Nine Maxims for the Ecology of Cold-Climate Winters

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Frozen winters define life at high latitudes and altitudes. However, recent, rapid changes in winter conditions have highlighted our relatively poor understanding of ecosystem function in winter relative to other seasons. Winter ecological processes can affect reproduction, growth, survival, and fitness, whereas processes that occur during other seasons, such as summer production, mediate how organisms fare in winter. As interest grows in winter ecology, there is a need to clearly provide a thought-provoking framework for defining winter and the pathways through which it affects organisms. In the present article, we present nine maxims (concise expressions of a fundamentally held principle or truth) for winter ecology, drawing from the perspectives of scientists with diverse expertise. We describe winter as being frozen, cold, dark, snowy, less productive, variable, and deadly. Therefore, the implications of winter impacts on wildlife are striking for resource managers and conservation practitioners. Our final, overarching maxim, "winter is changing," is a call to action to address the need for immediate study of the ecological implications of rapidly changing winters.

Keywords: adaption, ecology, ice, frozen, snow, winter

Many ecologists have treated winter as a biologically dormant season in locations that experience freezing temperatures, which has limited the historical motivation for asking ecological questions during this season. However, contemporary concerns surrounding the impacts of climate change on northern ecosystems have revealed large gaps in our understanding of the ecological role that this dormant season plays (Groisman et al. 2004, Campbell et al. 2005, Barnett et al. 2005). Following the identification of this blind spot in ecology, several studies have moved the field forward by focusing on winter ecology (Contosta et al. 2019, Kreyling 2010, Penczykovski et al. 2017, Williams et al. 2015). The challenge now is to define the boundaries of what is considered winter. Even so, this objective is particularly difficult, given the commonness of the term *winter*, the variability in what winter represents across different regions, and the diversity of environmental characteristics that distinguish the months of the year that define the winter season. Therefore, studies have tended to use idiosyncratic definitions of winter, often relying on regionally specific characteristics (e.g., temperature, presence of snow or ice) that limit the generalizability of study results and generate a requirement for thoughtful comparisons among studies and regions (see Contosta et al. 2019 and box 1 for a discussion of definitions).

In the present article, we provide a framework to define winter, by using knowledge that has been generated since interest in this season grew to create a more comprehensive definition and guide the field moving forward. This framework focuses on the concept of frigid winter (Contosta et al. 2019), which is experienced by over 30% of the world's landmass including temperate, boreal, and polar ecosystems (Lemke et al. 2007, Pauli et al. 2013). We are aware that this framework will not define all possible environmental conditions that are considered winter across the globe but believe that the key parameters we consider represent a majority of winters and that exceptions to our framework will be just as instructive as the inclusions.

We propose nine maxims (a maxim is a concise expression of a fundamentally held principle or truth) for distinguishing winter as a focal season in ecological studies (see figure 1), drawing on the experience of scientists with diverse expertise. Our goal in the present article is to capitalize on the increasing enthusiasm for winter ecology to broadly contextualize winter and help define the emerging field, as well as to coalesce thinking and stimulate research into frequently overlooked aspects of winter ecology. Given the reality of anthropogenic climate change and the associated reduction or even disappearance of the winter conditions that we define in the present article, now is the time to define this season, what it means to organisms, and the

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Box 1. Winter defined.

Winter's multidimensionality—spanning conditions related to temperature, photoperiod, and, at higher latitudes, snow and ice—and winter's variability, differing from one place to another and from one year to the next, precludes a single definition of winter that is both general and precise.

Prioritizing generality over precision, winter can be defined as the 3-month period (if a year is composed of four seasons of equal length) that coincides with the shortest days and the coldest temperatures of the year. This definition situates photoperiod and temperature as codefining winter conditions. Given photoperiod and temperature attain their annual minima on different dates, then defining winter requires a compromise across these two conditions. The 3-month period that includes the months of December, January, and February in the Northern Hemisphere and the months of June, July, and August in the Southern Hemisphere, achieves this compromise by including both the photoperiod minimum (around December 21 or June 21) and the temperature minimum (typically 2–8 weeks later) and, more generally, captures the three coldest and darkest months of the year.

The duration and intensity of sunlight is, in fact, the causal condition. Winter happens because the Earth's axis of rotation is not perpendicular to the plane of its orbit around the sun; winter occurs where sunlight strikes least directly, and summer occurs where sunlight strikes most directly. The Northern Hemisphere's winter solstice, usually December 20 or 21, is the date (and orbital position) when the Northern Hemisphere is most directly angled away from the sun and, as a result, when day length is shortest (above the Arctic Circle, there is no day at all, because the sun remains below the horizon). June 20 or 21 is the Southern Hemisphere's winter solstice. Temperature variation is a consequence of this photoperiod cause. Short days, long nights, and indirect solar radiation combine to create a negative heat balance, which causes the air, land, and water to cool. The thermal inertia of landmasses and water bodies, and (at high latitudes) the time required for ice and snow to accumulate and contribute to albedo, means that minimum winter air temperatures occur sometime after the winter solstice.

When seasonality is applied to landscapes containing diversified microclimates and exposures (e.g., because of varied topography, water body volume or flow rates, vegetation cover, etc.), seasonal transitions still happen everywhere, but at different times in different places. For example, in the mountains in autumn, you can see winter coming; the snow line moves down the mountain over time, because the winter conditions of freezing air temperatures and snowfall occur first at high elevations and later at low elevations. The reverse pattern occurs in spring when, for example, the winter ski season remains open at high elevations long after it has closed at lower elevations. The varied size and thermal inertia of water bodies creates similar diversity in the timing of seasons. In early spring, frogs are calling in open-water ponds when lakes are still frozen. Earlier in the winter, boats and ships are still moving through large bodies of water when snow machines and trucks are traveling on the ice covering smaller lakes. Although these phenological differences are most obvious from mountaintop to valley or Great Lake to pond, they occur everywhere, albeit at smaller temporal and spatial scales, including in places in which topographic and land cover variation is more nuanced. In a general sense, it can be winter in one place, when it is still autumn or already spring in another.

Flipping the definition to prioritize precision over generality, winter can be alternatively defined as the period of the year when a specific condition exceeds or drops below a threshold. For example, in a continental US context, winter has been defined as when daily maximum temperature is below 0 degrees Celsius, or when snow is on the ground, or the days between the first and last frost (Mayes Boustead et al. 2015). These condition-based definitions of winter have the advantage of recognizing location and year specificities in the timing of winter, but also the limitation of isolating one or a few conditions and thresholds as winter defining. Therefore, not only does winter vary in length from year to year and from place to place, but winter does not occur in years and places that do not cross the threshold. The flexibility of condition-based definitions of winter also facilitates recognition that every place in a landscape can be its own season.

implications of rapidly shifting winter conditions. Finally, we recognize the importance of increasing awareness of the ecological implications of winter among resource managers and conservation practitioners. Although our nine maxims may not be equally applicable to all species and systems, we expect our framework will inspire or provoke inclusion of winter into ecological and theoretical frameworks, and create an interest in ecological studies that span all seasons.

Winter is colder

Low temperatures have a pervasive effect on almost every aspect of ecology and biology (for a summary, see Clarke 2017). Enzyme-mediated processes slow exponentially or cease altogether (Brown et al. 2004), and some proteins are denatured in the cold. Biological membranes lose fluidity and lipids become more viscous or even solidify (Somero et al. 2017). Organisms whose body temperature varies with that of the surrounding environment (ectothermic animals, plants, and microorganisms) often have biochemical and phenological adaptations to resist these effects (Campoy et al. 2011, Tattersall et al. 2012, Preston and Sandve 2013). Endothermic organisms (mammals and birds) avoid these effects by expending energy to warm tissues (except hibernators, which lower their body temperature to save energy; Tattersall et al. 2012) or migrate to avoid these harsh

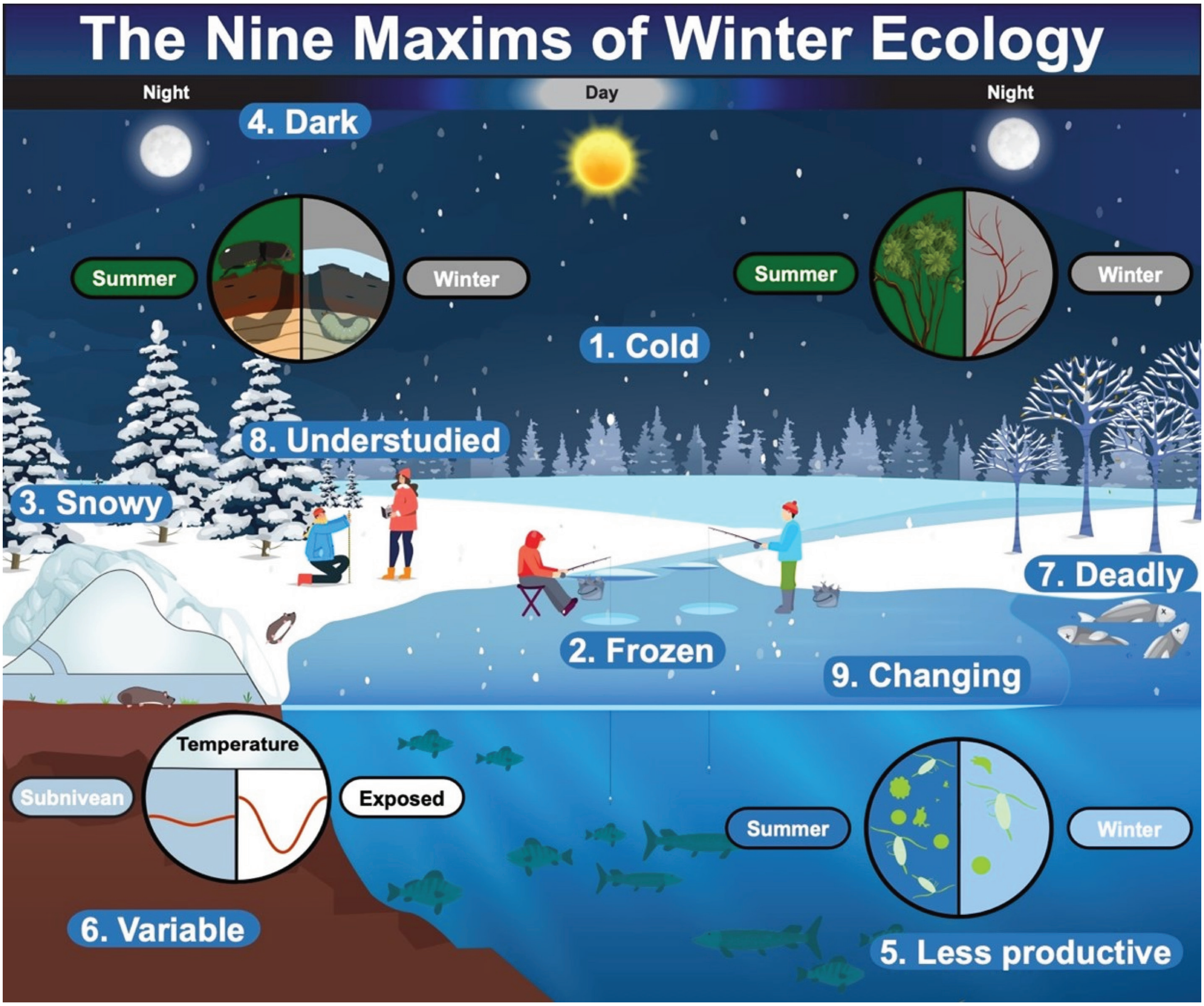

Figure 1. Schematic of a winter scene that highlights the nine maxims. Included within the winter scene are four insets highlighting winter influences on (clockwise from the top left) invertebrate life cycles, plant productivity, aquatic productivity, and thermal buffering of subnivean environments.

conditions (Alerstam et al. 2003). Not all processes slow at an equal rate. Photon capture by photosynthetic organisms that persist in winter, for example, continues at the same rate in the cold, despite a slowdown in the biochemical processes that receive that energy (Hüner et al. 1998); similarly, passive drift of ions and water across epithelia continues, even if active regulation stops (Tattersall et al. 2012). These direct effects of temperature on the biochemical, cellular, and organismal levels cascade to the ecosystem level, meaning that biological processes and ecological interactions in winter may be fundamentally different from those in other seasons. We note that cold is not necessarily bad; some plants (Chouard 1960) and insects (Williams et al. 2015) require low temperature exposure to synchronize phenology or initiate development, and low temperatures are instrumental for energy conservation for overwintering ectotherms (Sinclair 2015).

Winter is frozen

Water changes from liquid state to solid at or below 0 degrees Celsius (°C), depending on the pressure, the concentration of dissolved solutes, and the presence of ice nucleators. Therefore, freshwater freezes at higher temperatures than seawater or the water inside organisms. In some instances, water can remain unfrozen below its freezing point, yielding freezing rain when supercooled droplets hit surfaces and allowing some ectotherms to remain unfrozen at temperatures below −40°C (Clarke 2017). Water expands by as much as 9% when it freezes (Clarke 2017). In soil, this expansion can cause frost heave, driving erosion and bulk movement of nutrients (Hayashi 2013). In water, less-dense ice floats on the surface, partitioning the liquid water from the air, and preventing movement of organisms, gas exchange, modifying light transmission, and minimizing evaporation and heat loss to the atmosphere (Kauko et al. 2017). Therefore, surface ice can form unfrozen refugia that remain above 0°C. This allows aquatic life to persist and flourish in certain frozen conditions, including seasonal blooms of ice-associated phytoplankton (e.g., Phillips and Fawley 2002) that sustain aquatic food webs. However, ice encasement can render water bodies, soil, and near-ground habitats hypoxic (Nürnberg 2002, Williams et al. 2015). Ice on water bodies is reflective, and both sea and freshwater ice influence global climate patterns via ice–albedo feedback (Serreze et al. 2007, Brown and Duguay 2010, Kashiwase et al. 2017). Freezing poses a variety of physical and physiological challenges to organisms. Some organisms cannot survive internal ice formation, but many taxa, including arthropods, mollusks, turtles, frogs, fungi, and plants readily tolerate internal ice formation (Clarke 2017). If the majority of an ecosystem's water is locked up in ice, then this can induce physiological stress in terrestrial biota. Evergreen trees are challenged by excessive light absorption in winter when soil water is frozen (Berg and Chapin 1994), soil microbes must survive dehydration (Jefferies et al. 2010), and some insects rely on dehydration to increase their cold tolerance (Williams et al. 2015). A lack of access to fresh water in winter also affects mammals; polar bears preferentially eat fat over muscle to retain the water needed to digest protein (Nelson 1987), and hibernating black bears survive winters without drinking or urinating by avoiding protein catabolism, recycling proteins, and reabsorbing any urine that is produced (Spector et al. 2015).

Winter is snowier

During winter, precipitation typically falls as snow at high latitudes and altitudes. Accumulated snow blocks light transmission, inhibiting photosynthesis in those plants that retain their leaves. Snow cover buffers air temperature extremes, and its albedo diminishes heating from solar radiation (Berteaux et al. 2016). Therefore, years with less snow expose organisms in soils or aquatic ecosystems to extreme cold, whereas years with deep snow moderate subnivean temperatures but lengthen snow cover duration because it takes longer to thaw in the spring (Williams et al. 2015). The buffered environment within the snowpack and especially at the soil–snow interface provides a thermal refugium (Thompson et al. 2018, Pauli et al. 2013) and, as such, supports an active terrestrial subnivean community of invertebrates and small mammals; some larger mammals depend on this buffered environment for denning (Petty et al. 2015). Buffering by snow also influences the depth of frost penetration in the soil, affecting plant growth and composition in the following summer (Kreyling et al. 2012). Some organisms, such as snow algae, live on the snow surface for a portion of their life cycle (e.g., Hamilton and Havig 2017). Above the snow, travel becomes easier for small animals, because the underlying habitat complexity is homogenized, but more difficult for larger animals that sink into the snowpack (Williams et al. 2015). Snow also gives access to vegetation that is not reached by herbivores in other seasons by raising ground level or lowering branches (Nordengren et al. 2003). Snow camouflages white animals but increases the risk of predation for dark animals (Atmeh et al. 2018). All of these properties mean that an absence of snow in ecosystems that historically experience snow can have profound effects from the loss of thermal refugia to altering species interactions.

Winter is darker

Winter nights are long, and with the albedo of winter snow reflecting more solar radiation back into the atmosphere, many organisms overwinter in microhabitats with reduced light exposure. This lack of photoperiodic cues can blunt circadian responses in mammals that overwinter in burrows (Williams et al. 2012). Conversely, spring-spawning fishes use the combination of winter photoperiod and temperature cues to synchronize energy allocation and the progression of the reproductive cycle (Migaud et al. 2010, Brown et al. 2019). In terrestrial ecosystems, endotherms experience more radiative heat loss under dark night sky conditions, increasing thermoregulatory costs and reducing cold tolerance; for example, weasels exposed to daytime sun can tolerate air temperatures that are 32°C colder than weasels exposed to clear night sky conditions (Chappell 1980). Darkness affects biological function and ecological interaction from increasing thermal costs, creating photoperiod cues, and constraining diurnal species.

Winter is less productive

The combination of winter being colder and darker than other seasons of the year severely constrains all forms of production. All else being equal, more sunlight leads to more primary production by plants, phytoplankton, and macrophytes (figure 2), which enables increased secondary and tertiary production by heterotrophs. In addition, colder temperatures reduce photosynthetic rates (Berry and Björkman 1980, Yamori et al. 2014), slow metabolism in ectotherms (Speers-Roesch et al. 2018), and increase thermoregulatory costs for endotherms (Rezende and Bacigalupe 2015). Most plants suspend primary production and remain dormant and primed through winter, ready to capitalize on light and warmth when it next becomes available (Jónsdóttir 2005, Berge et al. 2015). Those plants that don't become dormant typically have little or no photosynthesis when temperatures are cold but have low amounts of photosynthesis during periodic warm spells (Oquist and Huner 2003, Grosbois et al. 2017). As ectotherm functionality is dependent on temperature, feeding is not possible at cold temperatures and as such they must rely on energy conservation to survive winter, with most species entering dormancy and stopping production (Voituron et al. 2002). However, in aquatic

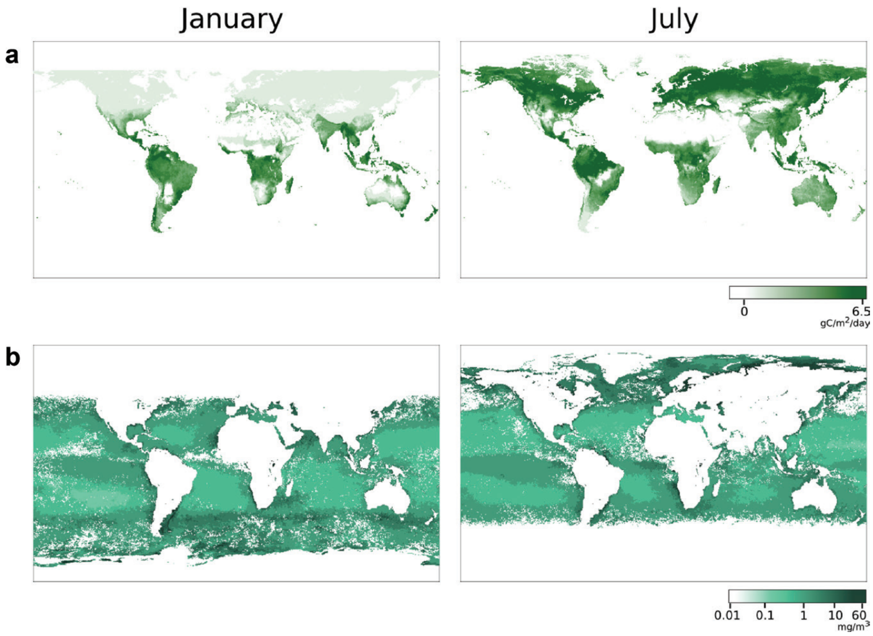

Figure 2. Productivity decreases during winter. Both net primary production on land (a) and chlorophyll concentrations in oceans (b) are greater in July (2016) than January (2016) in the Northern hemisphere. The figures were generated from MODIS data (https://neo.sci.gsfc.nasa.gov) using NASA algorithms for net primary productivity and chlorophyll concentrations (Carder et al. 2004, Running et al. 2004).

environments in which temperatures remain above freezing, ectothermic species maintain some productivity, albeit at reduced rates relative to summer (McKnight et al. 2000, Vincent et al. 2008, Shuter et al. 2012, Hampton et al. 2017). Aquatic invertebrates continue to play an important role in decomposition and nutrient mineralization during winter, including shredders that breakdown terrestrially derived materials (Cummins et al. 1989). For endotherms, low productivity combined with high thermal costs makes winter an energetically challenging period. To survive this bottleneck, many endotherms either migrate to areas in which conditions are less harsh (Alerstam et al. 2003) or use hibernation or torpor to conserve energy (Williams et al. 2016). However, some species remain active, and even reproduce in winter by using buffered subnivean spaces or relying on behavioral and physiological adaptations to minimize costs (Duchesne et al. 2011, Pauli et al. 2013, Menzies et al. 2020). Although, winter is very much alive, and winter productivity and activities are key to the life cycle of many organisms and to the function of many ecosystems, winter, as a whole, is a season of lowered productivity and energy conservation.

Winter is variable

Variability in winter exists at both an inter- and an intra-annual scale. Some winters are mild, whereas others are long and extremely cold. We see this variation geographically where latitude influences incoming solar energy. The characteristics of terrestrial winters are further influenced by geography (especially continentality, aspect, and elevation), whereas in aquatic systems, wind and water currents determine thermal stratification and ice formation, which, in turn, affect light and nutrient availability (Hampton et al. 2015). The energy required to thaw ice means that systems with greater thermal inertia, such as large water bodies or frozen ground, respond more slowly to seasonal changes and are more resistant to short-term perturbations (Arenson et al. 2015). Variation among winters can be driven by local-scale processes such as adiabatic cooling and global-scale processes such as climate cycles (the El Niño-Southern Oscillation) and polar vortices (Schoeberl et al. 1992). This variation can determine long-term population processes—for example, years with little snow cover yield range contraction of montane beetles (Rank and Dahloff 2002, Dahlhoff et al. 2019), years with unusually deep snow can delay phenology (Sambaraju et al. 2012), and extreme cold events are agents of natural selection (Stroud et al. 2020). Weather and climate patterns can also vary within a season. Warm spells mid-winter can melt snow, cause ice encasement, and disrupt growing cycles. Paper birch (*Betula papyrifera* L.) subjected to a mid-winter thaw suffered dieback of shoots and loss of conducting xylem (Cox and Malcolm 1997). Cold snaps in late spring can be particularly damaging; for example, a late frost event in northeastern United States in 2010 reduced productivity in regional forests by 7%–14% (Hufkens et al. 2012). As many biological processes (such as metabolic rate or digestive efficiency) change exponentially with temperature (Brown et al. 2004), the impact of temperature fluctuations is highly dependent on the average around which those fluctuations occur: Increasing the temperature from –10° to –5°C will have little impact on the metabolic rate of an overwintering ectotherm, but a shift from 5° to 10°C can increase metabolic rate considerably (Colinet et al. 2015). Whether it is between years or between days, variability defines winter with cascading impacts on organisms, food webs, and ecosystems.

Winter can be deadly

Across all forms of life, many individuals that are alive in autumn will be dead by spring. Winter is therefore a brutal annual selection event that filters out genotypes and phenotypes unable to endure its many challenges. As a result, winter has shaped the biology of many species, whether through the evolution of avoidance (migration and hibernation) or through the behavioral and physiological adaptations to winter conditions. Even avoidance strategies are not failsafe. Migrating birds that depart late or arrive early risk encountering lethal snow and ice conditions, such as the estimated 100,000 king eiders (*Somateria spectabilis*) that starved in spring 1964 when severe cold froze newly opened leads at migration staging areas in the Beaufort Sea (for a review, see Newton 2007). Insects can be killed directly by thermal stress; for example, the position and timing of cold air inversions determines survivorship of autumnal moth eggs (Neuvonen et al. 1999). Trees are not impervious to the effects of winter; for instance, a harsh winter in the northeastern United States during 2003 led to approximately 90% injury across red spruce (*Picea rubens* Sarg.), which may have led to further spruce declines and mortality (Lazarus et al. 2004). Fishes are susceptible to interacting abiotic and biotic stressors, especially in their first year of life (Hurst 2007). For example, large-scale fish kills can result from oxygen depletion (i.e., hypoxia or anoxia) in late winter because of nitrification in water bodies isolated from the air by ice (Hurst 2007) or from asphyxiation or stranding because of various ice formations (Brown et al. 2000). Winter-related death is not always a negative thing. It can create barriers to invasive species, pests, and pathogens (Weed et al. 2013). Despite increased mortality for some species, well-adapted species benefit from a lack of predation and relaxed competition in winter (McMeans et al. 2020). Indeed, some fishes can accumulate lipid in winter (Arctic charr, *Salvelinus alpinus*; Finstad et al. 2003) and are fattest during winter (Fernandes and McMeans 2019), and hibernating mammals can have higher survival rates in winter than in summer because they are freed from predation pressure (Turbill et al. 2011).

Winter is (traditionally) understudied

Winter is a relatively understudied season, reinforced by our training programs and conceptual frameworks. Reasons for this are many. Many of our undergraduate and postgraduate training programs focus on short courses, field schools and fieldwork during the summer season, with long-course requirements falling outside of summer months (Marchand 2014). Full-time attendance at some academic institutions is therefore typical in winter months, translating to barriers in planning winter field seasons (Campbell et al. 2005). Ecology education is focused on examples and theory based on the warmest months of the year, thereby shaping the questions on which our research programs are based. Winter field seasons are also expensive and come with significant risks. Expeditions in the winter require specialized sampling gear (e.g., for sampling under ice and at cold temperatures), additional health and safety conditions to prevent exposure to the elements, specialized training for working in cold weather conditions, and larger teams to mitigate field risks (Block et al. 2019). Winter fieldwork is commonly impeded or prevented by storm activity, and therefore jeopardizes student projects that depend on traveling to and accessing field sites. Despite all this, times are changing and interest in winter ecology is growing (Powers and Hampton 2016). With the threat of climate change looming, more researchers are turning their focus to winter, which is slowly shifting this maxim toward falsehood.

Winter is changing under climate change

The final maxim is more of a capstone, because it impinges on all of the other maxims described above. Winter is not what it used to be; indeed, winter is becoming “weird” (so-called winter weirding, a term that has been used by weather forecasters for some time and is recently being adopted by the scientific community; Wallace et al. 2014). There are many examples on which we can draw that demonstrate that winter is changing with respect to its duration and intensity. There is ample evidence for winter whiplash, with high variability in temperature (Cohen 2016, Casson et al. 2019) and precipitation (Swain et al. 2018) within a winter season. For example, extreme winter weather, including both extreme cold and extreme warm temperatures within a season, can now be expected at mid-latitudes (Francis and Vavrus 2012, Cohen 2016). In the 2016–2017 winter, California experienced an extreme drought and floods within a season (Swain et al. 2018). In addition, thousands of lakes that consistently froze every winter are now beginning to experience freeze–thaw events within a season and, in more extreme cases, winters without ice cover at all (Sharma et al. 2019). The warming climate is also likely to remove existing winter barriers for invasive species, paving new pathways for dispersion (Dukes et al. 2009). A small increase in temperature that removes seasonal snow cover may reduce habitat availability (see above), reduce insulation leading to paradoxically colder extremes in soils (Groffmann et al. 2001), and change albedo, increasing light and affecting microclimate. Changing winters that do not meet these vernalization requirements are already delaying the onset of spring green-up on the Tibetan plateau (Zhang et al. 2013). Furthermore, temperature and flow are key factors that influence hatch timing for fishes (Rooke et al. 2019), whereas snowmelt runoff induces large pulses of microbial activity as soil melts in the Arctic (Schimel and Clein 1996). These thresholds mean that small changes in conditions that may be negligible in the growing season can fundamentally change winter.

Why studying winter ecology is important

We conclude our presentation of the nine maxims by discussing why winter ecology, as we have defined it in the present article, is important and why it is critical that more studies focus on unlocking the impacts of winter on organisms and ecosystems.

Winter generates distinct ecosystem services. Winter conditions, specifically snow and ice cover, generate a range of ecosystem services that are important for humans, as well as for other organisms. Among the most critical ecosystem services furnished by winter conditions is cooling of land and water surfaces due to snow and ice albedo. In temperate forests that receive regular snowfall, radiative forcing associated with snow albedo can mitigate climate change more powerfully than forest carbon sequestration (Lutz and Howarth 2015, Sturm et al. 2017). Furthermore, the distribution and magnitude of the winter snowpack determines quality and availability of drinking and agricultural water for approximately 1.2 billion people globally (Sturm et al. 2017). Seasonally frozen water bodies provide habitats that support ecologically important populations, or facilitate the survival and genetic health of some species. During the late winter in large lakes, ice bottoms provide attachment substrata for large-celled, lipid-rich diatoms from the genus Aulacoseira (e.g., Twiss et al. 2012). This under-ice primary production is a key component of overall carbon budgets in these systems. In marine systems, the expansion of land-fast sea ice during the winter provides critical seasonal hunting habitat for polar bears (Hamilton et al. 2014) and bridges otherwise isolated islands, enabling propagule migration and gene flow among insular populations of large mammals such as caribou (Mallory and Boyce 2019). Ice-covered water supports human travel as well, ranging from people walking on ice to transport trucks using ice road networks. Snow and ice are also critically important to hunting, trapping, and fishing. Vibrant recreational ice fishing industries are sustained worldwide. In the United States, up to two million ice anglers spent US$178 million on equipment alone in 2011. The actual economic impact of ice fishing is much larger, including patronage of businesses near frozen water bodies (Knoll et al. 2019). As with other aspects of winter ecology, precise valuation of winter ecosystem services is challenging and remains largely unexplored. Rapid changes in winter conditions worldwide underline the need for accelerated efforts to study winter ecology and associated ecosystem services.

Winter is relevant to resource managers and conservation practitioners. When winter neglect extends beyond the scientific community to include resource managers and conservation practitioners, ecosystems and wildlife populations are put at risk. The extent to which that is realized is unclear (and certainly does not extend across all managers and practitioners), but that contention is consistent with our collective experience. Many organisms aggregate in winter refugia (hibernacula) that concentrate populations and may make them particularly vulnerable to exploitation and disturbance (Cunjak 1996, Hanson et al. 2007, Taylor et al. 2016). Safe and continuous migratory corridors are also required for animals to reach critical winter habitats (Sawyer et al. 2012, Simpson et al. 2016). Considering winter habitats and corridors are therefore important components of management strategies requiring international collaboration for species that cross through different country boundaries (Nevins et al. 2009, Zmelik et al. 2011). Exploitation activities (e.g., hunting, fishing) in the winter months can be reduced for organisms that would otherwise be too easy to harvest while hibernating (e.g., bears, snakes) or aggregated (e.g., some fishes). However, these activities do occur, and there can be unintended consequences (e.g., ice fishing bycatch; Lennox et al. 2018). Minimizing disturbance (e.g., from outdoor recreation or resource development) during periods of hibernation, quiescence, diapause, or general energy conservation can be important to reduce stress and associated energetic expenditure (e.g., Arlettaz et al. 2015). In some cases, winter is regarded as a period during which construction activities can occur, such as in wetlands or forests when machinery can traverse on frozen ice or ground that would otherwise destroy critical habitats. These so-called construction windows imply that ecosystems and organisms are less sensitive in winter than at other times of year, but this assumption may be incorrect (Rittenhouse and Rissman 2015, Cameron and Lantz 2017, Evans et al. 2016). In addition, restoration of degraded ecosystems requires understanding the winter tolerances and needs of both plants and animals to ensure the long-term hardiness of recovering populations (e.g., Taft and Haig 2003).

Almost all of these aforementioned observations are drawn from the physical environment (e.g., temperature, ice cover, snow cover depth) with comparatively little known about the consequences of changing winters on wildlife and ecosystems and how winter variability can be incorporated into management strategies. This is important as it represents a challenge for those managers and practitioners who already consider winter important and are trying to manage in the face of environmental change. Nonetheless, there are some examples that have emerged in recent years. For example, Wipf and colleagues (2009) showed the importance of considering variation in snow depth and snowmelt timing when attempting to predict responses of Arctic tundra plant communities to climate change. Williams and colleagues (2015) reviewed the effects of climate change on the winter ecology of terrestrial organisms and revealed that existing frameworks for predicting the impacts of climate change do not incorporate the complexity of organismal responses to winter, leading them to call for more research (and theory) on the topic. A similar review focused on the winter ecology of freshwater fish and concluded that many (but especially winter specialists) will be influenced by changes in winter phenology, with examples already becoming apparent (Shuter et al. 2012). The ecology of many marine fish in winter represents a major knowledge gap. For fish in fluvial systems, midwinter breakups and floods are becoming more common with unknown consequences on fish (Scrimgeour et al. 1994). The equivalent on land is mid-winter warm spells that can lead to restlessness or arousal in hibernating animals (e.g., bats; Sherwin et al. 2013). Likewise, plants rely in part on temperature cues for phenological events such as bud break and leaf emergence, leaving them vulnerable to false spring events (e.g., Marino et al. 2011), which can reduce subsequent growth and decimate that year's reproductive effort. However, assuming winter stress does not lead to immediate mortality, it remains unclear for many organisms the extent to which it could lead to carryover

Box 2. Adapting to winter research.

Recognizing that winter is neglected is a key first step to addressing this gap. Moving forward involves incorporation of winter into ecological theory, working with local communities to monitor and sample through the year (e.g., such as under the ice), and adjustments to equipment to ensure functioning during cold conditions (Block et al. 2019). Technological solutions now allow continuous remote observations that give a unique perspective of winter ecology. For instance, Oceans Network Canada at the University of Victoria monitors ocean conditions year-round at Cambridge Bay in Nunavut with an underwater camera and microphone, and a suite of sensors to measure seawater and ice properties (www.oceannetworks.ca/year-arctic-sea-ice). Winter radio tracking of large vertebrates has long been the norm, but GPS collars and better battery capabilities at low temperatures now yield fine-resolution winter data (Williams et al. 2016). Winter logistics in the Antarctic has expanded from base maintenance to year-round research capability and, at the time of writing, the German research vessel *PolarStern* has emerged from a winter locked in Arctic ice (see www.sciencemag.org/news/2019/08/arctic-researchers-will-lock-ship-ice-year-study-changing-polar-region). In response to these (and other) possibilities, there is a proliferation of winter-focused research networks, including Winternet (http://winternet.sites.sheffield.ac.uk). This is creating new opportunities to explore finer scale variation in environmental conditions within a season, and taking advantage of advances in sensing and predicting snow and ice cover. Incorporating winter in our understanding of how natural systems are and will respond to climate change (across all seasons) can only be advanced through efforts to advance field observations in the winter.

effects (O'Connor et al. 2014). Winter severity promotes different phytoplankton communities and ice algae that have different nutritional quality and therefore influence higher trophic levels (Özkundakci et al. 2016). Moving forward, it won't be good enough to simply study winter, but rather it will be necessary to understand how the aspects of change that we are experiencing and predicting changes will influence wildlife, communities, and ecosystems. This will require greater interaction between knowledge generators (and holders) and knowledge users.

Conclusions

For those that study ecology in winter, the idea that this season is cold, dark, and snow covered is not new. Given that winter places extreme physiological constraints on wild organisms and can be deadly, it is surprising that winter is less studied than other seasons. In the present article, we presented a set of nine maxims to define the boundaries of winter ecology as a discipline, but our discussions led us to recognize that context matters. These truths define winter for regions that experience frigid winter (30% of global land mass), but fail to capture the seasonality that exists in other regions. And although we believe these maxims are true of winter, there are always exceptions. What might apply to one species or ecosystem or geographic location in a given year may be dramatically different at a future time point. The ideas of winter weirding and weather whiplash are changing what winter means to wild organisms and what that will consequently mean to those tasked with managing and conserving biological resources in winter, as well as to those who study winter. There is increasing dramatic interannual variation in winter (e.g., duration, intensity), which emphasizes the need for long-term research to contextualize one's findings (Magnuson 1990). A 1-year study will almost certainly fail to capture the range of conditions that are experienced in the winter of today or tomorrow.

Recent evidence suggests that ecologists are starting to embrace winter and recognize its importance (box 2; Kreyling 2010, Williams et al. 2015, Hampton et al. 2017). The emergence of winter ecology as a formal subdiscipline is an important signal as to the uniqueness of the season. Our hope in writing this article is that we initiate a discussion as to what defines the boundaries of this new discipline: what is winter and what is not. The maxims presented in the present article can be reframed as testable hypotheses of the extent to which they are broadly applicable and the extent to which they will be relevant in a future of climate change and winter weirding. We hope the next steps will include critical evaluation of how these ideas are relevant to a changing world and the extent to which additional research is needed to move beyond general truths and develop context dependencies to improve our understanding of ecosystems and to enhance management and conservation.

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