to Conservation and Management Actions

From a conservation perspective, winter is often underappreciated. Suitable summer and breeding habitat are regularly identified and afforded strict protections, while the protection of winter habitat in cold-climates (not to be confused with the winter habitat of migratory species which travel south to warmer climates to overwinter) is frequently ignored or lacking the specificity needed for comprehensive species conservation (Cunjak, 1996; Courtois *et al.*, 2004; Simons-Legaard *et al.*, 2018; Goldberg *et al.*, 2020). In this section, we consider how winter can be integrated more effectively into various conservation and management actions. Using the IUCN-CMP *Conservation Actions Classification Needed* working document (Version 2.0; IUCN, 2022a) as a guide, we demonstrate practical winter conservation and management actions that could help maintain or promote biodiversity and resilience across terrestrial and aquatic ecosystems (for more details on the conservation and management action categories, see Table 2). It should be noted that, to reduce repetition, some sections have been combined.

1. Site/area & habitat/resource protection

Habitat protection regulations typically recognize the importance of wintering habitat, but do not specify the characteristics of those areas (e.g. Courtois *et al.*, 2004). In part, this lack of specificity results from an inadequate understanding of species-specific winter habitat requirements which impairs our ability to protect these areas (Weller *et al.*, 2018). A logical first step is to identify and characterize critical winter habitat, for which several tools already exist. For example, satellite, thermal infrared imaging and aerial surveys can be used to assess land use by wintering mammals (Fortin *et al.*, 2008; Atuchin *et al.*, 2021) and locate potential thermal habitats or refugia for fish (Brown *et al.*, 2011; O'Sullivan *et al.*, 2019). These methods can also be used to assess the efficacy of winter habitat protection in already established protected areas (Simons-Legaard *et al.*, 2018). Radiotelemetry or other locational devices can be useful in identifying key overwintering locations used for winter refugia (Browne and Paszkowski, 2010; Martino *et al.*, 2011; Taylor *et al.*, 2016; Goldberg *et al.*, 2020; Roe and Bayles, 2021). For larger mammals (e.g. bears), traditional tracking methods can also be useful for identifying winter refugia (Tammeleht *et al.*, 2020), and eDNA surveys can identify aggregations of brumating, freshwater turtles (Feng *et al.*, 2020). Further,

Table 2: Summary of the IUCN-CMP Unified Classification of Conservation Actions Needed (Version 2.0) detailing which threats should be included in each section

[a]IUCN-CMP Unified Classification of Conservation Actions Needed Exposition	
1. Site/area & habitat/resource protection	Includes actions to identify, establish or expand parks and other legally protected areas, as well as actions directed at conserving sites, habitats and the wider environment. This class contains all actions designed to directly protect biodiversity through parks, reserves, easements, or other similar means and contains all actions involved in directly managing habitats.
2. Invasive/problematic species control & limiting population growth	Controlling and/or preventing invasive and/or other problematic plants, animals and pathogens. This could arguably fit into *1. Site/area & habitat/resource protect*, but it is such a vital action it gets its own category. Limiting populations includes actions such as culling to keep a population within park carrying capacity, the sterilization of animals and other similar methods.
3. Habitat & natural process restoration	This category involves the restoration of degraded lands and natural processes opposed to the protection of existing ones.
4. Harvest & trade management	This class contains all actions involved in directly managing the harvest and trade of species. For example, setting fishing quotas, catch-size limits, trade regulations for specific populations, etc.
5. Species reintroductions & ex-situ conservation	Re-introducing species to places where they formerly occurred or benign introductions and protecting biodiversity out of its native habitats. Reintroductions are to areas where the species formerly occurred; benign introductions are to areas outside of the species' historic range, but within an appropriate habitat and are done deliberately for conservation reasons. This class also includes actions such as captive breeding, propagation of plants from seeds or cuttings, the artificial propagation of plants and other similar methods where conservation efforts seek to protect biodiversity outside of its native habitat.

[a]Note that these sections are combined or otherwise slightly modified from the original IUCN-CMP Unified Classification actions need working document

biologging devices can help record important variables like depth and temperature preference, allowing researchers to continuously monitor important trends in habitat use and physiological changes across winter months (Robichaud *et al.*, 2022; Reeve et al., In Prepartion). This information can then be used to identify ideal overwintering refugia and to assess the energetic costs of overwintering. Locating these areas is especially important considering that many species form winter aggregations in these refugia (Suski and Ridgway, 2009; Browne and Paszkowski, 2010; Taylor *et al.*, 2016; Weller *et al.*, 2018) and some species show strong long-term site fidelity (Smith, 2009; Bunt *et al.*, 2021). If species-specific habitat characteristics or overwintering locations are known, predictive models could be developed to inform habitat protection (Fortin *et al.*, 2008; Browne and Paszkowski, 2010; Tammeleht *et al.*, 2020). Importantly, once these areas are identified, efforts could be made to protect this winter habitat to maintain biodiversity.

Many species show profound inactivity to reap energetic savings during the resource-limited winter period (e.g. hibernation, torpor, brumation, dormancy). As a result, winter ranges in cold climates are often smaller than that of summer ranges and many species form tight aggregations (Allee, 1927). Thus, the protection afforded to winter habitat may not need to be expansive and, in some instances, small protected areas may be sufficient to effectively protect a given population. For example, in British Columbia, Canada, small protected areas (termed "wildlife habitat areas") were established based on communal overwintering sites to protect great basin gopher snakes (*Pituophis catenifer deserticola*), a known species of concern (Willams *et al*., 2012). However, careful consideration of species-specific winter habitat and continued monitoring is important to ensure the success of such protected areas. Some species may find refuge in urbanized or developed areas which may require creative solutions to provide protection. Bats, for example, hibernate in mines, urban drainage systems, tunnels, abandoned buildings and other anthropogenic developments (Baranauskas, 2006; Wojtaszyn *et al.*, 2013). Where applicable, restricting human access (e.g. using grilles or gates) to bat hibernacula has a positive effect on local population growth (Voute and Lina, 1986; Crimmins *et al.*, 2014). Importantly, the conservation of critical winter habitat supports the recovery of populations of concern, such as caribou (Wittmer *et al.*, 2005).

2. *Invasive/problematic species control & limiting population growth*

The monitoring and control of invasive and problematic species may be more effective in the winter. For example, winter burning has been used to control invasive plant species as winter burns are less likely to result in damage to human infrastructure (Middleton, 2002). Additionally, some overwintering species display aggregating behaviour, resulting in large portions of a given population inhabiting small areas for an extended period of the year (Allee, 1927). If aggregations of invasive or problematic species can be located, efforts can be streamlined, reducing removal costs and leveraging methods such as the Judas technique (tracking the movement of a "Judas animal" using electronic tags to locate conspecifics). This method is effective for species that aggregate during winter or exhibit narrow winter habitat preferences (Bruckerhoff *et al.*, 2021; Hessler *et al.*, 2021; Shaw *et al.*, 2021). Tracking "Judas animals" has been used to locate aggregations across several taxa (Taylor and Katahira, 1988; Woolnough *et al.*, 2006; McCann and Garcelon, 2009; Bajer *et al.*, 2011) and could be especially effective for locating invasive or problematic conspecifics during the winter. For example, Bajer *et al.* (2011) radio-tagged several common carp (*Cyprinus carpio*; one of the world's most invasive fish species) to locate larger aggregations during the winter which resulted in high removal rates (52–94%). This method may also be useful in conservation efforts to help identify critical overwintering locations or to locate species at risk.

Additionally, other forms of control benefit from reduced vegetation in winter. Trapping and hunting success is typically higher in the winter due to decreased resources and reduced vegetation, which can aid in the control of problematic mammalian species (Bonesi *et al.*, 2007; Rushton *et al.*, 2010; Lieury *et al.*, 2015). The use of aerial surveys to monitor animals may also be more effective in the winter. In particular, drones or planes equipped with thermal infrared imaging is an emerging technique to monitor large mammals. A thinner canopy layer and strong contrast between ambient temperature and the body temperature of the animal improves detection relative to other seasons. Researchers have already found this technique to be useful in monitoring ungulate populations such as wild boar and deer (Witczuk *et al.*, 2017; Atuchin *et al.*, 2021 preprint; Kim *et al.*, 2021). Once located, more targeted removals can be employed if needed.

3. Habitat & natural process restoration

Though underappreciated, winter is particularly relevant when planning for environmental restoration. Winter creates unique conditions that must be considered to ensure that restoration efforts are effective. For example, the cold tolerance of plants used for restoration needs to be considered as demonstrated by failed attempts to restore American chestnut (*Castanea dentata*) in the north-eastern United States (Gurney *et al.*, 2011). Similarly, fish stocking programs should consider the impacts of body condition during stocking, the availability of suitable winter habitat and winter temperatures on their overwinter survival and post-winter fitness to improve stocking success (Miranda and Hubbard, 1994; Quinn and Peterson, 1996; Fullerton *et al.*, 2000). Restoration efforts that consider species-specific physiology would ensure that restoration efforts create environmental conditions that are favourable to the native biota and could be used to refine restoration efforts (Cooke and Suski, 2008) but there is little evidence that such approaches were common when planning, doing, or assessing restoration.

In general, efforts to understand and incorporate the environmental requirements of species during winter (e.g. thermal stability that contributes to energy conservation for hibernators) into restoration could dramatically improve restoration success (Cowan *et al.*, 2021). For some small mammal and fish species where specific winter habitat is limited, the addition of structures can enhance overwinter survival and benefit population growth (Hodara *et al.*, 2000; Solazzi *et al.*, 2000; Sullivan *et al.*, 2012). Notably, the erection of artificial structures that mimic natural hibernacula benefit a range of organisms including newts (Latham and Knowles, 2008; Dervo *et al.*, 2018), snakes (Zappalorti *et al.*, 2014) and burrowing owls (*Athene cunicularia hypugaea*; Keppers *et al.*, 2008). However, consideration must be taken when selecting areas for structural enhancement. For example, Barrineau *et al.* (2005) assessed the effectiveness of instream restoration structures and found that when used in areas with groundwater influx, the addition of the structures led to significant frazil and anchor ice, both of which increase the risk of injury and mortality in fish. For larger animals, the restoration of suitable winter habitat may require the removal of anthropogenic developments which fragment critical habitats (see *1. Residential & commercial development* for more information on the impacts of anthropogenic developments) and reductions in human activity (see *6. Human intrusions & disturbance* for more information on the impacts of human activities). In Scandinavia, efforts to regulate human traffic, relocate trails and remove infrastructure and cabins were effective in facilitating the return of caribou to their historic winter ranges (Nellemann *et al.*, 2010). Moreover, for these efforts to be most effective, suitable protection must be afforded to these areas (see *1. Site/area & habitat/resource protection* for more information).

4. Harvest & trade management

Changing winter conditions are already impacting economically important species. For example, sufficient ice cover and/or winter length influences reproductive success in a number of fish species (Farmer *et al.*, 2015; Fernandes *et al.*, 2021). Therefore, recruitment following warmer winters and poor ice cover may be below projections that fail to incorporate changing winter conditions (Farmer *et al.*, 2015). In this context, applying adaptive fisheries management that accounts for the consequences of contemporary winter conditions on a rolling basis would prove beneficial. Additionally, for species that are known to be particularly sensitive to warming winter conditions, managers may seek to improve or restore critical winter habitat (see *3. Habitat & natural process restoration* for more details). Similarly, the production and survival of large game mammals can be strongly mediated by winter conditions. In winter-tolerant ungulate species like moose (*Alces alce*s), milder winters with recurring temperatures above their winter-time thermal maximum (−5°C) can cause heat stress (Renecker and Hudson, 1986). Warmer winters are also expected to improve the survival and incidence of ectoparasites, like the winter tick (*Dermacentor albipictus*), which already contributes substantially to moose winter mortality (23% of winter mortalities in Minnesota; Wünschmann *et al.*, 2015). Conversely, the geographic range of white-tailed deer *(Odocoileus virginianus*) is expected to increase as their northern range limits are largely constrained by the severity of northern winters (e.g. snow depth, minimum winter temperatures; Dawe *et al.,* 2014). Increased interaction strength between deer and moose may exacerbate disease transmission and drive further declines/range modifications in moose populations (Lankester, 2010). Considering this compounded pressure on moose population, increased harvest limits for white-tailed deer in regions where range expansions are expected and prioritizing the protection of critical moose habitat (especially wetlands) may help slow the disease-mediated decline of southern moose populations (see review by Weiskopf *et al.,* 2019). Milder winters are driving similar changes to the strength and geographical extent of ecological interactions across ecosystems (McMeans *et al*. 2020). The use of adaptive management will become increasingly necessary as these new and changing ecological dynamics begin to redefine northern ecosystems.

Unfortunately, our ability to predict how populations, communities and ecosystems will respond to changing winter conditions is constrained by our limited understanding of winter biology, complicating management decisions and policymaking. Implementing adaptive management practices will likely be necessary to appropriately handle this uncertainty and properly manage and allocate natural resources with unknown responses to rapidly changing winter conditions. Adaptive management is a cyclical iterative process which evaluates the results of past actions to inform and adjust future actions, thereby providing a useful framework for addressing and directing management decisions in changing ecosystems (Argent, 2009). Using this framework, management actions can not only function to manage biological resources under changing winter conditions, but can also help to identify and address future knowledge gaps.

5. Species reintroductions & ex-situ conservation

Species reintroduction is a well-established conservation practice where an organism is translocated to an area to re-establish a viable population of the focal species in a once extirpated region. The success of a given reintroduction program depends on a thorough understanding of the target species' ecology. In some instances, the target species' ecology is well matched for winter reintroductions. For example, bear reintroduction programs yield greater success when conducted in the winter, as the translocation of denning females with their young significantly reduces the likelihood of homing behaviour (a frequent challenge in bear reintroductions), increasing survival (Clark, 2009). Additionally, understanding the necessary habitat requirements of the target species is important in influencing the success of the reintroduction program. For some species, such as redside dace (*Clinostomus elongatus*), an inadequate understanding of winter habitat requirements could present roadblocks for their reintroduction success (Lamothe *et al.,* 2019). If the ideal winter habitat is known for a given species, such information should be used to identify appropriate reintroduction locations which can be further supported by predictive spatial modelling (Bleyhl *et al.,* 2015).

Ex-situ conservation is closely linked to re-introductions in that organisms generated in captivity are ideally released/-planted into the wild. *Ex-situ* conservation focuses on organisms (or germ cells) that have been collected in the wild and brought to zoos (Conde *et al.,* 2011), aquaria (Gusset and Dick, 2010), botanical gardens (Chen and Sun, 2018), seed/germ banks (Hamilton, 1994; Hiemstra *et al.,* 2006), or similar facilities to enable controlled propagation or storage or reproductive tissues for future use (Miller *et al.,* 2004). Such programs tend to be a last resort when *in-situ* conservation efforts fail and often involve reproductive science to increase the number of organisms (Holt *et al.,* 2003, 2014). From a winter context, there is little published that is specific to *ex-situ* conservation. Ideally, captive breeding programs mimic the environmental conditions the target population experiences in the wild. To that end, winter (or emergence from winter) can be necessary to trigger germination of some seeds (Nichols, 1934). Some mammals have long gestation periods that coincide with extended hibernation (e.g. brown bears, *Ursus arctos*; Friebe *et al.,* 2014), such that successful captive rearing involves recreating such conditions, or delayed ovulation (e.g. some temperate Vespertilionid bats; Buchanan, 1987; Wang *et al.,* 2008), which limits breeding success in captivity because the required conditions are unknown (e.g. Davy and Whitear, 2016). Another key aspect of *ex-situ* conservation is to ensure that the captive and wild conditions are similar so that, once released, organisms are not completely naive to the natural environment (Pritchard *et al.,* 2012). In that sense, ensuring that organisms are adequately prepared for winter prior to release/planting is essential for long term success. For example, if animals are being released prior to (or during) winter, then adequate energy reserves would be needed. For ectothermic animals, adequate time would be needed to acclimate to conditions anticipated in the field (Williams *et al.,* 2015; Carstairs *et al.,* 2019), whereas winter hardiness may need to be established (within biological constraints) in plants to reduce likelihood of post-planting mortality (Arora and Rowland, 2011). Determining the ideal time to release/plant organisms is also critical, especially in regions with distinct seasons (e.g. cold winters). Although winter is rarely considered in *ex-situ* conservation, it will be an important area of research and practice moving forward.

Synthesis and Conclusions

Winter in cold-climate regions is inherently challenging for biological life (physiological challenges that can result in mortality of individuals and alterations in populations, communities and ecosystems) and has therefore been the subject of much fundamental research to understand winter adaptations and organism-environment relationships (e.g. identifying physiological tolerances to cold conditions). Yet, winter

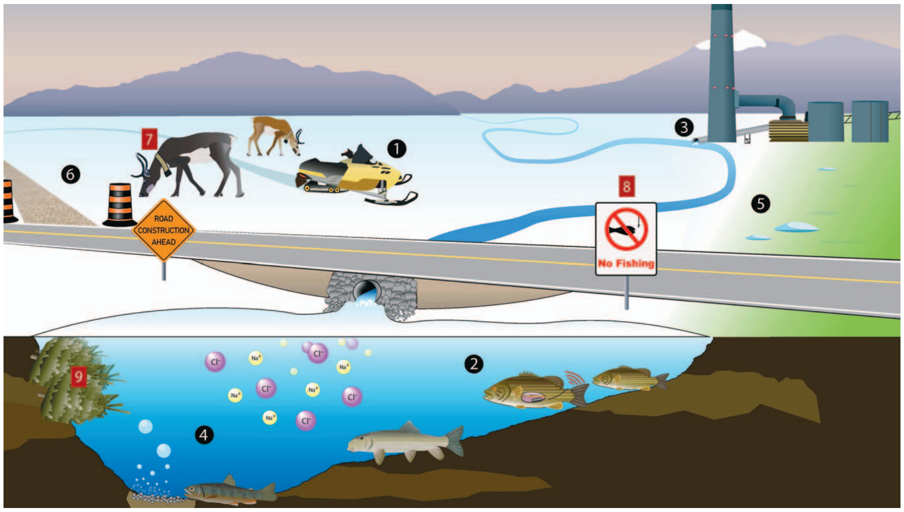

Figure 1: Examples of winter threats and conservation and management actions. Threats are shown using black circles: (1) anthropogenic disturbance to wintering wildlife (e.g. caribou: Ranger tarandus) such as those introduced by motorized vehicles; (2) poleward migrations of more southern species like smallmouth bass (Micropterus dolomieu), pictured here in our northern stream, and their interactions with wintering species (e.g. white sucker: Catostomus commersonii; brook trout: Salvelinus fontinalis); (3) pollution during winter, commonly in the form of thermal effluent from power plants and road salt inputs from roadways; (4) the understudied nature of winter, exemplified by our poor understanding of the characteristics and locations of critical winter habitat (e.g. groundwater upwellings) and consequences of winter disturbances (e.g. road salt pollution); (5) shifting phenologies of flora and fauna commonly signalled by earlier snowmelt and warmer winter temperatures; and (6) winter habitat loss from anthropogenic development (shown here is the construction of a new road). Conservation and management actions are shown using red squares: (7) locating and protecting critical winter habitat using tools like radio telemetry via collars (pictured here on caribou) or tags (which can be observed in the smallmouth bass); (8) adaptive management of natural resources leveraging strategies like flexible harvest windows; (9) habitat restoration/enhancement through the addition of critical habitat structure. This is not an exhaustive list and instead functions to highlight some of the more important threats and actions discussed. It should be noted that any singular threat highlighted here has numerous consequences to winter biota and could threaten biodiversity if not adequately dealt with or managed. Moreover, consideration should be taken whenimplementing these conservation and management practices to ensure their effectiveness. For example, inadequate habitat restoration can be harmful if implemented incorrectly (see 3. Habitat & natural process restoration for more details).

is also highly relevant for conservation and management of biological resources. Here, we examined the ways in which anthropogenic threats are relevant to winter and considered the relevance of different management and conservation actions to winter. We used well-established threat and action taxonomies to focus our efforts. For all the common threats explored here, there is evidence that they are as relevant to winter as they are for other seasons (Fig. 1 highlights winter-specific threats and actions). Moreover, climate change will intersect with baseline winter conditions and other stressors to potentially magnify threats and further complicate management (Dietz *et al.*, 2021; Srivastava *et al.*, 2021). For all management and conservation actions, we identified potential or existing relevance to winter. Many of the examples identified were quite recent, which could reflect a turning point in the importance of applied winter biology.

Perhaps the clearest conclusion arising from this synthesis is recognition that there is need for more research to understand the complex ways in which diverse anthropogenic threats (ranging from existing to emerging threats) manifest in winter to impact biological mechanisms and systems (Sutton *et al.*, 2021). Moreover, there is a need to better understand how various management and conservation activities can be used to avoid or mitigate those threats (Cunjak, 1996; Sutton *et al.*, 2021). Like Studd *et al.* (2021), we emphasize that winter is a unique season that requires explicit consideration for the conservation and management of biological resources. It is well-established that winter is understudied relative to other seasons (Sutton *et al.*, 2021). Yet, we suggest that winter is also overlooked when it comes to understanding threats and applying management and conservation interventions. There are some instances where winter creates unique opportunities that can be exploited by environmental managers (e.g. winter prescribed burns, removal of some invasive species) but for the most part, management actions, especially those that involve active intervention, are not used. Our synthesis revealed that there is a need for more active management of threats in winter or to consider how threats in other seasons may carry over to influence threats during winter (O'Connor and Cooke, 2015). There are many ways to make meaningful progress, from reforming the training of future resource managers and conservation practitioners (to include more winter-relevant content and case studies) to creating development opportunities for practicing professionals (Studd *et al.*, 2021). In addition, there are many unanswered questions about winter biology (spanning taxa, levels of biological organization and types of mechanisms/disciplines) that need to be addressed to better inform conservation and management actions (see Sutton *et al.*, 2021). Any and all efforts that elevate understanding of the relevance of winter to conservation and management has the potential to improve the state of biological resources during all seasons.

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Data Availability Statement

This is a synthesis article so there are no data or code to share.

Conflict of Interest Statement

Cooke is the Editor in Chief of the journal Conservation Physiology. The paper was handled at arms length from Cooke as per COPE guidelines to ensure integrity of the editorial process.

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