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Winter is changing: trophic interactions under altered snow regimes

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Abstract

Shifts in abiotic conditions can strongly influence not only the demography, ecology, and evolution of individual species, but also the networks of interactions that structure communities and ecosystems. Though many studies have addressed how changes in mean temperature or rainfall patterns will affect ecosystems, there has been far less attention on the impact of changing snow regimes. As climate change alters the abundance and persistence of snowpack in temperate and polar regions of the globe, novel reductions or accumulations of snow may dramatically impact the nature of interactions between organisms in these ecosystems. In this review, we focus on four major mechanisms by which snow cover affects food webs, by (1) generating an insulated subniveal environment, (2) providing a physical or visual refuge from consumption, (3) affecting movement of animals across landscapes, and (4) driving phenology. For each of these mechanisms, we explore examples of observational and experimental studies that have addressed the role of changing snow conditions on food web processes. Then we highlight open questions regarding the influence of changing snow cover on trophic interactions, and suggest types of experiments and tools that could advance this field of research. We conclude that more experimental work is needed to understand the net effect of altered snow cover for food webs, particularly because snow cover may simultaneously affect multiple trophic levels through different mechanisms.

Keywords: climate; insulation; movement; phenology; refuge; snowpack

1. Introduction

Understanding how climate change affects not only single species, but entire food webs, is critical for anticipating shifts in ecological communities and the ecosystem services they provide. Accordingly, recent studies have focused on food web or ecosystem responses to increasing temperatures or altered precipitation patterns (Barton and Ives, 2014; Ockendon et al., 2014; Rosenblatt and Schmitz, 2016; Van der Putten et al., 2010; Walther, 2010). However, more than 30% of earth's land mass – nearly all within the Northern Hemisphere – can be covered with snow for at least part of the year (Lemke et al., 2007). In such places, effects of climate change on food webs may be partly driven by altered snow regimes (Cooper, 2014). Snow is a major habitat feature and driver of phenology, yet the potential for changes in snow cover to affect the structure or dynamics of food webs has received less attention than other aspects of climate change.

The need for understanding how altered snow regimes impact food webs is particularly urgent because anthropogenic climate change is occurring most rapidly in regions of the world that have historically had cold, snowy winters (Anisimov et al., 2007; Vaughan et al., 2013). In the Northern Hemisphere, the duration of snow covered ground decreased by 5.3 days per decade from winter 1972/1973 to 2007/2008, due to earlier spring snowmelt (Choi et al., 2010). Spatially, the average areal extent of snow covered ground in March and April in the Northern Hemisphere decreased by 0.8% per decade (90% confidence interval: 0.5–1.1%) per decade from 1922–2012, and at the substantially faster rate of 2.2% per decade (90% CI: 1.1–3.4%) within the last three decades (1979–2012) of that time period (Vaughan et al., 2013). However, in some regions (e.g., northern high latitudes), projected increases in precipitation during winter may yield greater annual snow cover (Collins et al., 2013). Consequently, our review will cover food web responses to scenarios of both increased and decreased annual snow cover.

There are several interrelated mechanisms by which changes in the amount, timing, and persistence of snow cover can affect food webs. At the heart of these mechanisms are the physical properties of snowpack (Fig. 1). The insulating capacity of snow (*section 2*) creates vertical structure in the snowpack (*section 2.1*), and directly promotes the overwinter survival of a variety of organisms at different trophic levels (*section 2.2*). Snow crystals reflect solar radiation, thereby contributing to snowpack persistence (i.e., because less solar energy is absorbed to melt it), but also limiting primary production under snow (*section 2.3*). However, trophic interactions – even entire food webs (Aitchison, 1984; Bokhorst and Wardle, 2014) – may be facilitated by the insulation of snow cover (*section 2.4*). Organisms under snow may benefit not only from the insulating shelter from cold air, but also derive physical protection from consumers (*section 3*). Snowpack can serve both as a physical barrier to consumers (*sections 3.1 and 3.2*) and a visual refuge for cryptically colored (i.e., white) organisms (*section 3.3*). In addition, some animals may use snow as a refuge from parasites (*section 3.4*) or to store and protect caches of food (*section 3.5*). Snow can influence predation above the snowpack as well, by directly inhibiting movement of attacking predators or escaping prey (*section 4*). Finally, when snow melts, the increased availability of light and liquid water triggers emergence of many plants and invertebrates; thus, changes in the timing of snow melt may generate phenological mismatch, or novel interactions, between consumers and resources (*section 5*). In discussing these mechanisms by which snow cover affects food webs, we draw insight from key literature. We then conclude by recommending types of experiments and tools that could be useful for addressing open questions on this topic and improving predictions of population, community, and ecosystem responses to changing winter conditions (*section 6*).

2. Snow cover as insulation

2.1. Insulating properties of snowpack

The insulating properties of snowpack stem from the low density arrangement of ice crystals in fresh snow (Fig. 1; (Singh, 1999; Sturm et al., 1997)). As snow accumulates, ice crystals fuse together and the density and mechanical strength of the snowpack increases (Colbeck, 1983). However, this internal compaction is counteracted by an upward movement of water vapor which creates open space at the base of the snowpack (Colbeck, 1983). During this process, heat emitted from the ground warms the base of the snowpack, while heat and moisture are lost from the top of the snowpack to the colder, drier air above. Diffusion of water vapor upward through this gradient of temperature and humidity generates more water vapor through sublimation at the base of the snowpack, leading to the creation of an open, snow-free subnivean space (the “subnivium”, (Pauli et al., 2013)) that can serve as an insulated shelter for a diverse range of taxa ((Aitchison, 2001; Pruitt, 1970), and examples below). Given sufficient snow depth (ranging from ca. 15–20 cm in relatively mild climates to ca. 25–30 cm in colder climates), this space is maintained at near 0 °C and 100% water saturation even when temperatures above the snowpack are much colder (Aitchison, 2001; Pruitt, 1970).

A variety of forces can collapse the subnivean space and diminish the insulating properties of snowpack. On small spatial scales, the subnivean space can be destroyed and thermal conductivity of snow can be increased by compaction from vehicles (e.g., snowmobiles, (Neumann and Merriam, 1972; Pesant, 1987); skis, (Hadley and Wilson, 2004)) or large animals

(Creel and Christianson, 2009). Melting due to warm air temperatures or rain can cause deterioration of snowpack on a much larger spatial scale (Vaughan et al., 2013). Rain-on-snow events not only destroy the subnivean space and insulating capacity of snow, but subsequent freezing also creates ice layers that block herbivores from their forage plants and block the exchange of gases with the atmosphere (Cooper, 2014; Williams et al., 2015).

2.2. Direct effects of insulation on overwinter survival

Many terrestrial organisms in the Northern Hemisphere rely on the insulating properties of snow in order to survive winter (Aitchison, 2001). As such, the amount and duration of snowpack may set limits for these organisms and determine their influence as resources and/or consumers in food webs.

Microbes

Insulating snow can also promote overwinter survival and activity of microbes. While viable cells of spore-forming and non-forming bacteria have been isolated from Siberian permafrost layers dated at ca. 40,000 years old (Bakermans et al., 2003), survival and/or growth of bacteria and fungi is typically enhanced by insulating snow cover (Aanderud et al., 2013; Bokhorst and Wardle, 2014; Larsen et al., 2007; Monson et al., 2006; Nikrad et al., 2016; Penczykowski et al., 2015). In temperate and subalpine forests, distinct soil microbial communities can be found in winter and growing seasons (Aanderud et al., 2013; Monson et al., 2006), suggesting that seasonal snow cover may promote microbial diversity over annual scales. Changes in microbial community composition, including shifts from dominance by bacteria to fungi during winter, may contribute to temporal patterns in nutrient mineralization (Aanderud et al., 2013; Larsen et al., 2007). Rates of respiration by soil microbes have been shown to increase with the warmer temperatures provided by deeper snowpack in mid- as well as high-latitude ecosystems (Aanderud et al., 2013; Larsen et al., 2007; Monson et al., 2006; Sullivan et al., 2008). In a high-latitude heath, total soil respiration during late winter and spring-thaw was approximately half of net primary production during the growing season, suggesting that microbial respiration under snowpack can play a substantial role in annual carbon budgets (Larsen et al., 2007). During spring snowmelt, microbial biomass can vary over short time intervals, likely due to a combination of mortality from stressful freeze-thaw events and increased grazing by subnivean invertebrates (Larsen et al., 2007). The lysing of microbial cells during such die-off events releases microbial nutrients that can be rapidly taken up by surviving microbes and emerging plants (Larsen et al., 2007).

Plants

Freezing temperatures can directly reduce the overwinter survival of vascular plants through mechanisms including frost damage to above-ground tissues, freezing injury to root systems, and impaired uptake of water and nutrients from frozen soil (Blume-Werry et al., 2016; Charrier et al., 2015; Kreyling, 2010; Tierney et al., 2001). However, snow cover can ameliorate these potential causes of damage and mortality to plants. Experimental manipulation of snowpack in a boreal forest demonstrated that snow protects understory dwarf shrubs from frost damage to above-ground tissues (Blume-Werry et al., 2016). Moreover, by keeping soil from freezing, snowpack protects fine root structures from injurious physical stresses of ice formation, and decreases plants' risk of desiccation and nutrient limitation. Such protective effects of snow on root structures have been experimentally shown for perennial grasses (Vankoughnett and

Henry, 2013), mature trees (Charrier et al., 2015; Gaul et al., 2008; Tierney et al., 2001), and understory plants (Blume-Werry et al., 2016; Kreyling et al., 2012). Reduced snowpack and more frequent freezing of soil can affect plant communities by decreasing overwinter survival of susceptible taxa (Blume-Werry et al., 2016; Kreyling et al., 2012), which would translate into an altered resource base for herbivores. Moreover, freezing damage to root and soil microbial cells releases nitrogen (N) into the soil at a time when plant uptake of nutrients is impaired; thus, lack of snow can enhance N losses from soil and alter nutrient cycling through the ecosystem (Gaul et al., 2008; Tierney et al., 2001; Vankoughnett and Henry, 2013).

Persistent snow cover may be especially beneficial for plants by minimizing the number of freeze-thaw events during winter (Cooper, 2014). Repeated freeze-thaw cycles have been experimentally shown to decrease viability of seeds of the perennial bunchgrass *Elymus canadensis* through a combination of physical stress and fungal pathogen attack (Connolly and Orrock, 2015). Therefore, by staving off cold stress events, persistent snow cover may promote seed viability. Even in the absence of persistent snowpack, occasional snowfall may benefit plants. For example, accumulations of snow on leaves of Arctic evergreens can protect the trees from death by desiccation when the soil is frozen (Billings and Mooney, 1968), and snow may also prevent physical abrasion by wind-blown ice particles (Marchand, 2014). However, as we discuss below (*section 2.4*), the net effect of snow on plant survival depends on the balance between these direct positive effects of insulation, and indirect negative effects due to increased overwinter survival of plants' enemies – herbivores and pathogens (Hsiang et al., 1999; Kreyling, 2010; Olofsson et al., 2011; Penczykowski et al., 2015).

Animals

Animals have a range of strategies for surviving freezing temperatures, and many of these strategies involve decreased body temperature and physiological rates. While reduced activity may increase an organism's susceptibility to predation (Aitchison, 1984), it can boost the probability of survival during periods of cold temperatures and resource scarcity. For endotherms including the eastern chipmunk (*Tamias striatus*) and North American brown bear (*Ursus arctos horribilis*), decreased metabolic rate during hibernation lessens the need to find and intake food during winter (Craighead and Craighead, 1972; Landry-Cuerrier et al., 2008). Some 'freeze-avoidant' ectothermic insects (e.g., larvae of the goldenrod gall moth, *Epiblema scudderiana*) avoid intracellular and extracellular freezing through supercooling (Storey and Storey, 2012). Other 'freeze-tolerant' insects (e.g., the woolly bear caterpillar, *Pyrrharctia isabella*, (Marshall and Sinclair, 2012)), as well as herptiles (e.g., the wood frog, *Rana sylvatica*, (Sinclair et al., 2013)), undergo controlled freezing of extracellular tissue to prevent lethal intracellular ice formation (Storey and Storey, 2012). The stable thermal environment provided by insulating snowpack may enhance survival of hibernating, freeze-avoidant, or freeze-tolerant animals, while loss of snowpack may lead to more frequent freeze-thaw cycles and episodes of energetically costly reactivation. For overwintering animals that do not eat during winter and are therefore operating on limited stored energetic reserves, reactivation during freeze-thaw cycles may increase the risk of starving or freezing to death (Bale and Hayward, 2010; Sinclair et al., 2013; Williams et al., 2015). On the other hand, freeze-tolerant insects may need to consume more of their lipid stores in subnivean environments that are continuously above freezing; for such species, loss of snow can be energetically advantageous if winter air temperatures remain below freezing (Irwin and Lee, 2002; Marshall and Sinclair, 2012).

A broad range of animal species not only survive under insulating snowpack, but remain active throughout winter. For example, small arthropods (e.g., in the orders Acari [mites] and Collembola [springtails]) can be active throughout the snowpack (Aitchison, 2001; Bokhorst and Wardle, 2014; Hoham and Duval, 2001; Merriam et al., 1983). Microtine rodents (e.g., lemmings and voles) and shrews are active in the subnivium, and rely on snow cover both for insulation and protection from predators ((Duchesne et al., 2011; Hansson, 1999; Henttonen, 1985); *section 3.2*). Active organisms must either have sufficient fat stores or a continuous supply of resources to survive winter, and the insulated environment under snowpack helps them conserve energy at times when resources may be scarce (Duchesne et al., 2011; Neumann and Merriam, 1972).

Some mammals give birth under the protective insulation of snowpack, including microtine rodents (Duchesne et al., 2011), bears (Craighead and Craighead, 1972), and ringed seals (*Phoca hispida* and *Pusa hispida;* (Auttila et al., 2014; Ferguson et al., 2005; Kunnasranta et al., 2001)). For these mammals, offspring survival may depend on both the insulation and refuge from predation (*section 3.2*) afforded by snow. For example, the population recovery of endangered ringed seals in Lake Saimaa, Finland, has been hampered by low snow cover in recent years, which has limited the seals' ability to build subniveal lairs in which pups are birthed and suckled (Auttila et al., 2014). Human-made snowdrifts may be effective conservation tools for this charismatic mammal in Finland (Auttila et al., 2014). However, this strategy would not be feasible for conserving ringed seals in the Arctic, where models project that milder winters with more rainfall will decrease potential habitat for ringed seal reproduction (i.e., snow drifts of at least 20 cm during April) by 70% over the 21st century (Hezel et al., 2012). Adult ringed seals consume 4000–7000 Kcal of fish and crustaceans per day during winter (Auvinen et al., 2005), are a primary food source for polar bears (*Ursus maritimus*), and are preyed upon by a wide range of other marine and terrestrial species in their subarctic and Arctic habitats (Kelly et al., 2010). Consequently, the demise of ringed seal populations due to snow loss would sever a major link between aquatic and terrestrial food webs.

Other species use snowpack as temporary shelter to survive periods of extreme cold. Birds including grouse (*Tetraonidae*), finches (*Fringillidae*), and chickadees (*Paridae*) will burrow down into the snow from above, creating a subnivean space above ground level (Andreev, 1999; Marjakangas, 1992). Small carnivores such as American martens (*Martes americana*) seek shelter from extreme cold in subnivean cavities associated with coarse woody debris, which confers more structure to their resting site (Taylor and Buskirk, 1994). Larger mammals such as foxes and wolverines also occasionally reside in the subnivium to avoid wind chill in the tundra (Pruitt 1984), although their use of this space may decrease in the future due to "global stilling" (SI: Cherry and Barton, *in review*). For species that only temporarily use snow as insulation, the ability to travel long distances (i.e., migrate) or access alternative forms of insulation (e.g., tree cavities, (Gruebler et al., 2014)) may help them survive bouts of extreme cold when snowpack is absent. Under scenarios of reduced snowpack, species that are forced to migrate to a more hospitable latitude, altitude, or habitat type would be effectively lost from the local food web, despite no actual decrease in population size.

2.3. Primary production under snow

Primary production under snow may determine fluxes of energy and nutrients through food webs both during winter and subsequent seasons (Hampton et al., 2015). While the refractive properties of snow crystals (Fig. 1) limit absorption of solar radiation (depending on the depth and density of snow; (Marchand, 1984)), enough light may still penetrate through snowpack to allow photosynthesis in terrestrial as well as ice-covered aquatic ecosystems. Measurements of solar radiation in alpine snowfields indicate that penetration of 0.1% of the surface radiation may be sufficient to trigger spring blooms of cryophilic algae in the snowpack (Curl et al., 1972). Vascular plants such as evergreen sedges and dwarf shrubs have been shown to photosynthesize under snow cover (Starr and Oberbauer, 2003), and many spring ephemerals or winter annuals (e.g., *Erythronium* and *Claytonia* spp., and winter cereals) start or continue their growth under snow cover (Salisbury, 1984). Given sufficient light, primary production may be enhanced by the buildup of carbon dioxide (i.e., from respiration of microbes, plants, and other active organisms, (Aitchison, 2001; Bokhorst et al., 2013; Merriam et al., 1983; Monson et al., 2006)) as well as water-saturated air and relative warmth under snowpack (Billings and Mooney, 1968). Whether future reductions in snowfall increase or decrease winter primary productivity in terrestrial systems will depend on accompanying changes in temperature: if winter temperatures are consistently mild and soil is maintained in a thawed state, then reductions in snow should promote primary productivity due to increased light transmittance; however, even occasional spells of freezing temperatures can damage both above- and below-ground plant tissues in the absence of insulating snow (*section 2.2*).

In ice-covered aquatic systems, snow cover is typically a strong limiter of primary productivity (Hampton et al., 2015). Yet some Arctic algal species are adapted to such low light conditions and able to photosynthesize when only 2% of incident light is transmitted through the snow and ice (Cota, 1985). Primary producers adapted to extremely low light have also been found at the bottom of Antarctic lakes (Priddle, 1980). Production by such species may fuel aquatic food webs through winter (Hampton et al., 2015). By allowing light transmittance to greater depths, reductions in snow cover would likely increase primary productivity in many aquatic systems.

2.4. Trophic interactions under snow

There is evidence for direct protective effects of insulating snowpack on survival of diverse taxa from across several trophic levels (*section 2.2*), as well as for primary production under snow (*section 2.3*). Thus, snow-covered habitats can be a rich setting for trophic interactions, and the benefit of snow's insulation to any one species will be tempered by positive effects of insulation, or of other properties of snowpack (Fig. 1), on that species' competitors and consumers (Fig. 2).

First, consider how snow cover represents a double-edged sword for plants. While insulation from snow may improve survival and growth of plants on their own (*sections 2.2 and 2.3*), snow cover can also increase rates of herbivory and infection by plant pathogens (Kreyling, 2010). Small mammals active in the subnivium may benefit from insulation and relaxed predation risk under deep snow (*sections 2.2 and 3.2*), and consequently forage more intensely on herbaceous as well as woody plants. Winter herbivory by voles (*Microtus* and *Myodes* spp.), in particular, can hamper conifer tree regeneration in temperate forests (Hansson, 1999; Sullivan and Sullivan, 2008). Under deep snowpack, these microtines can limit natural forest recruitment (i.e., in cutover forest and natural stands) or survival of transplanted seedlings (i.e., in nurseries). Microtines can also damage or kill juvenile and mature trees by consuming bark in the subnivean, and the frequency and severity of this damage may be greater under deeper snow (Gill, 1992; Hansson, 1989; Littlefield et al., 1946). At the same time, the influence of subnivean herbivores on their plant resources will depend on their own vulnerability to predators (Fig. 2).

While snowpack may impede generalist predators including foxes and raptors (Duchesne et al., 2011; Jędrzejewska and Jędrzejewski, 1998; Jędrzejewski and Jędrzejewska, 1992; Olsson, 1984), winter specialists may still impose top-down control on their subnivean prey (*section 3.2*). For example, microtine rodents and shrews are vulnerable to predation by small mustelids (e.g., least weasels, *Mustela nivalis,* and short-tailed weasels, *Mustela erminea*), even under snowpack (Duchesne et al., 2011; Henttonen, 1985).

In addition to increased herbivory, plants may face greater pathogen pressure under snow. Many parasitic fungi – such as "snow molds" pathogenic to perennial turfgrasses and winter cereals – thrive in the cool, moist conditions of melting snowpack (Bokhorst and Wardle, 2014; Hsiang et al., 1999). In a snow manipulation experiment in the tundra heathland of northern Sweden, greater snow cover increased growth of the evergreen dwarf-shrub *Empetrum hermaphroditum* over several years, until an outbreak of a fungal parasite occurred (Olofsson et al., 2011). The parasite was more devastating to its host under increased snow cover, where it reduced gross photosynthesis and net ecosystem carbon exchange (Olofsson et al., 2011). Other pathogens must produce resting spores to survive winter periods when host tissue is absent, including *Podosphaera plantaginis*, a powdery mildew pathogen of *Plantago lanceolata* (Tack and Laine, 2014; Tollenaere and Laine, 2013). An observational study of more than 4000 populations across 13 years revealed that overwinter persistence of *P. plantaginis* was lower in years with more days that were both freezing (< 0 °C) and snowless (Penczykowski et al., 2015).

Green plants are not the only resources available to primary consumers in the hospitable subnivean environment. Pitfall trapping in a deciduous forest near Ottawa, Canada, revealed that a variety of beetles and adult flies are active in the subnivean space (Merriam et al., 1983). Insulating snowpack may increase rates of consumption of leaf litter and fungi by these and other arthropods ((Bokhorst and Wardle, 2014); Fig. 2), though the degree to which snow cover increases litter decomposition has been experimentally shown to vary with the age and species composition of the litter (Bokhorst et al., 2013). Moreover, the abundance and influence of arthropods in and under snowpack will depend in part upon densities of winter-active insectivores such as shrews ((Henttonen, 1985); Fig. 2).

3. Snow cover as a refuge

Refuges from consumption – physical locations or temporal periods where the risk of consumption is low – directly influence energy transfer within and between trophic levels (Finke and Denno, 2006; Pace et al., 1999). Refuges lower efficiency of consumers (i.e., herbivores, predators, or parasites) by decreasing their rates of finding and successfully consuming resources (Begon et al., 1995; Lima, 1990).

3.1. Snow cover as refuge from herbivores

Subniveal herbivores may consume plants under snowpack (*section 2.4*), yet snow cover can protect plants from supraniveal herbivores such as ungulates ((Cooper, 2014); Fig. 1; Fig. 2). In northern temperate and Arctic systems, ungulates dig away shallow snow to reach consumable plant material (Hansen et al., 2010; Nellemann and Reynolds, 1997; Schaefer and Messier, 1995), which can also facilitate foraging by other taxa (e.g., ptarmigans, (Cooper, 2014; Pedersen et al., 2006)). However, deep or dense snow can prevent ungulates from reaching subniveal resources (Helle and Kojola, 2008; Kumpula, 2001; Miller and Gunn, 2003). Therefore, in regions where winter climate change increases snow depth, the frequency of rain-on-snow events, or the thickness of ice at the base of snowpack (Collins et al., 2013), inaccessible resources may lead to declines in ungulate population growth (Aanes et al., 2002; Kohler and Aanes, 2004).

Snow cover can also protect primary producers from trampling by ungulate herbivores (Christenson et al., 2014; Cooper and Wookey, 2001; Helle and Aspi, 1983; Roy et al., 2004). Fragile taxa such as lichens and cryptogamic crusts may be especially susceptible to damage by trampling herbivores, and may also take a long time to recover from this type of damage (Cooper and Wookey, 2001). Such primary producers can be important contributors to carbon and nutrient cycling (Elbert et al., 2012; Housman et al., 2006) and may be seasonally important resources for some primary consumers (Holleman et al., 1979; Kumpula, 2001). Thus, studies evaluating how altered snow regimes affect the base of food chains should consider the role of snow cover in protecting primary producers from both supraniveal consumption and trampling.

3.2. Snow cover as refuge from predators

Snow cover can serve as an opaque, physical barrier against detection and capture of subnivean animals by supraniveal generalist predators (Fig. 1; Fig. 2). For example, foxes scratch or pounce on the snow to capture subnivean microtine prey, and deeper snow restricts their hunting efficiency (Duchesne et al., 2011; Jędrzejewska and Jędrzejewski, 1998; Jędrzejewski and Jędrzejewska, 1992). Lemmings (*Dicrostonyx* spp.) may take advantage of this by concentrating their nesting sites in locations with deeper snow (Duchesne et al., 2011; Reid et al., 2012). Increased snow depth can then drive foxes to switch from preferred microtine prey to less preferred, supraniveal food (e.g., hares, forest rodents, ungulate carcasses; (Jędrzejewska and Jędrzejewski, 1998). Raptors can adopt similar strategies when their hunting is limited by deep snow: some migrate seasonally away from regions of deep snow, but others switch to more apparent supraniveal prey items (e.g., passerines) during severe winters (Olsson, 1984). For prey species, therefore, snow cover may offer the dual benefit of increased insulation (*section 2.2*) and decreased predation. Such is the case for ringed seals in subniveal breeding dens (Furgal et al., 1996; Kelly et al., 2010).

While deeper snow may decrease the hunting efficiency of generalist predators, winter specialists such as small mustelids are less likely to be impeded (Duchesne et al., 2011; Henttonen, 1985). Consequently, altered snow regimes may lead to shifts in the contribution of generalist and specialist predators to mortality of small mammals (Fig. 2). For example, under scenarios of shallower snowpack and earlier snowmelt, generalist predators may consume more small mammals, dampening cycles of microtine abundance through time (Ims et al., 2008). Increased prey availability for winter generalist predators may also influence other energy fluxes within food webs. For example, red foxes (*Vulpes vulpes*) and Arctic foxes (*Vulpes lagopus*) can have significant diet overlap (Elmhagen et al., 2002), and some evidence suggests red foxes may competitively exclude Arctic foxes, particularly when shared resources are scarce (Tannerfeldt et al., 2002). If decreased snow cover limits small mammal abundance, competition for prey may become intense between these fox species, potentially increasing the frequency of antagonistic interactions (including intraguild predation, (Tannerfeldt et al., 2002)), and indirectly altering the strengths of other interactions within the food web (Fig. 2).

3.3. Crypsis and snow – winter's diminishing visual refuge

Snowy environments can also provide a backdrop for evolution of cryptic coloration (Fig. 1). In regions with reliable snow cover in winter, animals with white feathers or fur may derive a fitness advantage from being able to hide from their visually hunting predators or evasive prey

(Caro, 2005; Zimova et al., 2016). A subset of these animals are not white year-round, but use photoperiod as a biophysical cue to change their color to better match the white, snow-covered environment. Coat and feather polyphenism is apparent in disparate taxa across multiple trophic levels, including primary consumers (e.g., Arctic, mountain, and snowshoe hares; Peary caribou; *Dicrostonyx* lemmings; Siberian hamsters; white-tailed, willow, and rock ptarmigans) and secondary consumers (e.g., least, short-tailed, and long-tailed weasels; Arctic foxes). Under climate change, reduced extent of snow cover and earlier snow retreat may increase the visibility and predation-caused mortality of snow-adapted animals as their white fur or feathers generate a sharp contrast with their novel snow-free environment (Imperio et al., 2013; Zimova et al., 2016). Under a reduced snow scenario, greater predation on influential primary consumers (e.g., snowshoe hares) may in turn release plants from browsing pressure, potentially affecting both plant abundance and the maintenance of defensive chemistry in their target plants (Bryant et al., 1983; Reichardt et al., 1984; Reichardt et al., 1990).

3.4. Snow patches as refuge from pests

Patches of late season snow may serve as spatial refuges mitigating mammal–insect interactions. In alpine habitats during late spring and summer, large ungulates (e.g., feral horses [*Equus caballus*], (Keiper and Berger, 1982); woodland caribou [*Rangifer tarandus caribou*], (Anderson and Nilssen, 1998; Ion and Kershaw, 1989; Toupin et al., 1996)) may selectively move to snow patches to escape from biting insects (e.g., mosquitoes, blackflies, warble flies, deer botflies). Greater wind velocities and colder temperatures limit the number of ectothermic pests found in snow patches (Ion and Kershaw, 1989; Toupin et al., 1996), and ungulates that lie on the snow may further reduce their surface area exposed to biting insects, although this behavior also confers thermoregulatory benefits (Anderson and Nilssen, 1998; Downes et al., 1986). Loss of these snow refuge patches to generally warmer winters may increase the likelihood of insect harassment on some ungulate species. Intense insect harassment can generate significant energetic costs for ungulates at high latitudes or in alpine systems (e.g., time and energy diverted from foraging to insect avoidance behaviors), and may reduce body condition and reproductive fitness (Vors and Boyce, 2009; Weladji et al., 2003). Because warming winters are predicted to increase epidemic pest burdens (Harvell et al., 2002), the coincidence of more severe insect harassment and fewer snow patch refuges may exacerbate the negative effects of biting insects in these ungulate herds (Vors and Boyce, 2009), potentially increasing ungulates' risk of insect-vectored diseases, altering ungulate resource use, and affecting ungulate quality as food for predators and scavengers (Fig. 2).

3.5. Food cache refuges in the snow – nature's icebox

Caches of collected food items are essential winter resources for some consumers, and may be protected from decomposition and pilferage by storage in the snow (Vander Wall and Smith, 1987) (Fig. 1). Wolverines (*Gulo gulo*), for example, occasionally store their fresh kills or other recently deceased food (e.g., carrion) within the snow, ensuring food availability and quality during later, resource-scarce periods of the year. Resources hoarded overwinter are essential for healthy reproduction of wolverines (Magoun, 1987; Rauset et al., 2015) and may also facilitate the winter survival of other scavengers (e.g., Arctic fox, (Elmhagen et al., 2000; Pagh and Hersteinsson, 2008)). An opaque bulk of snow cover may limit both visual and olfactory detection of caches by pilferers, and too much snow accumulation may even make it difficult for an organism to relocate or access its own cache. However, reductions in the amount or duration of snow cover may decrease the number of suitable snow-covered sites available to store food, and decrease the efficacy of such sites for protecting caches against pilferage and decomposition. Because food caches provide nutrition during resource-scarce periods, their loss may have deleterious demographic consequences for cache-makers and scavengers (Fig. 2).

4. Moving through the snow

One strategy for surviving the harsh conditions of winter is to migrate to a warmer climate; however, for non-migratory mammals that remain active during winter, movement through a snow-covered landscape presents unique challenges. Walking through snow is more difficult than walking on top of snow, leading to higher energetic costs and reduced speed and agility (Crete and Lariviere, 2003; Fancy and White, 1985; Moen, 1976; Parker et al., 1984). Whether or not an animal sinks in the snow is largely a function of the snow's characteristics (e.g., snow depth, crust hardness; Fig. 1) and the animal's morphology (Telfer and Kelsall, 1984). Foot load is a useful metric to compare how easily different species move across snow-covered landscapes (Fig. 3). A high foot load (large mass: small foot) results in animals falling through the snowpack, whereas a low foot load (small mass: large foot) allows animals to move on the snow's surface.

Although other physical characteristics (e.g., leg length or chest height) and behavioral adaptations of animals may influence the effect of snow on their movement (Telfer and Kelsall, 1984), foot load provides a useful index for predicting how different species may be affected by changing snow depth. A compilation of foot loading values for 20 northern latitude mammals reveals a striking pattern (Fig. 3). Although snow can impede movement of both predators and prey, large carnivores generally have lower foot loading than their ungulate prey. This means carnivores are more likely to travel on snow, whereas their prey often must push through it (which reduces their speed and agility, and is more energetically costly). Even when the snow does not support their weight, predators have an advantage in that they are chasing the prey: breaking new trails in deep snow is difficult, so the leading animal that is breaking a new trail will incur a higher energetic cost than the animals that follow (Duquette, 1988; Fancy and White, 1985; Lundmark and Ball, 2008). These differences suggest that years with deep snow will benefit predators and strengthen top-down effects, while decreasing snow due to climate change could benefit prey by weakening top-down effects of predators. This is commonly observed in wolf (*Canis lupis*)–ungulate systems, where kill rates (Hebblewhite, 2005; Huggard, 1993; Nelson and Mech, 1986) and hunting success of wolves (Peterson and Allen, 1974; Post et al., 1999) generally increase with snow depth (Fig. 2). Further, by increasing predation on herbivores, greater average snow depth can indirectly benefit primary producers. This type of trophic cascade was demonstrated on Isle Royale during the 20th century: during periods of shallow snow, predation by wolves decreased, resulting in larger moose (*Alces alces*) populations and greater herbivory, which reduced biomass of fir trees (Post et al., 1999).

While larger carnivores often have an advantage in deep snow over ungulates in terms of foot loading, ungulates are likely to avoid deep snow where they are more vulnerable to predation. On a fine scale, ungulates may favor habitat with less snow due to topography or dense vegetation cover (Armleder et al., 1994; Rachlow and Bowyer, 1998; Schmidt, 1993), which could drive heterogeneous patterns of predation and herbivory across the landscape (Gorini et al., 2012; Kauffman et al., 2007; Nelson and Mech, 1986). Prey species may also migrate long distances to areas where there is less snow and more resources. Thus, accumulating snow may benefit entire communities of plants by reducing herbivory, while simultaneously generating negative indirect effects on distant plant communities where the herbivores relocate. Such indirect effects may extend beyond the plant level and winter season, generating effects that cascade through the ecological community and persist throughout the year. For example, elk (*Cervus canadensis*) in Arizona, USA have mediated the indirect effects of declining winter snowfall on the nesting success of summer breeding passerines (Martin and Maron, 2012). Historically, elk migrate out of high elevation habitats as snow accumulates in late fall and early winter. However, declining snowfall has allowed elk to remain in alpine environments later in the year, where they browse heavily upon deciduous woody vegetation (e.g., canyon maple [*Acer grandidentatum*], quaking aspen [*Populus tremuloides*], and New Mexican locust [*Robinia neomexicana*]; (Martin, 2007; Martin and Maron, 2012)). As a consequence, deciduous species have decreased and forest vegetation is more open, increasing nest predation and ultimately reducing songbird abundance in drainages where elk now overwinter (Martin, 2007).

4.1. Case study: coyotes and lynx in the boreal forest

A specific case study may best demonstrate how behavioral (e.g., habitat selection) or physical adaptions (e.g., foot loading) to moving and hunting in the historically snow-covered landscapes will influence food web interactions under altered regimes of snow cover. Specifically, differences in foot loading may help explain the increasing distribution of coyotes in northern boreal forests. In these systems coyotes (*Canis latrans*) compete with lynx (*Lynx canadensis*) for snowshoe hare prey (*Lepus americanus*) (Murray and Boutin, 1991). Coyotes are a recent arrival, colonizing the boreal forest in the last century (Chubbs and Phillips, 2005). Like most canids, coyotes are cursorial predators that evolved to run down prey (Andersson and Werdelin, 2003; Wang and Tedford, 2008). They are “built for speed”, with long legs and small feet that allow them long gait and a fast pace (Garland and Janis, 1993). In contrast, lynx have long evolutionary histories in the boreal forest (Repenning, 1967), and are highly adapted for hunting in the snow. While the two carnivores are similar in mass and chest height, the feet of lynx are approximately four times larger than those of coyotes. Consequently, lynx have a much lower foot load (< 30g/cm2; Fig. 3) than coyote (> 100g/cm2), which translates into a better ability to move over soft, deep snow without sinking (Murray and Boutin, 1991). This morphological adaptation permits lynx to hunt in habitats across a wide range of snow depth and softness.

Coyotes display remarkable behavioral adaptation that may compensate for morphological disadvantages in competition with the lynx (Murray et al., 1995). Coyotes use the landscape differently than lynx, using habitats and adopting a variety of hunting strategies that increase their probability of success. Murray and Boutin (1991) tracked coyote and lynx in the Canadian Yukon and found coyotes altered their behavior to mitigate the negative effects of deep snow by restricting their hunting to lower elevations with shallower, harder snow. Coyote were also more likely to use trails made by other animals, which can decrease the energetic costs of travel (Duquette, 1988; Fancy and White, 1985; Lundmark and Ball, 2008) as well as increase their chances of encountering carrion to scavenge (Murray and Boutin 1991).

Lynx hunt hare in a wide variety of habitats, and alter their hunting technique (e.g., stalking, ambush, or chase) in different habitat types. If the initial attack is unsuccessful, the low foot loading of lynx allows them to continue chasing their prey through the snow (Murray et al., 1995). In contrast, snow greatly reduces coyotes' ability to run down their prey in long chases, restricting their hunting locations to dense spruce thickets with abundant understory where they can stalk and pounce on their prey. Murray et al (1995) found that when the initial attack was unsuccessful, coyotes rarely gave chase, probably because hares have a significant advantage over coyotes in soft snow (e.g., lower foot loading, Fig. 3). However, even though coyotes initiated fewer attacks than lynx, their probability of success was higher (34% vs. 29%).

Deep snow may have limited the northern range of coyotes historically, but multiple aspects of global change may facilitate their expansion into boreal forests and competition with lynx. Coyotes will benefit not only from less snow, but also from the harder snow crust that is likely with increased winter temperatures, as harder crust is likely to increase the maximum foot loading capable of easily moving over the snow. Further, the opportunistic use of paths made by humans may facilitate both the range expansion (Kolbe et al., 2007) and, possibly, the hunting efficiency of coyotes. Together, these changes may alter the strength of competition between coyotes and lynx, with implications for hare populations and possibly the plant communities that hares consume (Bryant, 1987; John and Turkington, 1995).

5. Snow as a driver of phenology

Snowpack plays a major role in the timing of plant and invertebrate emergence as a protective insulator, light limiter, and source of water (Cooper, 2014; Kreyling, 2010; Wipf and Rixen, 2010) (Fig. 1). Earlier snowmelt due to reduced snow depth and/or warmer spring temperatures can drive earlier emergence of plants and many invertebrates (Bale and Hayward, 2010; Cooper, 2014; Iler et al., 2013b). However, other environmental cues such as air temperature and day length drive the reactivation, reproduction, and migration of many animal species (Bale and Hayward, 2010; Doiron et al., 2015; Inouye et al., 2000; Post and Forchhammer, 2008). For consumers and pollinators with different phenological drivers than their resources, changes in the abundance of snow and timing of snowmelt may lead to phenological mismatch between trophic levels and resulting population-level effects that may propagate through food webs.

All else equal, advances in plant phenology due to earlier snowmelt might be expected to prolong the growing season, increasing gross primary production to the benefit of higher trophic levels. However, earlier loss of snow cover may instead harm plants by exposing them to damaging spring frosts, as has been shown for montane wildflowers and temperate deciduous woody plants (Augspurger, 2013; Inouye, 2008). Such constraints may contribute to nonlinear trends in flowering with date of snowmelt, where more flowers are produced in years with later snowmelt, but only above a threshold date of snowmelt (Iler et al., 2013a; Inouye, 2008). More generally, nonlinear trends in flowering phenology with date of snowmelt have been found to be relatively common (ca. 20% of species) in Arctic and subalpine plant communities, suggesting that many species are at or near their limits of phenological change in response to snowmelt (Iler et al., 2013a). Plants may also face constraints when their emergence and flowering, driven by earlier snowmelt, precedes emergence or migration of their invertebrate pollinators (Kreyling, 2010). For example, populations of the dwarf alpine shrub *Phyllodoce aleutica* that emerged earlier were pollen limited due to later emergence of their bumblebee (*Bombus hypocrita sapporoensis* Cockerell) pollinators (Kameyama and Kudo, 2015). In turn, changes in the timing of snowmelt may affect pollinator population dynamics through a combination of direct and indirect mechanisms. For example, earlier snow melt had a negative indirect effect on fecundity of the alpine butterfly *Speyeria mormonia* through frost effects on its preferred floral resources (*Erigeron speciosus*), as well as a direct negative effect on survival of larvae or pupae in the following year (Boggs and Inouye, 2012). Analysis of the phenology of a community of montane wildflowers and their generalist syrphid fly pollinators, however, showed that earlier snowmelt may actually increase the overall window of overlap between the plants and syrphids (Iler et al., 2013b). Indeed, increasing asynchrony in phenology between plants and their pollinators should be especially problematic for specialist interactions, while plants with multiple pollinators or pollinators with many nectar sources may be buffered from negative effects of mismatch in any one pairing (Williams et al., 2015).

With changing winter climates, mismatches in the timing of plant emergence and the arrival, emergence, or reproduction of herbivores have been documented for a wide variety of taxa. For example, yellow-bellied marmots (*Marmota flaviventris*) are emerging from hibernation earlier due to increased air temperature, but confront food scarcity due to increased snow cover or delayed snow melt in some areas (Inouye et al., 2000). Herbivores may be limited not only by the quantity, but also the quality of plant resources available at critical times. Canada geese (*Branta canadensis*) and greater snow geese (*Chen caerulescens atlantica*) are larger and healthier at fledging if they hatch concurrently with the emergence of high quality forage plants; however, if earlier snowmelt and emergence of high quality forage is not accompanied by equally early hatching, goslings may miss these high quality resources and suffer reductions in body size and first-year survival ((Brook et al., 2015; Doiron et al., 2015); Fig. 2). Similar patterns of asynchrony have been detected for large ungulates and their resources. For example, earlier snow melt and emergence of alpine snow bed vegetation results in decreased availability of high quality resources to domestic sheep (*Ovis aries*) later in the season, and smaller body mass of lambs in autumn (Mysterud and Austrheim, 2014). In the Arctic, caribou time their seasonal migration to calving grounds based on day length, while plant emergence at the calving grounds is driven by snowmelt. As snowmelt has advanced, caribou have suffered decreases in offspring production due to arriving after the peak of high quality forage ((Post and Forchhammer, 2008); Fig. 2).

The consequences of phenological mismatch can extend beyond adjacent trophic levels, as has recently been documented for an Arctic food web consisting of a flowering plant community, arthropods (nonbiting midges [Chironomidae] and house flies [Muscidae]), and wading birds (ruddy turnstone [*Arenaria interpres*], sanderling [*Calidris alba*], and dunlin [*Calidris alpina*]) (Mortensen et al., 2016). Analysis of a long-term dataset from this system showed that earlier snowmelt affected all three trophic levels, through a combination of direct and indirect effects on the phenology and performance (abundance or reproductive success) at each level (Mortensen et al., 2016). Through consideration of multiple pathways of effects, the authors found that direct negative impacts of earlier snowmelt on performance of plant and wader communities were at least partially offset by indirect biotic interactions within the food web (Mortensen et al., 2016).

6. Conclusions and future directions

Winter is a season of harsh abiotic conditions for many species (e.g., (Coltrane and Barboza, 2010; Huitu et al., 2003; Tack and Laine, 2014; Thieltges et al., 2004)), but can also be the setting for dynamic ecological interactions (Cooper, 2014; Williams et al., 2015). However, even as our knowledge of the role of winter in the ecology of plants, animals, and microbes develops, ecologists face the challenge of trying to understand and predict how rapidly shifting climatic conditions will alter the structure and function of entire ecological communities. In this review, we explore several examples of how climate-mediated alterations in snow pack may change the outcomes of ecological interactions. Our review is not exhaustive, and other aspects of snow cover may also affect food webs. For example, reductions in average snow cover or pollution with contaminating particles may decrease albedo (i.e, reflectance) of the landscape (Vaughan et al., 2013). Changes in albedo would influence primary productivity both above and below snowpack, the ability of snow to serve as a visual refuge from consumption, and rates of snowmelt. Importantly, the mechanisms explored in this review (snow as insulation, refuge, barrier to movement, and driver of phenology; Fig. 1) operate simultaneously, and different mechanisms may have synergistic or opposing effects on a given species or interaction. For example, snow provides dual benefits as an insulating shelter and refuge from predation for many species. However, the benefits of snow cover for a given species are less certain if an antagonist species also benefits from snow. For example, the net effect of snow on a plant may depend on tension between the benefit of insulation for the plant and the benefit of insulation to its pathogens. Thus, predicting the consequences of altered snow cover for a given species requires understanding how snow directly affects that species and the network of interactions in which it is embedded.

Our understanding of the role of snow in food webs, particularly in temperate ecosystems, is limited due to a paucity of data derived from hypothesis-driven experiments that manipulate components of the winter environment and evaluate how species interactions respond. While most studies have used natural variation to evaluate the effects of different snow characteristics on species interactions, experimental manipulations are becoming more common (Wipf and Rixen, 2010). Removal or addition of snow with shovels is a relatively easy and insightful approach, but great care must be taken not to damage plants or the soil surface with the shovel, or to create unnatural levels of compaction (e.g., (Groffman et al., 2011; Hardy et al., 2001)). Another method is to construct structures with roofs and partial walls (e.g., made of tarp) to prevent snow from accumulating on plots; an advantage of this method is that the roofs can be cut prior to snowmelt so that the total amount of moisture and compounds received from the snowfall is ultimately the same between control and manipulated plots (Blume-Werry et al., 2016). However, the potential for roofed structures to limit light transmittance should also be considered (Kreyling et al., 2012). Snow fences are another more passive approach to manipulating snow, and already exist in many areas to reduce snow drift on roads and highways. Data from snow fences have provided great insight on the effects of altered snow regimes on plants, including that increased snow depth can facilitate plant invasions (Blumenthal et al., 2008) and reduce plant community diversity (Wipf and Rixen, 2010). Because snow fences require relatively little maintenance, they are especially conducive to long-term manipulations of snow regimes (Walker et al., 1999), but only in habitats that experience winds strong enough to generate a predictable distribution of snow depths. The next logical step involves the use of snow fences to study effects of snow on networks of ecological interactions spanning multiple trophic levels. For example, manipulations of microbial communities (e.g., pathogens, mutualists, decomposers) in the lee of snow fences would allow investigation of relationships between plants and microbes over gradients of snow depth. Such experiments may allow for disentangling the effects of snow on multiple trophic levels, and yield insight into the net effect for food webs and ecosystem processes. Long-term studies on effects of altered snow regimes on food webs are particularly important, as effects of short-term manipulations (i.e, snow addition or removal over one or a few years) may not scale proportionally to longer-term (i.e., decade or more) consequences due to temporally confounded changes in other environmental factors, evolutionary or community compositional changes, or other sources of nonlinearities in species responses (Blume-Werry et al., 2016; Iler et al., 2013a; Wipf and Rixen, 2010).

Several recent technological advances may help uncover previously hidden food web processes below snowpack, and their consequences at the community and ecosystem level. While small mammal and insect pitfall trapping are well-established methods for determining animal activity beneath snow (e.g., (Hansson, 1999; Merriam et al., 1983)), these methods do not easily reveal what the animals were consuming. However, tools including DNA barcoding (Wirta et al., 2015) and stable isotope analysis of rodent teeth (Calandra et al., 2015) can shed light on trophic interactions under snow. For larger animals (e.g., ungulates and canids), improved devices for tracking animal movement and body temperature may yield insight on their winter foraging activities (Cooke et al., 2004). Extensive studies of food web and ecosystem dynamics can then be paired with remote sensing technologies that allow for analysis of snow coverage patterns over large spatial and temporal scales (Brennan et al., 2013; Street et al., 2015; Zhu et al., 2017). Finally, these empirical data should be complemented with modelling studies to make generalizable predictions about how altered snow regimes affect networks of interacting species (Archey et al., 2015; Trainor et al., 2014).

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FIGURE LEGENDS

Figure 1. Conceptual map linking properties of snowpack (blue ovals) and dynamics of snowpack structure (orange rounded rectangles) to key mechanisms by which snowpack affects food webs (green rectangles).

Figure 2. Hypothesized changes in a simplified Arctic food web under a future low snow scenario, adapted from (Aitchison, 1984; Legagneux et al., 2012). Blue lines indicate trophic interactions, with arrows pointing in the direction of energy transfer, and green lines indicate competitive interactions. The line type (thin, thick, or dashed) indicates the likely change in interaction strength in a shift from a typical amount of snow to a year of low snow amount and/or persistence. Under a low snow scenario, some interactions are likely to decrease in strength (thin dashed lines), others are likely to increase in strength (thick solid lines), and others might either increase or decrease (thick dashed lines).

Figure 3. Foot loading index for 20 northern latitude mammals, designated as predator (grey) and herbivore (black) species. Foot loading is calculated as body mass (g) divided by the surface area of all four feet (cm^2). Animals with smaller values are better adapted to walk on snow, where animals with larger values are more likely to sink into snow. Figure adapted from (Buskirk, 1999; Klein, 1992; Telfer and Kelsall, 1984).

Figure 1

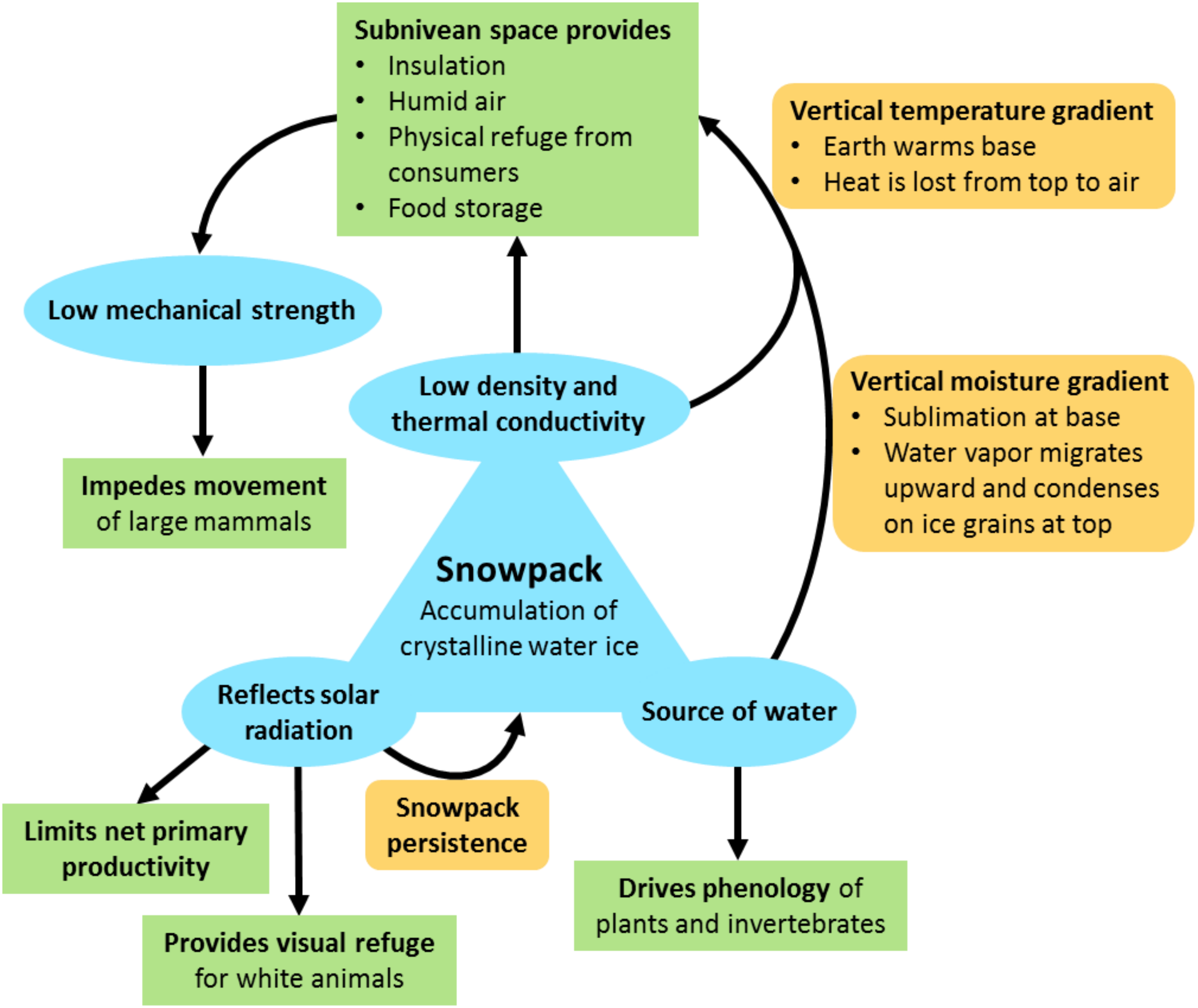

Subnivean space provides
Insulation
Humid air
Physical refuge from consumers
Food storage
Vertical temperature gradient
Earth warms base
Heat is lost from top to air
Low mechanical strength
Low density and thermal conductivity
Impedes movement of large mammals
Vertical moisture gradient
Sublimation at base
Water vapor migrates upward and condenses on ice grains at top
Snowpack
Accumulation of crystalline water ice
Reflects solar radiation
Source of water
Snowpack persistence
Limits net primary productivity
Provides visual refuge for white animals
Drives phenology of plants and invertebrates

Figure 2

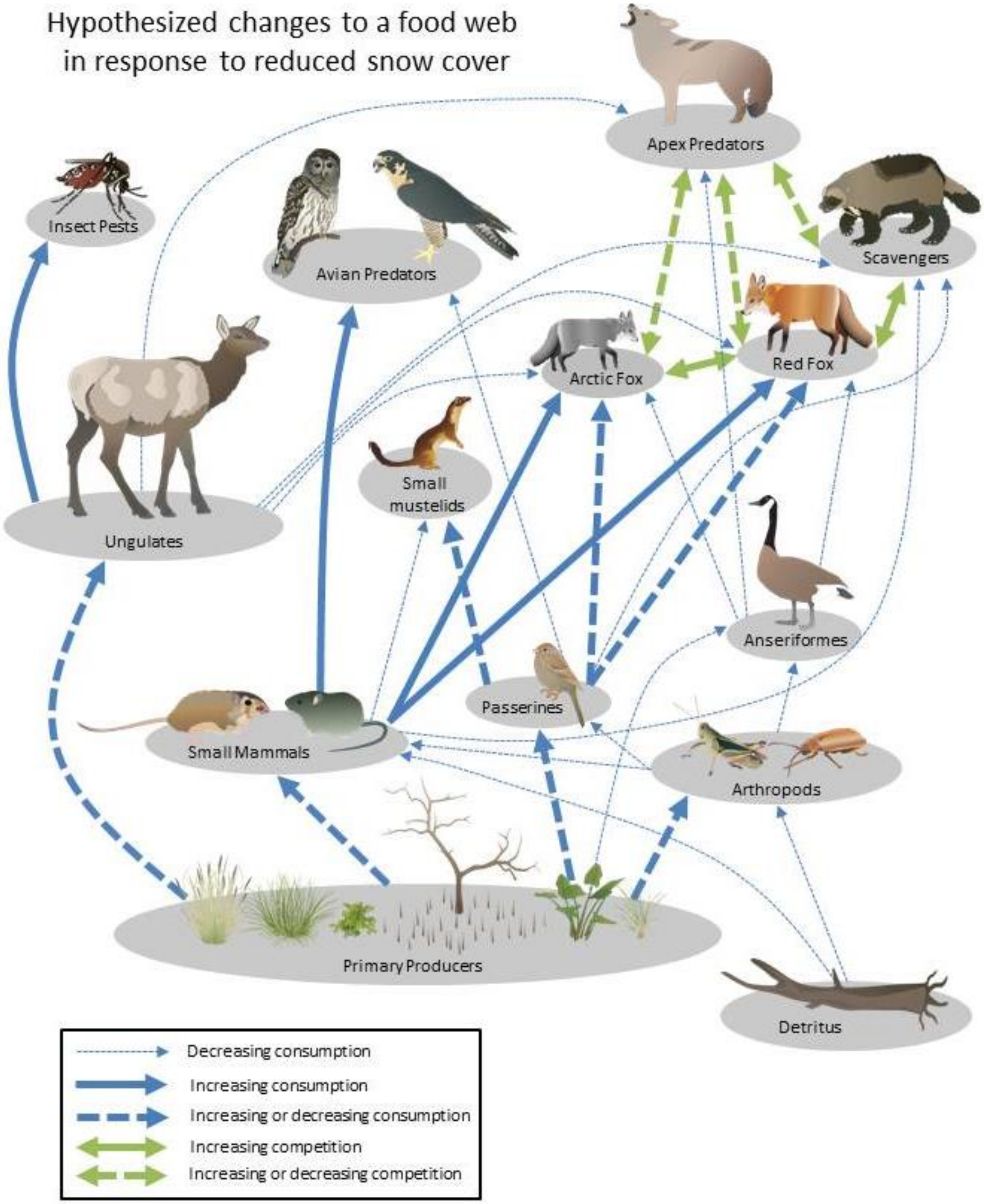
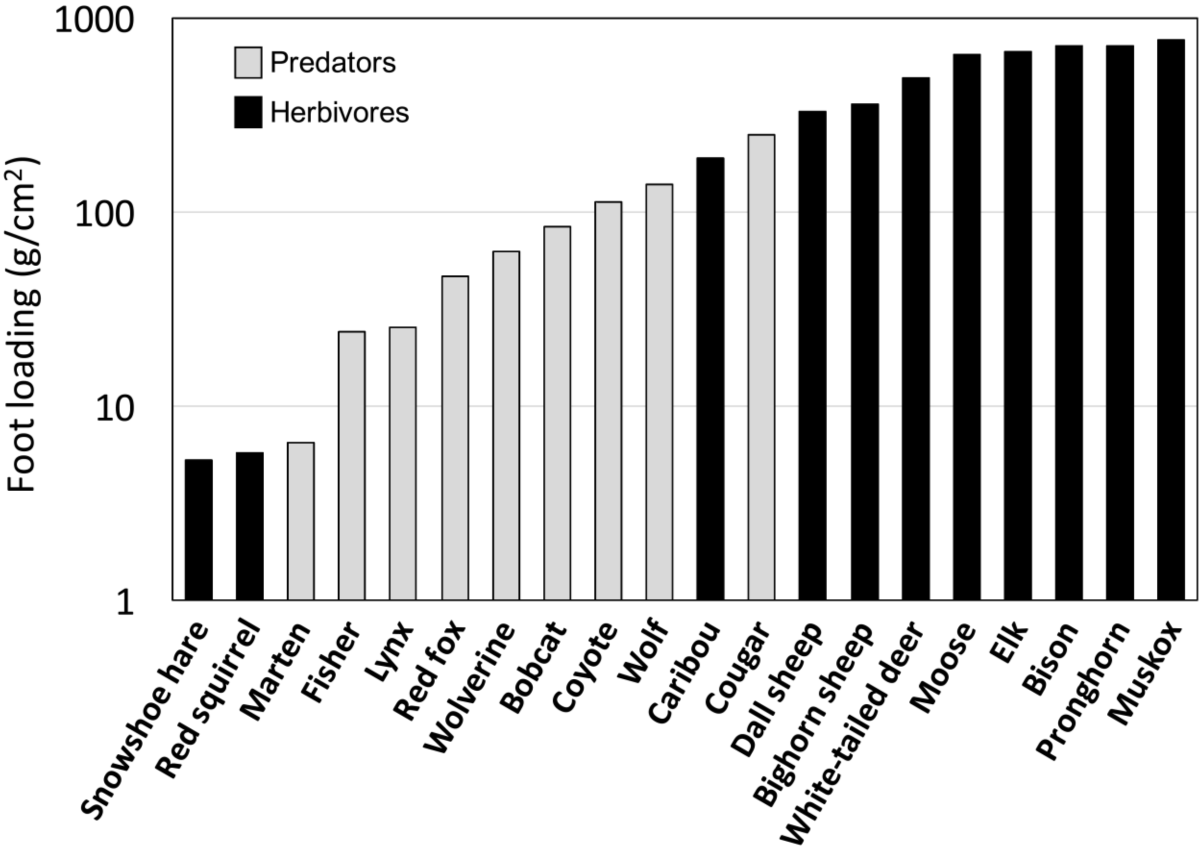
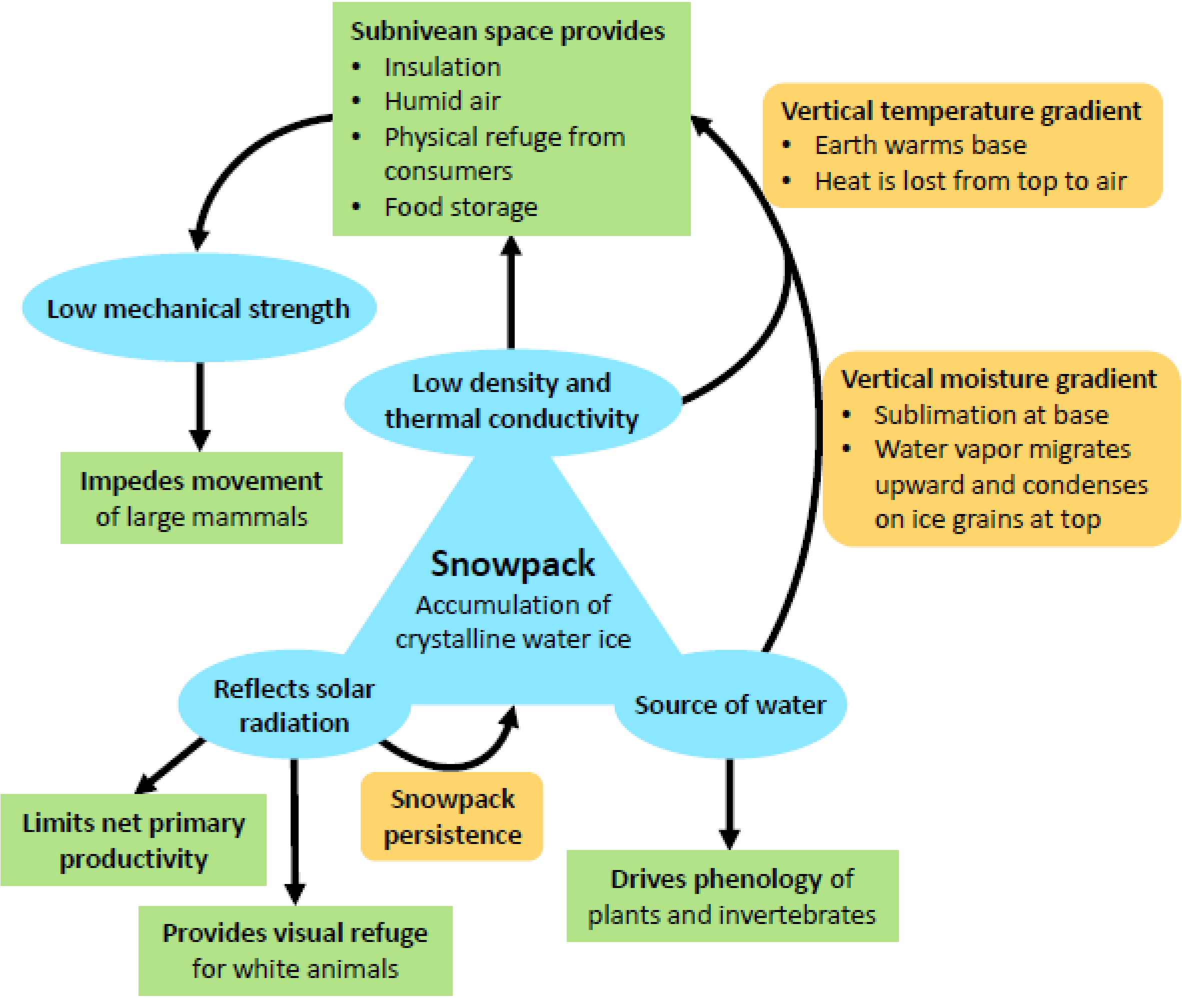

Hypothesized changes to a food web in response to reduced snow cover
Apex Predators
Insect Pests
Avian Predators
Scavengers
Arctic Fox
Red Fox
Small mustelids
Ungulates
Anseriformes
Passerines
Small Mammals
Arthropods
Primary Producers
Detritus
Decreasing consumption
Increasing consumption
Increasing or decreasing consumption
Increasing competition
Increasing or decreasing competition

Figure 3



Foot loading (g/cm²)
1000
100
10
1
Predators
Herbivores
Snowshoe hare
Red squirrel
Marten
Fisher
Lynx
Red fox
Wolverine
Bobcat
Coyote
Wolf
Caribou
Cougar
Dall sheep
Bighorn sheep
White-tailed deer
Moose
Elk
Bison
Pronghorn
Muskox



Graphical abstract