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PERSPECTIVE

Frozen out: unanswered questions about winter biology

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Abstract: Winter conditions impose dramatic constraints on temperate, boreal, and polar ecosystems, and shape the abiotic and biotic interactions underpinning these systems. At high latitudes, winter can last longer than the growing season and may have a disproportionately large impact on organisms and ecosystems. Even so, our understanding of the ecological implications of winter is often lacking. Indeed, even what exactly defines winter is currently unclear, and boundaries that delineate this season are blurred across marine, freshwater, and terrestrial realms and fields of biology. Here, we discuss the complexity of defining winter, and highlight the importance of maintaining the capacity to test hypotheses across seasons, realms, and domains of life. We then outline questions drawn from diverse fields of research that address current gaps in our understanding of winter ecology and how winter influences multiple levels of biological organization, from individuals to ecosystems. Finally, we highlight the potential consequences of changes to both the length and severity of winter due to climate change, and discuss the role winter may play in mediating ecosystem function in the future.

Key words: climate change, communities, ecosystems, individuals, populations.

Résumé : Les conditions hivernales imposent des contraintes dramatiques aux écosystèmes tempérés, boréaux et polaires, et elles façonnent les interactions abiotiques et biotiques qui soutiennent ces systèmes. Aux hautes latitudes, l'hiver peut durer plus longtemps que la saison de croissance et il peut avoir un impact disproportionné sur les organismes et les écosystèmes. Malgré cela, notre compréhension des implications écologiques de l'hiver est souvent insuffisante. En effet, même ce qui définit exactement l'hiver n'est pas clair actuellement et les frontières qui délimitent cette saison sont floues à travers les domaines marins, d'eau douce et terrestres et les champs de la biologie. Les auteurs discutent ici de la complexité de définir l'hiver et soulignent l'importance de maintenir la capacité de tester des hypothèses à travers les saisons, les royaumes et les domaines de la vie. Ils présentent ensuite des questions tirées de divers domaines de recherche qui visent à combler les lacunes actuelles dans notre compréhension de l'écologie hivernale et de la façon dont l'hiver influence de multiples niveaux d'organisation biologique, des individus aux écosystèmes. Enfin, ils soulignent les conséquences potentielles des changements de la durée et de la rigueur de l'hiver dus aux changements climatiques et discutent du rôle que l'hiver pourrait jouer dans la médiation de la fonction des écosystèmes dans le futur. [Traduit par la Rédaction]

Mots-clés : changements climatiques, communautés, écosystèmes, individus, populations.

Introduction

Ecologists have traditionally regarded winter as a dormant time of year; a time when most organisms actively or passively depress their metabolism or seek out warmer climates until spring arrives. This view, in combination with the arrangement of academic calendars and logistical difficulties associated with field work during the coldest months of the year, has restricted the scope of research conducted during winter and thus there is an under-representation of the ecological importance of winter (Marchand 2013; Studd et al. 2021). Despite the many challenges, a growing number of ecologists who brave winter conditions are striving to reveal its many snow-covered and ice-encased secrets. In direct contrast to historical attitudes around winter ecology, recent studies have provided strong evidence that the winter

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environment is far from dormant (Berge et al. 2015; Hampton et al. 2017; McMeans et al. 2020). In some systems, winter can be a period of unexpectedly high productivity (Darnis et al. 2012), while in others, specialized organisms remain active year-round, maintaining interactions and energy flow between species (Humphries et al. 2017), and even underpinning species coexistence (McMeans et al. 2020). Regardless of an organism's overwintering strategy, winter conditions can shape survival and reproduction (Berteaux et al. 2017), population dynamics (Kreyling 2010), and food web structure (Tremblay et al. 2012; McMeans et al. 2015). Thus, winter is a critical period for which we need a better understanding.

Winter imposes unique challenges to survival for many taxa; however, it can also introduce ecological opportunities, such as reduced competition and access to otherwise rare resources that are critical for many species at high latitudes (Bokhorst et al. 2009; Farmer et al. 2015; Forrest 2016). However, at high latitudes, winter is changing more rapidly than any other season (IPCC 2013). With the continued acceleration of global climate change, boreal and arctic systems have experienced some of the most dramatic warming on the planet, with annual average temperatures rising 2.7 °C in the past 30 years (IPCC 2013; Box et al. 2019), much higher than rates of change in tropical (0.26 ± 0.05 °C; Malhi and Wright 2004) and temperate systems (0.9 °C; Zhang et al. 2000). Water bodies that historically froze for months every year now go full winters without freezing over (Sharma et al. 2019). In less extreme situations, freeze–thaw events are becoming more common, owing to the ever-increasing frequency of winter whiplash — drastic and rapid oscillations in temperature and precipitation (Cohen 2016; Swain et al. 2018; Casson et al. 2019). For organisms and systems that are adapted to cold, dark, and snowy periods, a warming climate that drives winter temperatures beyond critical thresholds (e.g., 0 °C, the freezing point of water) will alter outcomes at all levels of biological organization and introduce a cascade of biological consequences across systems.

Recent climate change research has led to the realization that winter warming and winter weirding (i.e., deviations from traditional norms of winter) may have far greater impacts on biodiversity than previously appreciated, generating increased motivation for studying winter and the effects of winter conditions on the ecology of species and ecosystems. As more researchers begin to focus on this understudied season, there is a need to pause and identify the major knowledge gaps. Here, we bring together a group of scientists with diverse expertise across ecosystems, taxa, and biological scales to pose questions we believe are most crucial to advancing our understanding of how winter influences individuals, populations, communities, and ecosystems, and how climate change impacts these relationships. We start by discussing how researchers have attempted to define what winter is, highlighting the range of perceived definitions and the complexity that exists in defining this season across systems and organisms. We then underscore the importance of using a definition of winter that allows for explicit hypothesis testing about the role of winter in shaping biological phenomena across time, taxa, and systems. Next, we focus on fundamental questions that will advance our understanding of natural systems, explicitly considering organism-, population-, community-, and ecosystem-scale impacts. We conclude by considering the management implications of continuing to ignore the impacts of winter on wildlife and highlight current knowledge gaps surrounding winter in the context of continued climate change.

What is winter?

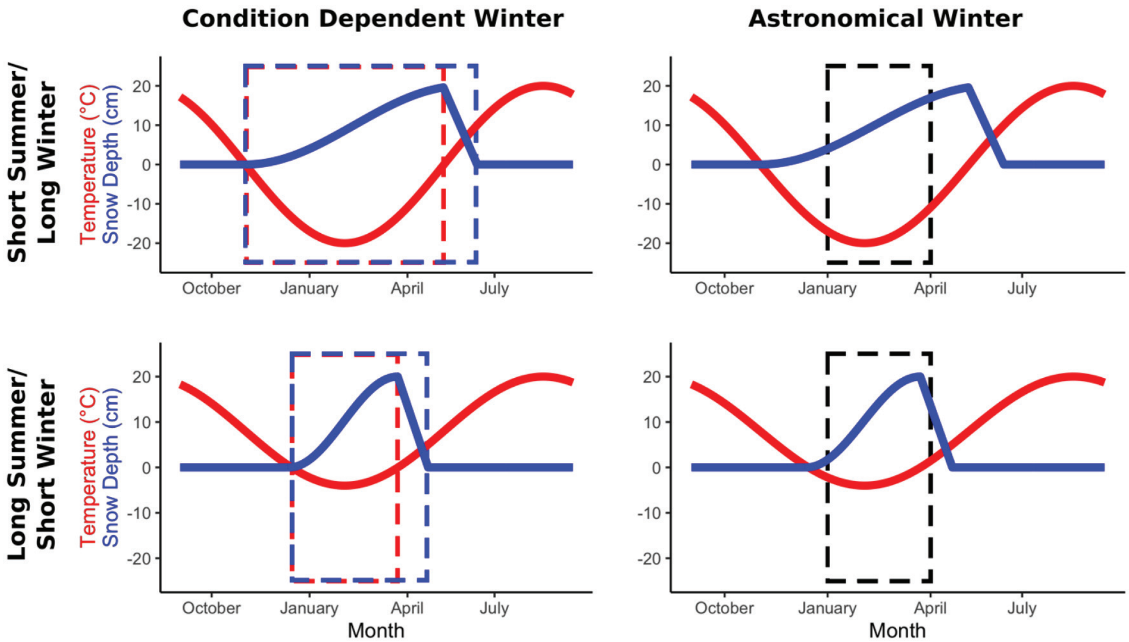
Images of temperate, boreal, and Arctic winters commonly depict snow, ice, and cold weather; however, defining winter for these latitudes can be difficult. In the broadest terms, winter is the coldest season of the year, caused by the shifting of the Earth's rotational axis during its migration around the sun, which results in spatially heterogeneous fluxes of incoming solar radiation. While each part of the planet goes through "winter", the seasonal amplitude of temperature is most severe in the northern hemisphere (Serreze 2015; Turner 2015), driven primarily by the interactions of land mass and oceanic heat fluxes. Land masses increase average summer temperatures and decrease average winter temperatures, whereas water masses reduce variation in average annual temperatures (Kraus and Morrison 1966; Dickinson 2015). In the northern hemisphere at north-temperate and Arctic latitudes, winter is characterized by long, cold, dry periods, where temperatures can reach –49 °C, and daylight can be almost entirely absent (Serreze 2015). These fluxes of energy, heat, and light from solar radiation underlie variation in what winter is, but are not necessarily accounted for when authors define winter itself.

Defining winter remains a contentious issue, and definitions are often specific to a focal system or geographic area. Meteorological definitions confine winter to the three coldest months of the year (Huschke 1959), whereas more recent works suggest delineations of winter that depend on the satisfaction of specific environmental criteria, such as maximum daily temperatures (Mayes Boustead et al. 2015) or lake and river ice cover (Shuter et al. 2012). However, these definitions of winter can vary dramatically between biomes, geographical locations, terrestrial and aquatic ecosystems, and even freshwater and marine systems (e.g., Kielland et al. 2006; Contosta et al. 2019). Such definitions may limit the range of testable ecological hypotheses, because they outline a "bounding box" for winter that depends on focal variables (e.g., ice cover, temperature). As such, the focus is shifted towards the temporal axis on which winter's bounding box sits (i.e., the length and timing of when winter-defining characteristics are achieved), as opposed to the focal variables themselves. Compartmentalized definitions that constrain "winter" to system-specific conditions hinder our ability to adopt a general framework for describing winter, and likely limit the translation of existing knowledge between levels of biological organization and across geographic locations (Fig. 1).

In light of ongoing climate change, it is imperative to forecast how continuing changes in climate will impact organisms. Although characterising winter at a local or system-specific scale has value, generalizing more broadly will also allow for an understanding of how winter is changing across space. This could, in turn, allow researchers to identify ecosystems that are experiencing the most rapid changes, or even quantify how variation in winter conditions influence individuals, populations, communities, and ecosystems. Without a generalizable definition outlining the bounds of winter, or how to characterize winter outside of single focal systems, it will be difficult, if not impossible, to develop broad characterizations of how winter is changing and how these ongoing changes influence organisms.

Numerous studies have proposed unifying definitions of winter to facilitate broader comparisons across geographic areas and between ecosystems (e.g., Ladwig et al. 2016; Contosta et al. 2020). These proposed definitions attempt to define winter based on select characteristics and typically rely on the fact that winter is considered to be a "frigid" season (Contosta et al. 2020). For example, Ladwig et al. (2016) defined the timing and duration of winter based on the 90% freeze/frost probability for each site in their analysis. Similarly, Contosta et al. (2020) define the start and end of winter based on the occurrence of four days of below freezing air temperatures and snow cover within a seven-day period. In contrast to these meteorological definitions of winter that rely on temperature or snow cover data, we propose a two-step approach that can be used to test hypotheses across temporal (e.g., interannual) and spatial (e.g., between systems and geographically) scales. First, we propose that photoperiod should be

Fig. 1. Conceptualization of how different definitions outlining the boundaries for winter have imposed divergent interpretations of winter across the years. In instances where winter is defined by specific focal conditions, the period defined as "winter" is mobile and adjusts to changes in these conditions across years. Thus, the length of winter is the predominant characteristic that varies. However, when winter is defined by a fixed, photoperiod window, conditions within that window are likely to change. In this way, winter processes can be more easily compared longitudinally and geographically. Blue lines represent seasonal snow depth, with the blue boxes representing winter as defined by minimum snow depth. Red lines represent seasonal water temperature, with the red boxes representing winter as defined by temperature. The black boxes represent winter defined by photoperiod.



used as the overarching characteristic to bound winter to facilitate temporal comparisons ("meteorological" definition of winter), because photoperiod represents a causal mechanism driving seasonal conditions. Although the magnitude of photoperiodic variation can be extensive and varies widely based on latitude, the phenology of photoperiodic cycles changes little from year to year, and is relatively consistent across biomes and geographic regions. By delineating boundaries that are relatively static in time, the magnitude and phenology of focal variable fluctuations within that window can be used to quantify system-specific winter conditions, while also facilitating comparisons across time.

Once photoperiod has been used to bound the length of winter, a condition-dependent definition using maxims (a maxim is a fundamentally held truth or principle) can be leveraged to outline the characteristics of contemporary winters that facilitate and motivate hypothesis generation in winter ecology (Studd et al. 2021). Studd et al. (2021) proposed nine maxims of winter (1. Cold, 2. Frozen, 3. Snowy, 4. Dark, 5. Less productive, 6. Variable, 7. Deadly, 8. Understudied, and 9. Changing) that provide a clear way to both define and compare winter between systems, and spatial and temporal scales (Fig. 2). For example, maxims can highlight similar constraints between systems imposed by a suite of environmental factors. Predictable changes in photoperiod lead to dark winters and phenomena like "polar night" (when night lasts for longer than 24 hours) at high latitudes, while snow and ice cover can cause winter to be dark in aquatic systems. Additionally, while these maxims clarify "what winter is", they also allow for broad comparisons to be made across systems, and can be used to assess the relative impact that predictable changes in abiotic conditions (i.e., shorter photoperiods and colder temperatures) have on organisms, populations, communities, and ecosystems. Maxim seven ("winter is deadly") illustrates this point, because in terrestrial ecosystems winter mortality may be driven predominantly by low temperatures and snowfall. In contrast, in limnic and marine environments, winter may be deadly not because temperatures fluctuate greatly, but because of ice cover that potentially limits oxygen concentrations, or the growth of photosynthetic organisms that many species rely on for food (Studd et al. 2021). Establishing maxims that exist for various regions that experience winter can help to guide ecological research and provide a way to organize comparisons between systems that otherwise seem disparate.

We have outlined a series of questions within the context of these maxims of winter, arranged according to levels of biological organization (Organisms, Populations, Communities, Ecosystems). The final sections review potential challenges to natural resource management and climate change research driven by winter processes (Management Concerns, Climate Change). All of these questions are preceded by a brief review of the known influences of winter on each level of organization and key areas of uncertainty, where questions are referred to explicitly in-text to help direct the reader. All of the questions focus on the direct and indirect effects of winter at each level of biological organization to highlight key uncertainties and expand our understanding of the importance of winter (Fig. 3). Many of these questions can be applied across systems and taxa to understand the broad consequences of winter. However, some questions are specific to a particular system (e.g., terrestrial, limnic, or marine) and we state alongside these questions which system or taxa they are directed towards in these cases.

Organisms (general and physiology/behaviour)

Environmental stressors are experienced, and responded to, at the individual level, and thus a comprehensive understanding of organismal biology is central to determining the effects of winter. The reduction of temperature-dependent biochemical reaction rates, coupled with the threat of chill injury and thermal stress has given rise to many unique survival strategies (questions 1–3;

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Fig. 2. Winter can vary across space and between systems, for example, with respect to snow and ice cover (e.g., A–C). Additionally, winter can vary over time (D and E represent the same lake in different years) with potentially high interannual variability in environmental conditions. Researchers interested in understanding the consequences of this variability can experimentally manipulate winter conditions (F) and monitor the effects on individuals, populations, communities, and ecosystems. As climate change continues to cause winter to change, it is imperative to understand how winter influences a variety of ecological processes at different biological scales. Photo credits: (A) Antóin M. O'Sullivan; (B) Brian Hayden; (C) Ocean Networks Canada; (D); (E) Alex O. Sutton; (F) Pamela H. Templer.

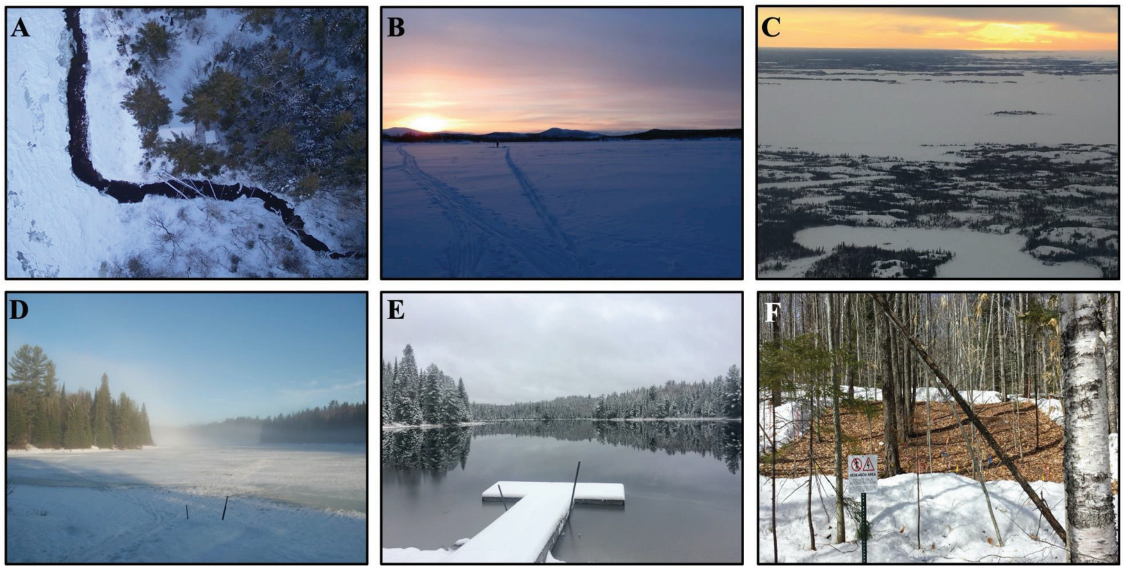
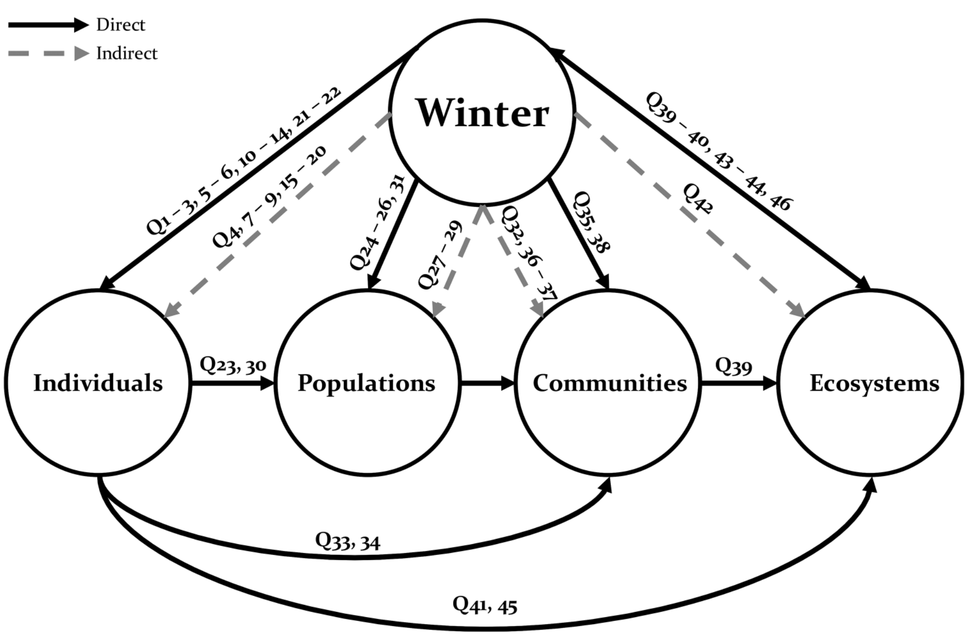


Fig. 3. Conceptual diagram outlining the direct and indirect effects of winter on various levels of biological organization, with unanswered questions highlighting where key uncertainties remain in winter biology. This diagram demonstrates that uncertainties exist across all levels of biological organization, and is a non-exhaustive list of the possible interactions within or between levels of biological organization. Furthermore, it displays the range of impacts, both direct and indirect, that winter can have. Climate change also has the potential to influence all proposed interactions and is likely to influence the magnitude of the effects of winter on all levels of biological organization. Questions that appear throughout the text have been mapped onto this diagram to identify what effects of winter these questions address. Black arrows represent direct effects, gray arrows represent indirect effects, and the arrowhead represents the direction of the proposed effect. Single headed arrows indicate a unidirectional relationship, whereas two-headed arrows represent bi-directional relationships.



Sinclair 1999; Shuter et al. 2012; Convey 1996; Bartlett et al. 2020). Despite an ability to (partially) mitigate the effect of stressors and mortality, performance nonetheless varies across a myriad of dimensions (e.g., taxa, thermal variability; Williams et al. 2012*a*, 2012*b*), and this context-dependency will necessitate the consideration of many intrinsic and extrinsic factors (questions 4 and 5). Colder temperatures can also induce oxidative stress, and the efficacy of physiological strategies to cope with radical production varies extensively (questions 6 and 7; Lalouette et al. 2011; Stier et al. 2014; but also see Blagojevic et al. 2011). How these stressors influence organism life history and overwinter survival outcomes remains very poorly understood (questions 8 and 9). Moreover, while ectotherms can benefit from reduced energy depletion, costs increase for endotherms as temperatures fall below their thermal-neutral range (i.e., the range of temperatures in the environment at which an individual can maintain a normal body temperature without needing to use energy beyond its normal basal metabolic rate; Romano et al. 2019). These unique winter maintenance and activity costs likely influence other aspects of organismal physiology, including immunity and the microbiome (Question 10); however, very little has been done to directly quantify these influences.

Exposure to the cold is also necessary for the initiation of many life history processes. Many insects and plants have minimum chilling requirements prior to the resumption of development (Sung and Amasino 2004; Forrest 2016). Some fish species also require low temperatures during winter to optimize reproductive success (Farmer et al. 2015); however, cues (e.g., photothermal regimes) that emerge during winter and their resultant influences have yet to be fully unpacked. Extensive snow and ice cover limits oxygen availability in terrestrial and aquatic systems (although oxygen saturation through convective mixing is still possible in large lakes; Yang et al. 2017); introduces thermal refugia for endotherms (Pauli et al. 2013); influences mobility (Parker et al. 1984; Richard et al. 2014); and attenuates light (Blanchfield et al. 2009). The consequences of these environmental conditions on organism life history are not well studied, although they likely mediate activity, survival, and reproductive outcomes across systems.

Consequences of winter stress are further modulated by variability in abiotic conditions (Question 11; e.g., extreme events: Bokhorst et al. 2009). Both mid-winter warm spells and cold snaps impact energetics (Question 12; ectotherms, Hahn and Denlinger 2011; endotherms, Humphries and Umbanhowar 2007), and can induce injury or death across both terrestrial and aquatic systems (Salt 1961; Donaldson et al. 2008; Lukatkin et al. 2012). Often, these temperature extremes occur in quick succession, resulting in weather whiplash and freeze–thaw cycles (Question 13). Snowmelt, for example, exposes organisms to refreeze, with consequences ranging from cold injury and ice encasement, to substantial energy savings (Gudleifsson 1993; Hoback and Stanley 2001; Marshall and Sinclair 2012). Likewise, the exposure of soils to cold temperatures can result in frost heave and damage to plant roots (Question 14; Groffman et al. 2001; Bergsten et al. 2001). Although generally more stable, convective upwelling and wind-fetch in marine systems can drive large daily temperature swings upwards of 18 °C (Bates et al. 2018). Our understanding of how these winter processes influence organism-level outcomes remains rudimentary in many systems, despite their potentially far-reaching implications.

Beyond temperature fluxes, winter also presents a unique suite of anthropogenic disturbance regimes. Artificial snowscapes such as managed ski trails can alter habitat quality for arthropods (Negro et al. 2010). Similarly, ice manipulation along shipping lanes facilitates the penetration of light and oxygen into the water column. Even for a given disturbance that can be experienced across multiple seasons (e.g., catch and release angling), the combination of intrinsic and extrinsic conditions specific to the winter period might influence organism responses. Our ability to predict how anthropogenic disturbances will affect overwintering organisms is limited by the lack of current consideration for such relationships (Question 15). Quantitative analyses across disturbance gradients are needed to better understand and manage systems that are impacted by anthropogenic activity during the winter.

Winter effects are often considered in a short-term context (e.g., acute metabolic changes, mortality), but can also be expressed over time as individuals exhibit chronic and sublethal energetic costs of winters past (questions 16 and 17). Abnormally warm winters lead to, for example, delays in the emergence of invertebrates (Stålhandske et al. 2015). Winter experiences can also result in stress "memories", encoded in the form of epigenetic markers with transgenerational consequences (questions 18 and 19; Bruce et al. 2007). In addition to winter experiences dictating performance in other seasons (i.e., through carry-over effects), the reverse is also true, because processes such as resource accumulation, behavioural modification, and physiological preparation during the active season can all play essential roles in subsequent overwintering success (questions 19 and 20; Gilbert et al. 2010; Sinclair 2015; Fernandes and McMeans 2019). The number of seasonal cycles experienced may also shape these seasonal strategies and their resultant outcomes (Question 21). However, the identification of these relationships has only recently begun. Developing a better understanding how winter conditions directly or indirectly shape individual physiology and ecology will be central to successful management moving forward.

Questions

1. How entrained are (aspects of) winter strategies, and how much do the strategies utilized depend on individual experience, energetic condition, and environmental context?
2. What winter conditions drive the breakdown of seasonal buffering mechanisms, and what are the sublethal implications of such a breakdown?
3. To what extent is behaviour constrained by physiological state during winter?
4. What is the relative importance of intrinsic vs. extrinsic cues and triggers that influence decisions (e.g., when to stir) during winter?
5. How do light, temperature, and oxygen (aquatic only) regimes experienced during winter interact to shape life history outcomes and decisions (e.g., reproduction, growth, migration) in both the short and long term?
6. How do winter conditions influence the relative risk and impact of oxidative damage?
7. What role does the production and accumulation of reactive oxygen species play in mediating physiological responses to winter and winter-time decision making?
8. What are the critical winter oxygen levels for survival and activity in aquatic organisms?
9. To what extent does aerobic scope constrain the activity of ectotherms at low temperatures?
10. How does winter shape the microbiome of wild organisms?
11. To what extent do the frequency, duration, intensity, and timing of winter stressors affect performance?
12. How do the consequences of weather whiplash events differ amongst ectothermic and endothermic organisms?
13. How much more costly are weather whiplash events for terrestrial species relative to temperature fluctuations that remain below the important biophysical and physiological threshold of 0 °C?
14. What is the relative importance of physical effects driven by winter processes (e.g., frost heave, frazil ice, wave regimes/wind fetch) for determining stress/physiological risk in organisms?
15. What is the impact of winter disturbance (e.g., anthropogenic noise, capture and handling, storms, forest harvest) on individual performance relative to disturbances experienced in

other seasons, and how does this cost vary when the disturbance is the same (e.g., catch-and-release angling) vs. season-specific (e.g., winter ice storms vs. summer heat wave)?

16*i*. How do levels of stress imposed by winter (e.g., freezing, hypoxia) interact or shape the ability of organisms to cope with stress during the summer (e.g., heat, drought)?

16*ii*. Do traits that maximize survival during harsh winters trade-off with those that maximize survival during harsh summers?

17. What is the influence of winter stressors relative to other factors (e.g. natural enemies, host quality) in the establishment of alien organisms?
18. What is the relative importance of carry-over effects that emerge in winter vs. from winter?
19. To what extent are winter carry-over effects responsible for shaping major life history events (i.e., migration, spawning cycles, post-winter emergence phenology)?
20. What is the role of nutritional quality (e.g., micro- and macronutrients) in preparing for or sustaining life in winter, and are there specific micronutrients that are most limiting?
21. What is the relative energetic cost of seasonal acclimatization?
22. To what extent do winter stressors drive life history characteristics in short- vs. long-lived organisms?

Populations

Although environmental conditions during winter can directly shape ecological and physiological consequences at the individual level, emergent properties that only manifest at higher levels of biological organization necessitate broad-scale questions and investigations (Question 23). Studies of a variety of taxa from diverse biomes have found that winter is an important portion of the annual cycle with consequences on population vital rates and population growth (Altwegg et al. 2005, 2006; Gamelon et al. 2017; Woodworth et al. 2017; Bargmann et al. 2020). However, despite the growing recognition of the importance of winter in understanding population growth, there remains a wide array of questions to be answered about the influence of winter on populations.

Leveraging the growing number of published studies investigating how winter influences populations can provide insight into broader trends of the mechanisms by which events in winter influence populations, and how interspecies variability in life history traits may influence their susceptibility to the effects of winter (Question 24; Altwegg et al. 2005). Abiotic winter conditions are a potentially important selective filter, but variation in the behavioural and physiological responses of individuals to these harsh abiotic conditions can also buffer or magnify the effects of these conditions on populations (Leirs et al. 1997; Coulson et al. 2001; Uelmen et al. 2016; Froy et al. 2019; Masoero et al. 2020). Broader life-history characteristics, such as life span (Sæther and Bakke 2000), overwintering strategy (e.g., hibernation, migration or remaining active), and behaviour during winter (Sutton et al. 2016, 2021), could also mediate or enhance the effects of winter on population vital rates (questions 25–27). Additionally, if animals aggregate in smaller patches of suitable habitat, it will also be important to understand how density-dependent processes are likely to interact with winter to shape population dynamics (questions 28 and 29).

Understanding broader patterns that describe the varying impacts of winter can predict population-level responses to winter for data-deficient species and future population trends from across a species' range, rather than restricting inference to a single population. The evidence suggests that populations at certain range extents may be more sensitive to winter severity and changes to environmental conditions (Ringsby et al. 1999; Veteli et al. 2005; Waite and Strickland 2006). These populations could be used to predict future responses to winter conditions as climate change continues to cause shifts in environmental conditions. Furthermore, comparative analyses of multiple populations across a species' range, may provide insight into the generalizability of responses to winter and allow us to better predict how species, not just focal populations, respond to a range of winter conditions (Question 30). Synthesis across systems (e.g., aquatic vs. terrestrial) will also help to identify possibly divergent mechanisms by which winter can influence population dynamics (Question 31).

Questions

23. To what extent do carry-over effects on individuals contribute to population dynamics?
24. Does winter have a disproportionate effect on certain population vital rates (e.g., survival, fecundity)?
25. Relative to other environmental processes, what is the role of winter as a selective filter on populations?

26*i*. To what extent do winter conditions currently serve as environmental filters against the persistence of species in regions of mid/high latitude/elevation?

26*ii*. What are the most important filters in terrestrial vs. aquatic systems?

27. Are certain types of species (e.g., R vs. K selected species) more susceptible to winter as a selective filter?
28. How does winter interact with density-dependent processes to influence population growth?
29. How do aggregations of wildlife in the winter interact with environmental conditions to modulate density-dependent processes?

30*i*. How flexible and variable are responses to winter within species or populations?

30*ii*. How generalizable are certain winter "strategies" across individuals, populations, or species?

31. Does winter have similar effects on both aquatic and terrestrial population dynamics?

Communities

The mechanisms that regulate the composition, structure, and dynamics of biological communities remain poorly understood. Community composition is broadly influenced by ecological filtering, dispersal capabilities, and environmental tolerances of the component species, while structure (relative abundance and distribution of taxa) and dynamics are shaped by species' environmental preferences (i.e., optima), and by the nature and intensity of their interactions with one another and their environment. As with other subdisciplines of ecology, most of our understanding of community processes has been derived from tropical systems or examinations of temperate areas during the warmer months (Hampton et al. 2015). At high latitudes, winter represents a relatively un-investigated period that is likely to yield novel insights into the manner by which species coexist under seasonally fluctuating environmental conditions and community interaction regimes (questions 32 and 33).

Outside of the tropics, seasonal fluctuations in solar irradiance are associated with often dramatic changes in basic habitat parameters, including ambient temperature, photoperiod, and the availability of liquid water. At the base of the food web, this often leads to decreased primary productivity (e.g., Bramburger et al. 2020) and associated reductions in food resource availability in many ecosystems. Sub-zero temperatures, oxygen limitations, and resource scarcity impose physiological constraints upon many taxa, and can be sufficiently harsh to induce mortality or dormancy in non-hardy taxa, driving migration and hibernation in others that can change their behaviour to avoid the most severe winter conditions. Further, snow and ice cover often constrains habitat connectivity and limits the dispersal of propagules among suitable patches. Consequently, winter communities are effectively less diverse than their summer counterparts. The duration and severity of winter conditions are often potent structuring agents of regional biodiversity, and taxa that thrive in areas characterized by harsh winters are often specifically adapted to winter conditions and can capitalize upon the effects of winter on species that are less well-adapted (Question 36).

The relative lack of biological activity during the winter presents various challenges and opportunities for overwintering species, resulting in shifting community dynamics. For taxa that are active during the frozen season, particularly consumers, the relative inaccessibility of food resources can cause intensification of interspecific competition and shift the food web towards top-down pressure on the few resources that remain (Humphries et al. 2017). In contrast, with fewer organisms active under harsh conditions, those species that are tolerant may enjoy a release from competitive interactions, predation, or grazing pressure (Question 36; McMeans et al. 2020). Scarce food resources and changes in consumer abundance or pressure can also de-couple the trophic linkage characteristics of warmer seasons and could restructure winter food webs (questions 34 and 35). A poignant example of this decoupling in both aquatic and terrestrial food webs is migration out of a system or metabolic arrest (e.g., hibernation, diapause), which effectively cuts off species interactions (McMeans et al. 2015; Humphries et al. 2017). Re-structuring can occur when consumers shift their diet towards different resources during winter. For example, in aquatic and terrestrial food webs, allochthonous, detrital-based pathways may become more important (McMeans et al. 2015). Several reports also suggest that aquatic consumers shift towards benthic or littoral prey during winter, which may be less susceptible to winter declines in abundance than their pelagic, phytoplankton-supported counterparts (Question 35; Caldwell et al. 2020).

The presence of winter-active organisms may indirectly affect other members of the community that are only active in warmer months, by modifying or consuming a shared resource (Question 36). For example, a winter active predator may shift its diet to feed on a small herbivore that is abundant during the winter but otherwise ignored when other prey species are available. Decreases in the number of those herbivores as a result of winter predation could lead to food shortages in spring for other predator species that hibernated through the winter. In contrast, winter-active organisms could facilitate spring- or summer-active organisms. For example, winter-active detritivores could break down leaf-litter deposited in autumn, making nutrients more readily available for spring-active detritivores that are lower down in the detrital processing chain (Heard 1994). This is particularly relevant in lotic systems, where terrestrial-derived allochthonous material (predominantly leaf litter) may be decomposed and mineralized during winter, resulting in the availability of nutrients to fuel primary production in the spring (Question 37). Furthermore, differential responses to environmental conditions throughout winter could also cause shifts in species interactions, further modulating the strength of species interactions (Question 38).

Questions

32. Does the occurrence of winter stabilize or destabilize populations, food webs, and community dynamics?
33. Are taxa being differentially influenced by changing environmental conditions throughout winter, and what physiological (e.g., thermal preference, energetic status) and ecological traits (e.g., functional group) explain these differences?
34. Are winter food webs supported by fewer resources, characterized by fewer trophic linkages and dampened top-down regulation?
35. If primary production declines in the winter, do winter food webs shift towards reliance on detrital-based pathways?
36. How important is winter in providing a refuge from negative species interactions (e.g., by weakening competition)?
37. How does the seasonal input of terrestrial-derived material in fall and spring influence allocthonous–autocthonous reliance in stream and river communities?
38. How do changing environmental conditions throughout winter influence the strength of trophic interactions (e.g., competition, predation)?

Ecosystems

Studies of ecosystems in the context of winter have focused primarily on how the movement, storage, and flow of energy (i.e., the carbon cycle) and nutrients (primarily nitrogen) vary in response to fluctuating winter conditions at a single site or among sites along climatic gradients. While biological activity, including productivity, decomposition, and nutrient mineralization, typically slows over winter, the contributions of processes in winter to annual cycles can be substantial in regions where winter is relatively protracted (Question 39; Hobbie et al. 2000). The transition from winter to spring (snow melt and soil thaw) can be a time of accelerated transport and loss of nutrients (Hobbie and Chapin 1996), and soil freezing and other stressors associated with winter can have a substantial effect on primary production over the subsequent growing season (Kreyling 2010; Reinmann et al. 2019). Many ecosystem-scale experiments have demonstrated the effects of current and projected changes in winter climate, through snow-removal, snow-addition, and snow-melt manipulation experiments (Campbell et al. 2014; Henry et al. 2018).

Despite recent progress in the study of how ecosystems function in winter and how these processes are likely to be altered by climate change (described in Sanders-DeMott and Templer (2017)), ecosystem studies can be limited by the spatial and temporal scales of experiments and observations, and by an inability to capture the complexity of the interactions involved. Specifically, ecosystem dynamics reflect an integration of biological processes at multiple scales of organization (i.e., organismal, population, community, and ecosystem scales) and are subject to the inherent shortcomings in quantifying these processes (Question 40). Ecosystem-scale experiments are further complicated by the influence of abiotic components (e.g., the geology, topography, climate, and hydrology of the system). When winter conditions are manipulated experimentally at the plot level using shoveling, shelters, heaters, etc., experimental artifacts often arise. For example, contrary to what would occur at the landscape level, plots subject to snow removal can remain artificially wet in spring because of runoff or groundwater recharge from the surrounding area. Likewise, regarding biotic factors, while plot level ecosystem experiments can address the responses of sessile organisms such as plants and soil microorganisms to variability in winter conditions, potentially important interactions with animals such as herbivores or detritivores can be underestimated (or when examined not completely understood) because these mobile organisms can move into and out of experimental plots (Question 41; Moise and Henry 2010; Templer et al. 2012). Regarding temporal scale, the manipulation of winter conditions in the short term can be useful for examining the direct effects of climate or weather on ecosystem processes, but important indirect effects that can occur via long term shifts in species composition (Komatsu et al. 2019) or legacy effects (Question 42) are often not captured.

A further characteristic of winter ecosystem experiments is that they have been conducted disproportionately at a select number of sites (Question 43). Gradient analyses across multiple sites have imparted greater generality to our understanding of how variability in winter conditions can affect ecosystem processes (Question 44), but they are nevertheless vulnerable to the influence of confounding factors. Combining both approaches by coordinating ecosystem experiments that manipulate winter conditions at many sites across natural climate gradients may be an ideal solution, but it requires greater logistical and financial support (Fraser et al. 2013).

Ecosystem-level responses to variability in winter conditions are particularly important to understand in the context of global climate change, given the key role of ecosystems in driving climate change feedback (questions 45 and 46; e.g., changes in the net flux of carbon in response to warming alter atmospheric greenhouse gas concentrations). Answering the following questions will help address the substantial knowledge gaps regarding the spatial and temporal scales of these responses, and the extent to which biotic complexity must be integrated into our understanding of these responses.

Questions

39. How does winter influence energy and nutrient transfer through communities and ecosystems?
40. How effectively can we scale up ecosystem processes measured in experiments conducted in specific sites to the regional scale, utilizing our understanding of geology, topography, and hydrologic connectivity?
41. Given that animals may operate at much larger spatial scales than experimental plots, how can interactions between animals and primary producers be better addressed in ecosystem-level winter experiments?
42. What are the legacy effects of acute frost damage in soils or to tree canopies on terrestrial ecosystems over the longer term (e.g., years to decades), and what mechanisms underlie these legacy effects?
43. What novel insights can be gained by coordinating winter ecosystem experiments across many sites along climatic gradients; what should be manipulated and measured?
44. Do ecosystem-level processes respond more to average winter conditions or to extreme winter events?
45. How does winter constrain or influence important plant functional groups such as vegetation with nitrogen fixers, pests, or invasive species, which can have disproportionate influences on ecosystem processes?
46. What are the contributions of biological processes in winter to annual carbon and nutrient cycles and to processes in other seasons, including the growing season, as well as shoulder seasons such as spring and fall?

Management concerns

Winter presents challenges to organisms in the wild, but also does so for those tasked with managing and conserving wildlife and plant populations, because of knowledge gaps in winter ecology and the difficulty in accessing field sites in the winter (Question 47). Winter climate regimes are shifting, increasing the need for adaptive natural resource management and consideration of winter processes (e.g., winter forest management; Rittenhouse and Rissman 2015). Indeed, failure to explicitly incorporate winter into management strategies can influence populations and management during other seasons (questions 48 and 49). Predictive tools are therefore required to incorporate both exposure and species' sensitivities to winter conditions, in particular at higher latitudes where life persists for more than half the year in winter conditions.

The capacity of both terrestrial and aquatic animals to be buffered from winter conditions, escape predation during the winter, and emerge from winter with adequate energy reserves have strong management implications. For instance, quantifying and identifying seasonal variability as a key climate-change driver of biological responses provides insights with significance for population biology, the trajectories of species invasions, and geographic range expansions (Rahel and Olden 2008; Pecl et al. 2017), and the outcomes of species interactions, such as disease dynamics (Question 50; Begon et al. 2009) and coexistence (Question 51; McMeans et al. 2020). Characterizing winter habitats of wildlife, especially for organisms that aggregate or have specific hibernation requirements, is essential for habitat management including both protection (e.g., limiting development activities; McKinnon and Hnytka 1988) and restoration (e.g., increasing prevalence of habitat types that enable overwinter survival; Elphick and Oring 1998; Taft and Haig 2003). This includes the availability of microhabitats for many species to survive winter during hibernation or torpor, such as animals that burrow within leaf litter and soil, or use rocky crevices as overwinter refugia. Moreover, understanding the vulnerability of important wildlife and ecosystems to different stressors such as human disturbance (e.g., wildlife responses to winter recreation; Cassirer et al. 1992) are also necessary to devise plans that reduce conflict between humans and wildlife (Question 52; Braunisch et al. 2011). Habitat used in the winter is rarely classified as "critical", which suggests that valuable winter habitat is more susceptible to loss or disturbance, potentially limiting population growth or recovery (Question 53; Cunjak 1996). Refining natural resource management policies and practices to consider events throughout the annual cycle has the potential to greatly improve management outcomes (Question 54; e.g., Zeug et al. 2012; Osnas et al. 2016), recognizing that carry-over effects are often manifested across seasons, especially in winter (e.g., Midwood et al. 2015).

Questions

47. What type of training is needed to prepare natural resource practitioners to consider winter in management decisions?
48. How do land use decisions, management/fishing regulations, and habitat restoration influence wild organisms during winter?
49. To what extent do winter threats contribute to the imperilment of wildlife?
50. How does winter contribute to disease dynamics (transmission, pathogenicity)?
51. How will invasive and range shifting species alter community structure and function during winter?
52. Are "so-called" winter construction windows beneficial or detrimental to wildlife, and how can they be altered to be more effective?
53. What specific types of policies and regulations are needed to protect critical winter habitats?
54. What are the management implications for rapid/unpredictable responses to changes in winter conditions/seasonal transitions (e.g., hunting/angling seasons and regulations, flow regulation in reservoirs + rivers during spawning runs and migrations, etc.)?

Climate change

Climate change is a dynamic process, involving changes to many environmental variables with distinct signatures in different seasons and many possible patterns of change. During summer months, shifts in air and ocean circulation cause increases in the frequency of extreme events, including heat waves and wildfires. However, climate change arguably has a greater impact in winter than summer, for example rates of warming in Northern Europe in winter outpace those seen in summer (Question 55; Elliott and Elliott 2010). The rapidity of such changes to high-latitude winters presents a unique challenge to researchers studying winter processes; as scientific interest in this season increases, so too do the forces driving its attenuation. In addition, winter conditions across the globe are changing in potentially very different ways, and it will be important to characterize how winter is changing and what factors may influence these changes across space and time (questions 56 and 57). In both freshwater and marine systems, the duration of ice-cover has been steadily decreasing over the last century (Sharma et al. 2016). This has reciprocal effects for biotic communities because spring melt occurs earlier in the year, causing disequilibria with the phenology of natural (Shuter et al. 2012) and managed events (Horstkotte et al. 2017). In terrestrial systems, a feedback loop whereby a reduced albedo effect increases winter warming is speeding up snowpack loss in northern regions (Kim et al. 2019), with implications for snow-associated biotic communities (Berteaux et al. 2017) and with potentially more devastating effects therein than for aquatic ecosystems, which may be otherwise buffered from climate change (Question 58). However, in some regions, instead of winter warming, harsher winters with longer cold spells are expected, including changes in lake and sea ice and storm regimes (Question 59). This presents ecologists with the variation necessary to investigate the consequences of different rates of climate change on natural systems and the potential to investigate the long-term consequences of these winter climate changes relative to climate changes during other seasons (Question 60).

In some cases, strong biological responses to these environmental changes have emerged. For instance, species' geographic ranges are extending polewards across multiple biomes as species are able to survive winter in regions that were once inhospitable (Parmesan 2006; Poloczanska et al. 2013; Pecl et al. 2015). Similar trends have been observed across a variety of taxa, including plant and algal communities, marine and freshwater fishes, plankton, mammals, and insects (IPCC 2014). While this pattern of warming winters and changes in resident biotic communities is well documented, the mechanisms through which changing winter conditions drive biospheric changes are less well understood.

At the individual level, it is important to understand how climate change may directly impact strategies used to cope with harsh winter conditions (Question 61) or the potential benefits of these strategies (Question 62). Tracking these shifts in coping strategies and the benefits of these shifts could also illuminate broader patterns of rapid evolution (Question 63) and the timescales over which changes in traits occur (Question 64). It could also shed light on the potential downstream consequences of changing environmental conditions on individuals (Question 65) or on broader scales (questions 66–68).

Because individuals are directly impacted by winter climate change, it is likely that interactions between species within a community will experience rapid change. Future research should investigate how the differential impacts of climate change on species may cause shifts in biotic interactions (Question 69). Additionally, it will also be important to characterize how changes in winter characteristics (e.g., length of winter, magnitude of temperature changes and precipitation) may simultaneously act to shape biotic interactions (questions 70 and 71).

Finally, effort should also be made to refine predictive models, with an emphasis on winter precipitation (Question 72). This could allow for targeted research on areas experiencing the greatest changes, and will allow researchers to better predict future climate change to forecast how species may continue to be shaped by changing abiotic conditions.

Questions

55. How is winter changing, and to what degree does this ongoing change vary geographically?
56. Are the effects of winter dependent on spatial scale (e.g., differ with size of the water body)?
57*i*. To what extent does vulnerability to ice loss vary spatially?
57*ii*. Are regions that are most susceptible to ice loss also experiencing the greatest amount of ice loss?
58. Will terrestrial organisms be affected by climate change more rapidly than aquatic/semi-aquatic organisms because aquatic environments are more thermally buffered (both to temperature extremes and variation in temperature) than terrestrial environments?
59. Can we define and predict the spatially explicit impacts of changing jet streams on winter conditions?
60. How do the legacy effects of winter climate change compare in magnitude to other aspects of climate change, such as summer warming, drought, and elevated levels of CO_2?
61. Are changing winter conditions influencing the behavioural/physiological strategies used to cope with harsh environmental conditions?
62. Under what conditions are different winter coping strategies best suited, and which strategies are likely to be most advantageous under climate change?
63. What species, or traits, will exhibit rapid adaptation to contemporary changes in winter and spring phenology?
64. Over what timescales will organisms respond to changes in winter and spring phenology, and how are these timescales associated with generation time and intrinsic variation in physiological/behavioural/ecological responses to environmental cues?
65. How will rapid misalignment between photoperiod and climatic cycles influence anticipatory physiological responses to the initiation and conclusion of "winter" and what are the downstream impacts of misaligned abiotic cues?
66. Which features of winter have the greatest influence on species and, consequently, ecosystem responses to climate change?
67. How does the increased prevalence of freeze–thaw/rain on snow events through winter impact terrestrial ecology at different scales (e.g., habitat quality/availability, mortality, metabolism)?
68. How do changing winters impact light transmission and winter primary productivity in aquatic ecosystems?
69. Given that species will be affected differently by changing winters, how will biotic interactions and energy transfer through food webs shift under winter climate change?
70. How will changing winter conditions influence the timing and magnitude of resource pulse dynamics in the coming years?
71. With the weakening of winter environmental filters as a result of climate change, what response do we expect from species formerly limited by them, and how will it impact local communities?
72. How can current climate change models be modified to better predict winter precipitation?

Conclusions

Although historically understudied, winter has recently been shown to be an important driver of ecological processes, with consequences on all levels of biological organization from individuals to ecosystems. We have endeavored to highlight some key questions that will advance our understanding of the importance of winter and continue to fill in knowledge gaps associated with winter ecology. In light of ongoing climate change it is imperative to understand not only the importance of winter as a driver of ecological processes, but how its impacts may be changing over time. We hope that these questions stimulate future work on understanding the important, but understudied season of winter.

Statement of authorship

All of the authors contributed substantially to the conception, writing, and revisions of this manuscript.

Data accessibility statement

No data was used in this manuscript and, as a result, there is no data to deposit in a public repository.

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