

Cold truths: how winter drives responses of terrestrial organisms to climate change

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ABSTRACT

Winter is a key driver of individual performance, community composition, and ecological interactions in terrestrial habitats. Although climate change research tends to focus on performance in the growing season, climate change is also modifying winter conditions rapidly. Changes to winter temperatures, the variability of winter conditions, and winter snow cover can interact to induce cold injury, alter energy and water balance, advance or retard phenology, and modify community interactions. Species vary in their susceptibility to these winter drivers, hampering efforts to predict biological responses to climate change. Existing frameworks for predicting the impacts of climate change do not incorporate the complexity of organismal responses to winter. Here, we synthesise organismal responses to winter climate change, and use this synthesis to build a framework to predict exposure and sensitivity to negative impacts. This framework can be used to estimate the vulnerability of species to winter climate change. We describe the importance of relationships between winter conditions and performance during the growing season in determining fitness, and demonstrate how summer and winter processes are linked. Incorporating winter into current models will require concerted effort from theoreticians and empiricists, and the expansion of current growing-season studies to incorporate winter.

Key words: snow, frost, cold, extreme events, average temperatures, freeze-thaw cycles, sub-lethal impacts, energetics, hibernation.

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I. INTRODUCTION

Terrestrial organisms in temperate, alpine and polar environments may spend more than half their lives overwintering. In these habitats, winter is the period during which sustained low temperatures (usually below freezing) occur, and snow accumulates on the ground for some period of time. Winter conditions vary geographically more than summer conditions (Bonan, 2003), and thus can delineate latitudinal variation in biological processes more starkly than conditions in the growing season. For example, the respective extreme maximum temperatures recorded in Montreal, Quebec (45°N) in Canada, and Miami, Florida (25°N) in the United States over 1997–2000 were 36.1°C and 36.7°C, whereas the respective extreme minimum temperatures at these locations, –37.8°C and –1.1°C, differed dramatically [data from NOAA National Climatic Data Centre (USA) www.ncdc.noaa.gov and Environment Canada climate.weather.gc.ca]. Extreme low winter temperatures constrain the geographic distributions of many species, presented most graphically in the plant hardiness zones used by gardeners and farmers: data on frost susceptibility are a key component underlying these maps (Daly *et al.*, 2012). Winter temperatures that directly cause mortality limit the northern distributions of organisms as diverse as mosquitoes in Europe (Caminade *et al.*, 2012), the Virginia opossum *Didelphis virginiana* in eastern North America (Kanda, 2005), the mountain pine beetle *Dendroctonus ponderosae* in western North America (Stahl, Moore & McKendry, 2006), the fungi that cause wheat rust (Roelfs, Singh & Saari, 1992), and citrus crops worldwide (Spiegel-Roy & Goldschmidt, 2008). Winter also poses indirect challenges. Many organisms overwinter in dormancy (and therefore cannot replenish energy reserves until spring). Those organisms that remain active face resource shortages, which may be compounded by the physical barriers presented by snow and ice and the increased cost of thermoregulation. Energetic deficits accrued during the winter can lead to mortality or reduce subsequent fecundity (Irwin & Lee, 2003; Hahn & Denlinger, 2011), and overwintering energetics constrain some species' distributions (e.g. Humphries, Thomas & Speakman, 2002).

In spite of the constraints, many species thrive in places with severe winters, and there are species that might be considered winter-dependent; for example, most Arctic vertebrates require snow and ice for their reproduction and survival (Gilg *et al.*, 2012), and some invertebrates disperse and hunt primarily in subnivean (beneath the snow pack) spaces (Addington & Seastedt, 1999; Pauli *et al.*, 2013). Some species that overwinter in a dormant state have evolved dependence on winter cues for termination of dormancy (Tauber, Tauber & Masaki, 1986; Amasino, 2004), and monarch butterflies (*Danaus plexippus*) rely on winter cold to reverse the direction of their autumn migration (Guerra & Reppert, 2013). Many ectotherms and hibernating mammals rely on low winter temperatures to reduce consumption of energy stores (Humphries *et al.*, 2002; Williams *et al.*,

2012*b*), while cold winters restrict the distribution of some plant pathogens, but not their hosts (Pfender & Vollmer, 1999). At the ecosystem level, freezing of soil in winter can mobilise nutrients (and/or damage roots), affecting nutrient availability and uptake, and therefore primary productivity, in the spring (Groffman *et al.*, 2001; Durán *et al.*, 2013). Likewise, winter conditions in many species can define organismal performance in the subsequent summer (Post *et al.*, 1997; Serrano *et al.*, 2011; Boggs & Inouye, 2012).

Repeated glacial/interglacial cycles, coupled with continental drift in and out of the tropics, mean that physiological and life-history adaptations to winter have evolved repeatedly in multiple lineages of organisms. The evolutionary impact of winter on life histories is significant – for example, the northern temperate winter may have been a primary driver of the evolution of migratory and hibernation phenotypes (Alerstam, Hedenstrom & Akesson, 2003; Turbill, Bieber & Ruf, 2011). Thus, predicting evolutionary trajectories into the future must take into account how changing winters will continue to shape organismal phenotypes. For ectotherms, microbes, and plants, the threat of internal ice formation has driven the evolution of physiological traits that allow them to withstand low temperatures (for example, freeze tolerance in insects and plants; Margesin, Neuner & Storey, 2007). Nevertheless, both endotherms and ectotherms suffer high mortality over winter (Hodges, Boonstra & Krebs, 2006; Stahl *et al.*, 2006; Roland & Matter, 2013), and the population dynamics of diverse animals including lemmings (*Microtus* spp.), moths (*Epirrita autumnata*) and bobwhite (*Colinus virginianus*) can be driven primarily by winter mortality (Dabbert, Lochmiller & Teeter, 1997; Virtanen, Neuvonen & Nikula, 1998; Callaghan *et al.*, 2004).

Anthropogenic climate change is rapidly altering biological systems, and winter conditions are changing particularly rapidly (IPCC, 2007). Differential sensitivity of organisms to climate change is restructuring biological communities due to disparate range and phenology shifts, and altered population dynamics (Walther, 2010; Chen *et al.*, 2011*a*). Where the proximate cause is known, many biological responses to climate change are driven by changes in winter conditions (e.g. Crozier, 2004; Battisti *et al.*, 2005). To guide mitigation efforts under global climate change, we must identify which species or populations will be 'winners' – benefitting from climate change, and which 'losers' will be vulnerable to changes (Somero, 2010). However, the interactions between snow and temperature that determine microclimate conditions combine with divergent ecological and physiological strategies for dealing with winter stress, leading to variation among species in susceptibility to winter climate change. In some cases, these idiosyncratic responses to winter likely underlie the failure of models to accurately predict species' responses to climate change (Cook, Wolkovich & Parmesan, 2012). A limited understanding of organismal responses to winter (and their cascading effects through communities and ecosystems) thus impedes prediction of the biological impacts of climate change in general.

The interaction between a species' traits (and the plasticity of those traits; Chown *et al.*, 2007; Somero, 2010) and changes in the abiotic environment will determine success or failure in a changing world (Foden *et al.*, 2013), so predictions would ideally utilise information on species traits combined with climate models to output vulnerability. Meta-analyses have shed some light on the relationship between species' traits and their responses to environmental change (e.g. Jiguet *et al.*, 2007; Thackeray *et al.*, 2010; Diamond *et al.*, 2011; Bokhorst *et al.*, 2012a). However, these analyses have not been in the context of winter, nor have they synthesised across diverse taxa and abiotic drivers. Thus, we need a framework to identify climate-change susceptibility that explicitly includes winter processes and incorporates evolution, ecology and physiology. An essential starting point is a synthesis of the mechanistic bases for the complex responses to interacting winter climate drivers across terrestrial taxa.

Here we present a multi-component framework for predicting the impact of change in abiotic winter drivers on terrestrial organisms. We begin by describing the predicted changes in winter climate, then synthesise the mechanistic bases for the biological impacts of winter climate change across terrestrial taxa and regions. We use this synthesis to identify key traits that make species susceptible to changing winter conditions, and integrate the current state of knowledge on impacts of winter climate change within the body of knowledge of growing-season processes. We focus on traits influencing exposure and sensitivity to a particular stress, which may arise from a number of drivers or interactions between drivers, and through both biotic and abiotic processes. Our review is not meant to be exhaustive in scope, but rather to draw on representative examples across taxa to illustrate the main biological impacts of winter across a range of terrestrial organisms, to provide a starting point for readers to access the literature relevant to their system, and to guide future research in the field of winter-focused global change biology. This framework is designed to provide researchers with the means to navigate from change in a climate driver to a list of potential biological impacts an organism may experience, and to make a qualitative assessment of the likelihood of any terrestrial organism to suffer a given biological impact.

II. WINTER CLIMATE CHANGE

Mean winter air temperatures are increasing globally, but the magnitude of predicted winter climate change varies by region (Fig. 1; IPCC, 2013), and is subject to complex feedback mechanisms and interactions between snow and ice cover and temperature. While increased temperature alone decreases snow cover, climate models predict that winter precipitation may increase, decrease or change in timing or duration depending on the region (Fig. 1B), which means that snow depth may stay the same or even increase in some regions, such as parts of the Arctic (Symon, Arris & Heal, 2005). Many organisms overwinter beneath snow, and

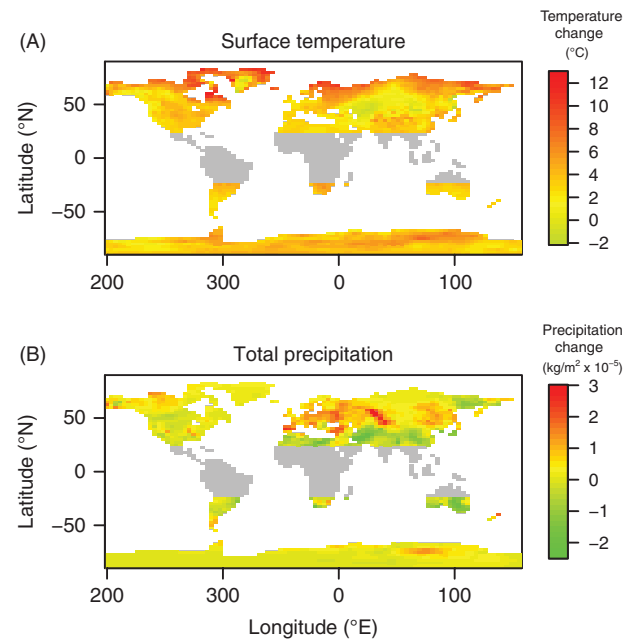


Fig. 1. Projected winter climate change in terrestrial systems over the next century. Predicted January (northern hemisphere) or July (southern hemisphere) differences between 2090–2099 and 2000–2009 in (A) mean surface air temperature and (B) total precipitation. Tropical regions (23°S to 23°N) that do not experience winter are in grey. Predictions are from the HADCM3 model, A2 scenario (Lowe, 2005); means for each cell over the early time period were subtracted from the means for the late time period to give projected changes.

snow cover is a critical mediator of soil microclimate; in particular, both reduced precipitation and increased mean air temperatures can increase the frequency and intensity of soil freeze–thaw cycles (Fig. 2; Brown & DeGaetano, 2011). Although the Arctic is predicted to experience the most extreme winter warming, changes in snow cover and soil freezing in this region are less sensitive to warming than in northern temperate regions, which feature a shallower snowpack and remain closer to melt temperatures over winter (Henry, 2008). The changing physical conditions of winter can also modify winter length; for example, ‘vanishing winters’ are predicted for low-latitude temperate regions, where persistent snow cover and soil freezing become rare or completely absent (Kreyling & Henry, 2011), and the ‘average’ winter may be getting shorter in temperate North America, where the first autumn frost has been getting later, and the last spring frost earlier, for several decades (Kunkel *et al.*, 2004).

In addition to changes in mean temperature and precipitation, an increased frequency of extreme weather events can increase the incidence, frequency and intensity of soil freezing, either as a result of unusually early or late winter frost events, or as a result of mid-winter warming (or rain) events that reduce snow cover and are followed by freezing temperatures (Fig. 2C). Increases in extreme minimum and maximum temperatures in recent decades

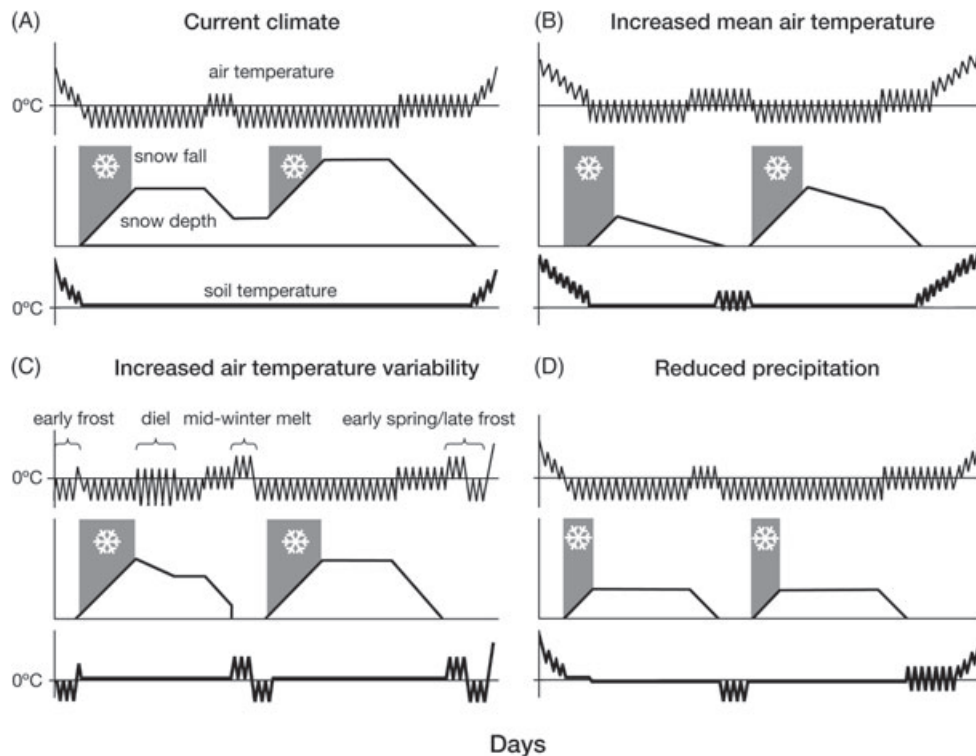


Fig. 2. Examples of the effects of changes in air temperature and snowfall on snow depth and soil temperature during winter. (A) Current climate. Note that snow cover buffers soil temperatures. (B) Increased mean air temperature results in increased soil freeze–thaw cycles during a mid-winter melt because the soils become exposed to warm air temperatures during the day and freezing air temperatures at night. (C) Scenarios whereby increased air temperature variability modifies soil freezing. In late autumn, an early frost exposes soil to cold air prior to development of the snowpack. Warm spells in either mid-winter or early spring melt the snowpack, leaving soils vulnerable to subsequent drops in air temperature. Finally, snow melt can be accelerated by increased diel air temperature variability. (D) Reduced winter precipitation leads to increased soil freeze–thaw cycles following a mid-winter melt and during spring melt as a result of reduced snow cover at these times.

have varied among seasons and among regions, but overall there has been an increased number of days of extreme high minimum temperature and a reduced number of days of extreme low minimum temperature (Easterling *et al.*, 2000; Caprio, Quamme & Redmond, 2009; IPCC, 2013). For example, across Canada the number of cold nights (minimum temperatures below the 10th percentile for the 20th Century) decreased by 15 per year between 1950 and 2003 (Vincent & Mekis, 2006). The frequency of both extreme high temperatures and longer mid-winter warm spells is expected to increase with climate change (Liu *et al.*, 2006), and although cold spells may be less frequent (or less intense) in some regions, there is debate as to whether they will be less severe or match current levels of severity (e.g. Kodra, Steinhäuser & Ganguly, 2011; Peings, Cattiaux & Douville, 2013). Much of this debate centres on how changes in atmospheric circulation patterns influence regional patterns of winter climate change. For example, the persistence of the negative phase of the North Atlantic Oscillation (NAO) caused a cold temperature anomaly in Europe during the winter of 2010 (Cattiaux *et al.*, 2010). While it has been hypothesised that disruption of the Gulf Stream could result in colder winters and increased snow

cover in Europe, cold temperature anomalies in this region have also been linked to interactions with other circulation patterns and to sea ice cover (Moore & Renfrew, 2012; Yang & Christensen, 2012). Thus, on balance, the complex interaction of multiple factors makes it difficult to predict temporal variation in winter climate at the regional level. However, from a biological perspective, there is a realistic expectation that some organisms (particularly those that are long-lived) could experience recurring cold spells similar to, or more severe than, those in the past, despite an overall trend of winter warming (Gloning, Estrella & Menzel, 2013).

Aside from thermal stress, interactions between temperature and moisture during winter can alter the occurrence of physical stresses such as ice encasement and frost heave (the uplift of soil when freezing water in soil expands). Both of these phenomena can lead to both physical and physiological stress for soil organisms and plant roots (e.g. Coulson *et al.*, 2000; de Chantal *et al.*, 2007). Increased rainfall over winter will increase the frequency of rain-on-snow events, which also contribute to ice encasement. Rain-on-snow events have increased in most Arctic regions, in some cases by up to 50% (ACIA, 2005). Furthermore, changes in albedo and permafrost depth can modify water retention by the soil,

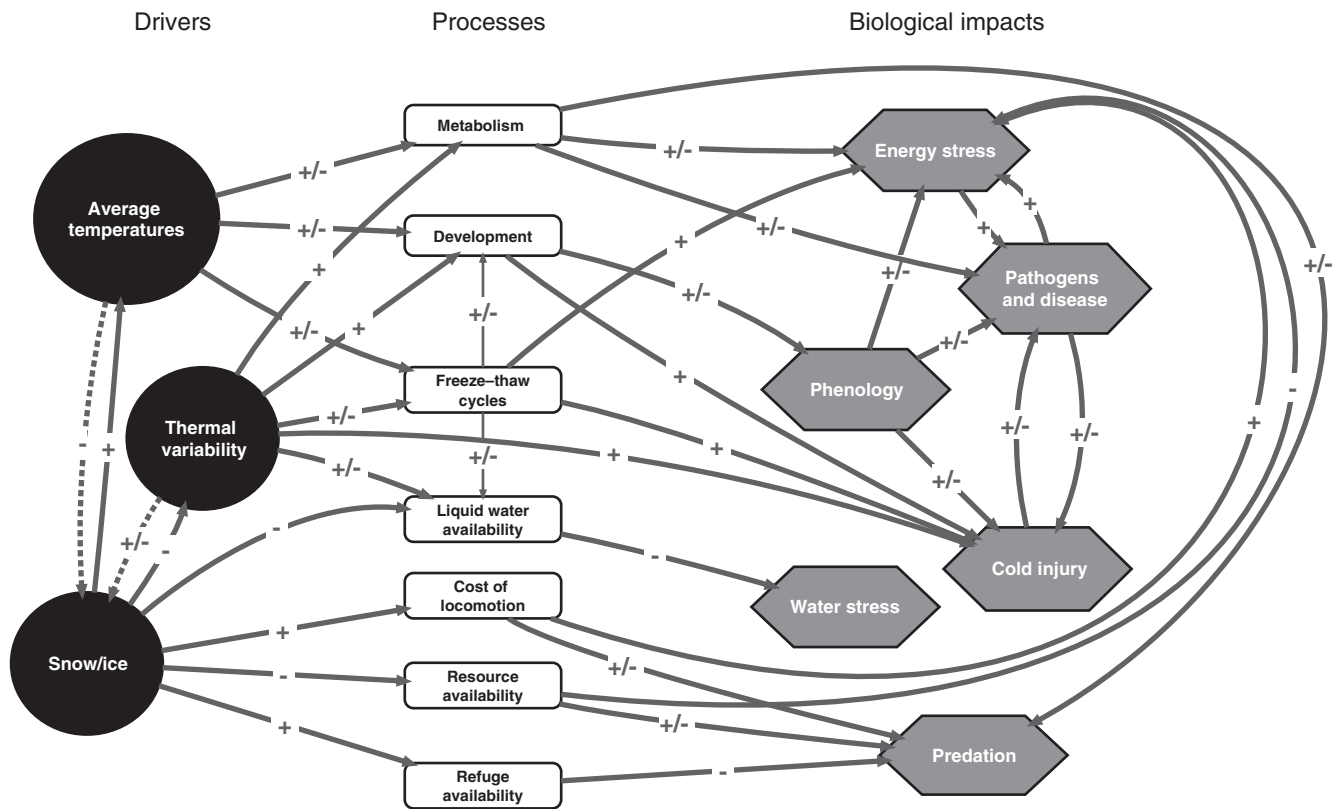


Fig. 3. A blueprint for predicting the biological impacts of winter climate change on terrestrial organisms. Abiotic drivers of winter climate change (black circles) alter physiological, biotic or abiotic processes (white rectangles) leading to biological impacts (grey hexagons). Signs on arrows indicate the direction of the relationship, and can be navigated with reference to Table 1 and examples in the text. The dashed line indicates that decreases in snow and ice occur in response to increased macroclimatic temperatures; all other relationships occur within organisms' microclimates.

which can alter the nature of below-ground freeze–thaw (Oztaş & Fayetorbay, 2003). Changes in sea or lake ice can also exacerbate terrestrial climate change, for example by increasing moisture availability, leading to increased snow depth in maritime areas, or by modifying albedo and accelerating spring melt (Deser *et al.*, 2010). With the emphasis on temperature effects in winter research, such interactions with moisture have often been overlooked, and consequently our discussion of these specific moisture effects remains speculative (and is often absent) throughout much of this review.

III. MECHANISTIC BASES OF THE BIOLOGICAL IMPACTS OF WINTER CLIMATE CHANGE

The primary abiotic drivers of the biological impacts of winter on terrestrial systems are temperature and snow cover. Temperature determines rates of biological processes, and thermal variability impacts the likelihood of crossing important biological thresholds (e.g. the freezing point of tissues). Snow strongly modifies both the physical and thermal environments. Changes in the absolute variability of these factors (as well as their timing and synchrony) can modify the

interaction and outcomes of snow cover and temperature. In Fig. 3, we describe how these drivers interact to determine biological impacts, and we show the direction of impact of changes in some of these drivers (which we elaborate below). Ultimately, the susceptibility of organisms to winter (see Table 1 for a description of the traits influencing vulnerability to winter changes), and the way these impacts combine and synergise with impacts of climate change during the growing season will determine the winners and losers under global climate change; understanding these processes will be essential for informed management of biodiversity in a changing world.

(1) Increased average winter temperatures

(a) Effects on metabolic rate

Increased average temperatures can arise either as a direct result of climate warming, for organisms whose habitats are not buffered from ambient temperatures, or from increased snow cover with associated thermal buffering (Figs 2A, B, 3). Increased average temperatures can impact energy stress and phenology by increasing rates of development or metabolism (Fig. 3). Temperature influences metabolism, and thus consumption of stored energy by (1) directly

Table 1. Organismal traits influencing vulnerability to winter climate change. Vulnerability is a product of traits that increase the likelihood of stress exposure (i.e. experiencing an increase in stress related to each of the underlined categories) in response to winter climate change, and traits that increase sensitivity to this stress (i.e. negative consequences of stress exposure at the whole-organism performance or fitness level). Sensitivity is conferred by a lack of either resilience (ability to recover from stress) or adaptive capacity (ability to adapt genetically or physiologically to stress). Climate drivers (indicated in italics, and with reference to the text and Fig. 3) are increased average temperatures (*AvT*), thermal variability [subdivided here into increased daily thermal variability (*DV*), extreme temperatures (*ExT*) and increased freeze–thaw cycles (*F/T*)], increased snow (*S+*) and decreased snow (*S-*).

Traits determining stress exposure	Traits determining sensitivity to stress	Proximal cause of vulnerability
Energy balance		
Thermoregulatory strategy (<i>AvT, DV</i>)	Reproductive strategy (<i>AvT, DV</i>)	• Consumption of finite energy reserves (<i>AvT, DV</i>)
• Poikilotherms > homeotherms	• Capital breeding > income	• Decreased resource availability
Energy intake and availability (<i>AvT, DV, S+</i>)	Energy storage (<i>AvT, DV</i>)	• Increased cost of locomotion (<i>S+</i>)
• No energy intake/limited food available > winter energy uptake	• Low > high pre-winter energy stores	• Decreased food access (<i>S+</i>)
Metabolic suppression (<i>AvT, DV, S+</i>)	Energetic recovery (<i>AvT, DV</i>)	
• Low > high suppression	• No post-winter feeding > feeds post-winter	
Metabolic plasticity (<i>AvT, DV</i>)	Feeding strategy (<i>S+, S-</i>)	
• Low > high plasticity	• Specialist > generalist	
Trophic position (<i>S+</i>)		
• Predator > prey		
• Heterotroph > autotroph		
Habitat (<i>S-</i>)		
• Subnivean > supranivean		
Phenology		
Chilling or vernalization requirements (<i>AvT</i>)	Trophic level (<i>AvT</i>)	• Reduction in length of growing season (<i>AvT</i>)
• Obligate > facultative dormancy	• Consumers > primary producers	• Trophic mismatches (<i>AvT</i>)
• Chilling requirement > non-thermal cues	Diet breadth (<i>AvT</i>)	• Habitat not available for reproduction (<i>S-</i>)
Habitat requirements (<i>S-</i>)	• Low > high	
• Snow-dependent > not snow-dependent	Overwintering stage (<i>AvT</i>)	
	• Early in life cycle > late in life cycle	
	Genetic variation in reaction norms (<i>AvT</i>)	
	• Low variation > high	
Cold injury		
Cold hardiness (<i>ExT</i>)	Rapid cold hardening (<i>ExT</i>)	• Direct injury from cold (<i>ExT</i>)
• Cold-susceptible > cold-hardy	• None > effective rapid hardening response	• Cumulative cold injury (<i>F/T</i>)
Cold-tolerance strategy (<i>ExT</i>)	Thermal plasticity (<i>ExT</i>)	• Energetic costs of repairing cold injury (<i>F/T, S-</i>)
• Seasonally programmed but readily deacclimate > constitutive protection	• No reacclimation > reacclimation	
Position of biological thresholds (<i>ExT, F/T</i>)	Cumulative impact of repeated stress (<i>F/T</i>)	
• Lower/higher than current conditions > near current conditions	• Cumulative > no cumulative impact/impact reaches asymptote	
Habitat (<i>S-</i>)		
• Subnivean > supranivean		
Water balance		
Susceptibility to waterlogging and ice encasement	Water balance strategy	• Hypoxia from waterlogging/ice encasement
• Hypoxia intolerant > hypoxia tolerant	• No winter water consumption > water consumption over winter	• Unavailability of liquid water when frozen
Predation		
Trophic position (<i>S-</i>)	Predator avoidance (<i>S-</i>)	• Increased mortality
• Prey > predator	• Low camouflage plasticity > high	
Habitat (<i>S-</i>)	• Low defences > high	
• Subnivian > supranivean	• High palatability > low	
	• Low alertness > high	
Pathogens, parasites and disease		
Cold tolerance of pathogens and parasites (<i>ExT</i>)	Immune response to cold (<i>ExT, AvT, F/T</i>)	• Increased mortality
	• Suppression > activation in response to cold	• Decreased fitness
Mismatch between immune system and pathogen thermal performance (<i>AvT</i>)	Cost of immune activation (<i>ExT, F/T</i>)	• Energetic costs

determining the rates of metabolic processes (such as respiration and carbon fixation) in poikilotherms, and (2) determining the costs of thermoregulation by homeotherms. Thus, increased average temperatures will increase rates of metabolism of poikilotherms, while for homeotherms below the thermoneutral zone, metabolic rates will decrease with increased average temperature due to the decreased cost of thermoregulation (Table 1).

A higher metabolic rate will increase the rate of use of stored energy reserves, which can expose non-feeding organisms to energetic stress (Fig. 3). For example, hibernating bats (*Myotis sodalis* and *M. lucifugus*) expend more energy when hibernaculum temperatures are above an optimal low temperature (Humphries *et al.*, 2002; Day & Tomasi, 2014), dormant hatchling turtles (*Chrysemis picta*) consume more energetic reserves and emerge in poorer physiological condition after warm winters (Muir *et al.*, 2013), and energy drain means that goldenrod gall flies (*Eurosta solidaginis*) that overwinter in relatively warm subnivean microclimates have reduced survival and fecundity compared to conspecifics overwintering in exposed, colder sites, because their metabolic rates increase exponentially with temperature (Irwin & Lee, 2003). All else being equal, this energy drain is likely to be more pronounced in organisms with high baseline metabolic costs, and less pronounced in organisms, such as diapausing butterfly pupae, that substantially suppress their metabolism during winter (Table 1; e.g. Williams, Hellmann & Sinclair, 2012a). Overwintering stage may also be important in determining energy drain as a result of winter warming: bees that overwinter as adults suffer greater energy drain than do those that overwinter as earlier life stages (Frund *et al.*, 2013).

Increased rates of biological processes may permit energy gain for organisms that can take up nutrients during the winter. For example, increased winter temperatures increase photosynthetic rates and thus carbon gain in non-dormant plants as long as water is available, although this effect is more pronounced in woody than in herbaceous species (Ensminger, Busch & Hüner, 2006). Similarly, the mineralisation of limiting nutrients such as nitrogen increases with soil temperature over winter (Sturm *et al.*, 2005), which can increase primary productivity, assuming that nutrient release and uptake are synchronised (Groffman *et al.*, 2001).

For homeotherms, the energetic costs of thermoregulation during winter can rival or exceed energetic costs of the breeding season, yet occur at a time when food availability may be low (Sgueo *et al.*, 2012). An increase in average winter temperatures will thus lower metabolic costs of thermoregulation in homeotherms that would normally experience winter temperatures below the thermoneutral zone, which may alleviate energetic stress (Fig. 3; Sears *et al.*, 2009). A release from energetic stress as a result of winter climate change may have led to recent increases in body size of American martens (*Martes americana*), either *via* decreased thermoregulatory costs or increased prey availability (which will reduce energetic stress by increasing nutrient uptake; Yom-Tov, Yom-Tov & Jarrell, 2008). Increased body

size and/or improved condition will likely translate into fitness benefits by decreasing overwinter mortality (Hodges *et al.*, 2006), or improving condition at the onset of the breeding season (e.g. Guillemain *et al.*, 2008). Alternatively, decreased thermoregulatory costs may increase fitness by reducing the need for pre-winter energy accumulation, which could mitigate trade-offs and predation risk associated with resource acquisition (Gentle & Gosler, 2001). However, overwinter physiology is not just driven by energetics, even in hibernating mammals: body mass (and presumably energy stores) is a poor predictor of hibernation duration in *Glis glis* edible dormice (Bieber *et al.*, 2014). By contrast, warmer winters may lead to summer energy drain for species such as polar bears (*Ursus maritimus*) that feed primarily during winter and fast in the summer. For polar bears, warmer winters reduce the length of the period during which the sea ice is sufficiently stable for hunting. This results in a shorter time over which polar bears can acquire their year's nutrients, offsetting any thermoregulatory benefits of warmer conditions (Robbins *et al.*, 2012).

However, direct evidence for energetic and performance consequences of winter warming in homeotherms is scarce. Changes in variables correlated with increased temperatures – such as snow cover, resource availability, and precipitation – make it difficult to isolate the impacts of temperature in observational studies, which form the majority of published work to date. For example, although they presumably provide a thermoregulatory advantage, warm winters reduced maternal investment in reproduction in red deer (*Cervus elaphus*), resulting in smaller offspring. This effect was probably driven by increased costs of locomotion incurred by deep snow in these winters, rather than by increased temperature *per se* (Post *et al.*, 1997). Thus, the impact in this case was driven by an interaction among abiotic drivers (Fig. 3).

(b) Effects on development and phenology

In addition to altering energy balance, increased average temperatures during winter generally promote development at times of year when it would traditionally be arrested, leading to activity earlier in spring, and later in autumn, for the majority of terrestrial taxa (Fig. 3; Jeong *et al.*, 2011; Walther, 2010). These phenological shifts have been particularly pronounced in cold regions such as the Arctic (Høye *et al.*, 2007). However, significant variation exists in phenological plasticity within communities; for example, phenological shifts in response to changing climate have been faster at lower trophic levels (Table 1; Both *et al.*, 2009; Thackeray *et al.*, 2010). Within the insects, these shifts are less pronounced in species with specialised diets or that overwinter at earlier life stages (Table 1; Diamond *et al.*, 2011), although the fitness consequences and trade-offs accompanying these shifts have not been well explored (Bale & Hayward, 2010).

For primary producers, or animals that are not limited by resource availability, performance is likely to be enhanced

by maximally-advanced spring activity and maximally-delayed autumn quiescence (Table 1), provided that such organisms do not participate in mutualistic interactions, such as plant–pollinator interactions, that will be disrupted by a phenology shift. Shortening the period of dormancy will allow greater resource accumulation during the growing season, and less energetic stress during winter. If this hypothesis is correct, performance will be enhanced in organisms whose phenologies are strongly temperature-sensitive and which can therefore respond to increases in average temperatures by rapid shifts in their growing season. Indeed, the ability to respond to climate change by advancing spring phenology strongly enhances fitness and persistence in plants (e.g. Fridley, 2012), presumably by lengthening the growing season and increasing resource accumulation (Pigliucci & Marlow, 2001). A recent evolutionary shift towards activity later in autumn has also been recorded in pitcher plant mosquitoes (*Wyeomyia smithii*), implying fitness gains from an extension of the length of the growing season (Bradshaw & Holzapfel, 2001), perhaps because resources are not temporally limited for mosquito larvae feeding on microbes in the contained pitcher plant ecosystem.

By contrast, phenological synchrony with crucial resources will likely be more important than growing season or winter length in determining fitness of organisms at higher trophic levels whose resources are temporally limited. This means that the optimal phenotype will depend on the phenology of the neighbouring trophic levels (Table 1). This dependence occurs because variation in phenological shifts can cause community mismatches, wherein resources for higher trophic levels are no longer synchronised with periods of demand. We will discuss the community-level implications in more detail in Section V, but the salient point at the organismal level is that a mismatch between food demand and availability is likely to apply strong selective pressure on higher trophic levels to maintain synchrony with the trophic levels below. Supporting the hypothesis that phenology may evolve to enhance synchrony with the trophic level below, winter moth caterpillars (*Opheroptera brumata*) have evolved a later spring hatching date in response to warming, which has increased synchrony with budburst of its host plant (oak, *Quercus robur*), and presumably imparted higher fitness despite a shorter growing season (van Asch *et al.*, 2013).

Thus, the pattern of selection on phenology likely differs among trophic levels, with producers or animals for which resources are available year-round experiencing consistent selection for maximal spring advances and autumn delays, while higher trophic levels experience divergent selection pressures that depend on the responses of the trophic level immediately below. This differential selection across trophic levels could explain why the responses of plant phenology to climate change show a strong phylogenetic signal (Willis *et al.*, 2008), while the responses of insect phenology do not (Diamond *et al.*, 2011): consistent selection on phenology in producers preserves the phylogenetic signal, while divergent selection on phenology at higher trophic levels reduces similarities across the phylogeny. Therefore,

although it is likely that phenological shifts will alter resource availability and thus energy stress for consumers whose resources are temporally restricted, determining whether the impact will be positive or negative requires consideration of the phenological responses of organisms at lower trophic levels (Fig. 3, Table 1).

Aside from predation, other types of interspecific interactions will determine the outcomes of phenological shifts. Mutualistic relationships such as plant–pollinator interactions depend on synchrony between interacting partners, and thus both partners will be under some degree of selection for phenological synchrony. The degree of selection will be determined by the degree of specialism on each side of the relationship; decoupling of synchrony will be highly deleterious for plants that depend on only one pollinator, or pollinators that depend on one nectar source. By contrast, generalist pollinators or plants may be buffered from negative effects to some degree (Biesmeijer *et al.*, 2006). Additionally, climate-change-induced phenological shifts could be advantageous for some species if they disrupt host–vector synchrony, thereby reducing pathogen spread (Garrett *et al.*, 2006).

Organisms for which seasonal timing is physiologically fixed (for example, univoltine insects with a fixed overwintering life stage; Danks, 2005) and that therefore have inflexible phenology, may suffer the most pronounced negative impacts of changing winter length and timing with climate change (Post & Forchhammer, 2008; Bale & Hayward, 2010). By contrast, organisms with multi-year life cycles or those that complete many generations per year are more flexible in their phenology, and are thus able to respond to variations in thermal units available for development by modifying their voltinism (Braune *et al.*, 2008; Altermatt, 2010), with concomitant performance advantages (Yamanaka, Tatsuki & Shimada, 2008; Bale & Hayward, 2010).

Many plants and insects have chilling or vernalisation thresholds that must be met before post-winter development can resume (Bale & Hayward, 2010). In these cases, warmer winters can slow development, leading to developmental delays (rather than advancement) in spring (e.g. Forrest & Thomson, 2011; Luedeling *et al.*, 2011). Most studies report an advance in spring development, although these are also intermixed with delays or lack of responses in many systems (Thackeray *et al.*, 2010); these delays are consistent with widespread effects of a reduction in chilling units (Cook *et al.*, 2012). Delays in spring activity or development have been well documented in meadow and steppe plant communities on the Tibetan Plateau, where the beginning of the growing season advanced in response to climate warming for the first half of a 20-year warming period, but was subsequently delayed despite continued climate warming (Yu, Luedeling & Xu, 2010; but see Zhang *et al.*, 2013). These delays are consistent with insufficient vernalisation (not enough accumulated cold exposure to end dormancy). However, these observations could also arise from the observed decrease in snow depth over this

period, which may have reduced the insulation of the roots and, counter-intuitively, resulted in colder conditions despite warming air temperatures (Yu *et al.*, 2013). There is no way to separate these proximal mechanisms from the available data, although this could be achieved through either autecological experiments on chilling requirements (e.g. Santiago *et al.*, 2013) or experimental snow manipulation (e.g. Groffman *et al.*, 2001).

Average temperatures will thus affect energy balance in two ways – directly, through rates of metabolism, and indirectly, through phenology and the resulting length of winter (Fig. 3). This introduces an important dichotomy in responses to winter climate change among dormant plants and insects: for cold-adapted species with high chilling or vernalisation requirements, increases in winter temperature will increase both overwinter energy use (by increasing metabolic rates) and winter length (by increasing development time). These changes will amplify the deleterious effects of warming for cold-adapted species. If failure to meet chilling requirements decreases the viability of populations, it may prove to be a proximate driver of range contractions at the equatorial range limit in some species. By contrast, for warm-adapted species that do not have chilling or vernalisation requirements, although warming will still increase overwinter energy use, it will also shorten the period of dormancy by advancing spring activity and development. Although this could mitigate the direct negative effects of winter warming on energetics of warm-adapted species, the resulting acceleration of snowmelt can advance spring phenology and increase exposure to extreme temperature events (Inouye, 2008); we elaborate on these dynamics in the next section.

(2) Altered thermal variability

Winter temperatures fluctuate on multiple temporal scales, ranging from diel temperature fluctuations, through short-term cycles associated with weather fronts, to seasonal changes (Gaines & Denny, 1993; Deere & Chown, 2006; Marshall & Sinclair, 2012*a,b*). The magnitude of these fluctuations varies spatially both with microhabitat (Marshall & Sinclair, 2012*b*), and across larger scales influenced by continentality, latitude and topography. Snow cover will drive much of this variability, so snow cover predictions must be taken into account to determine likely trends in variability in each of these components (Fig. 2). Changes in the seasonal timing of snow cover will exacerbate altered timing of extreme low temperatures (Fig. 2). Changes in thermal variability will impact energy balance, phenology, and cold injury through effects on metabolism, development, and freeze/thaw cycles as described below (Fig. 3). Species-specific sensitivity to changes in this variability may be particularly important in determining organisms' responses to winter climate change, although we note that changes in variability are extremely difficult to predict, even when only extreme events are considered (Easterling *et al.*, 2000). There are three salient components of fluctuations in winter thermal conditions: (a) the intensity and regularity of extreme

high and low winter temperatures, (b) the frequency with which temperatures cross important physical thresholds (e.g. the freezing point of water) or biological thresholds (e.g. thresholds for activity or cold-induced damage), and (c) the amplitude of thermal cycles on both diel and short-term scales (such as during storm events).

(a) Intensity and regularity of winter extremes

Extreme low-temperature events can cause cold injury, and winter mortality or injury is an important component of demographics for many species (e.g. Kanda, 2005; Sutherst & Maywald, 2005; Aukema *et al.*, 2008; Spiegel-Roy & Goldschmidt, 2008). Thus, a reduction in the intensity or duration of extreme winter low temperatures could increase winter and post-winter survivorship (Table 1; e.g. Tran *et al.*, 2007; Trotter & Shields, 2009), directly influencing the poleward or upper altitudinal range limit of a species (e.g. Neuvonen, Niemelä & Virtanen, 1999; Pfender & Vollmer, 1999; Crozier, 2004; Garrett *et al.*, 2006; Kasson & Livingston, 2012). However, there are cases where extreme low temperatures do not directly limit population persistence or geographic range. For example, the monophagous holly-leaf miner (*Phytomyza ilicis*) is more cold-tolerant than its host plant (holly, *Ilex aquifolium*), and its northern range limit in Europe is therefore likely set by the factors that set the host range, rather than directly by extreme low temperatures (Klok, Chown & Gaston, 2003). In such cases, amelioration of extreme low temperatures will not directly affect survival, but could still indirectly lead to range expansion if low temperatures are the primary determinant of resource availability.

Changes in thermal variability can modify the timing, predictability and sequence of extreme events over winter. Because many species have life-stage-specific tolerance to winter conditions [e.g. diapause-linked cold tolerance in insects (Leather, Walters & Bale, 1993); aquatic overwintering in adult frogs (Tattersall & Ultsch, 2008)], there is potential for changes in the seasonality of extremes to lead to mismatches between the occurrence of extreme events and the behavioural or physiological mechanisms that allow organisms to tolerate them (Bale & Hayward, 2010). In particular, organisms with seasonally programmed responses, or those which irreversibly lose cold tolerance during winter warm spells, will be more vulnerable to unseasonable temperature extremes than those with constitutively high or rapidly modified tolerances (Table 1; Bale & Hayward, 2010). For example, extremely warm mid-winter temperatures cause an irreversible loss of winter acclimatisation and the resumption of development in the emerald ash borer *Agilus planipennis* (Coleoptera, Buprestidae), making them susceptible to subsequent cold snaps (Sobek-Swant *et al.*, 2012). Extreme warm periods in spring can also lead to breaking of dormancy in plants, with subsequent extreme events killing buds and preventing reproduction or growth in the following season, as occurred in the unusual North American springs of 2007 (Gu *et al.*, 2008; Augspurger, 2009) and 2010 (Hufkens *et al.*, 2012).

Indeed, a 124-year temperature dataset combined with observations of frost susceptibility in Illinois, USA shows that the frequency of damaging spring frost events has increased in recent decades (Augsburger, 2013).

At the beginning of winter, unusual extreme events before organisms have accumulated programmed physiological protection can also lead to damage. For example, the grass *Bromus rubens* may be excluded from the intermountain steppe biome of western North America as a consequence of sudden freeze events in late autumn before the onset of (programmed) winter cold tolerance (Bykova & Sage, 2012). Thus, organisms that develop low-temperature tolerance in a programmed fashion (e.g. in response to photoperiod), or that have delayed the onset of winter hardening as part of a phenological shift, may be more vulnerable to changes in the occurrence of extreme events in autumn than organisms that can use temperature as a cue to rapidly increase early winter cold hardiness (Table 1).

(b) Frequency of threshold-crossing events

Changes in the frequency, intensity, or duration of extreme events could modify the frequency with which biologically important thresholds are crossed. For example, the 0°C threshold delineates the availability of liquid water and the beginning of soil freezing. Similarly, species-specific physiological thresholds exist, such as the temperatures at which ice formation and melting occur; crossing these thresholds can determine sub-lethal impacts (e.g. Marshall & Sinclair, 2010), survival (e.g. Régnière & Bentz, 2007) and overwinter energetics (e.g. Sinclair *et al.*, 2013b). In some regions (e.g. maritime-buffered habitats in the southern hemisphere; Chown *et al.*, 2004), temperatures already hover near the 0°C threshold: increases in mean temperatures will likely reduce the occurrence of freeze–thaw cycles in such environments, reducing the stress of threshold-crossing events. By contrast, increasing mean temperatures (or decreasing snow cover, see Section III.3) may increase the incidence of freeze–thaw in northern temperate habitats, and thus may increase the frequency of such transitions.

The implications of repeated freeze–thaw are not well understood, but the impacts appear to be largely negative. In invertebrates, repeated freeze–thaw can lead to a variety of deleterious consequences, due to both cold injury from the repeated cold exposure, and increased energy expenditure during repair and recovery in thaw periods (Marshall & Sinclair, 2012a). In freeze-tolerant *Rana sylvatica* frogs, carbohydrate energy reserves provide both fuel for the energy expended during freezing and the cryoprotectants for survival of freezing itself. In this species, repeated freeze–thaw both depletes energy reserves and reduces cold tolerance, suggesting the possibility for substantial fitness reductions with increased freeze–thaw (Sinclair *et al.*, 2013b). Repeated freeze–thaw cycles increase the risk of xylem embolism in conifers due to the expansion of gas bubbles during thawing that were formed upon freezing (Mayr, Gruber & Bauer, 2003). Increased intensity or frequency of soil freeze–thaw cycles can increase the lysis of soil

microorganisms and damage to plant roots, intensifying leaching and trace gas losses of soil nutrients (Groffman *et al.*, 2001).

In some cases, the impacts of repeated events such as freezing may not be cumulative. For example, elevated losses of soil nutrients may only occur in response to exceptionally severe frost soil events, and pools of frost-vulnerable materials in the soil are finite. Once the bulk of soil nutrients in these frost-vulnerable pools have been released, subsequent events may not result in further loss (Matzner & Borken, 2008). Thus, increased frequency of freeze–thaw can have detrimental effects in organisms for which the responses are cumulative, but for organisms or systems where the impact of repeated cold exposure reaches an asymptote (e.g. nutrient leaching), the impacts of repeated events may be less important (Table 1). However, at this point too little is known about the impacts of repeated stress (or about interactions among multiple stressors) to allow generalities to be constructed.

Increased thermal variability facilitates the more regular crossing of biological thresholds other than freeze–thaw. For example, decrease in temperature increases investment by hibernating mammals in thermoregulation, whereas temperatures above a threshold increase metabolic rate in a temperature-dependent manner, thus increasing consumption of energy reserves (Humphries *et al.*, 2002), so increased variability will lead to an overall increase in energy consumption. Activity thresholds of ectothermic animals (the ‘critical thermal minimum’, or CT_{min}) can be particularly important: below an activity threshold, an individual cannot feed (changing the dynamics of energy stores) and cannot move (Tattersall *et al.*, 2012). An inability to move prevents microhabitat selection and behavioural thermoregulation, increasing exposure to environmental stress (Dillon *et al.*, 2009; Huey & Tewksbury, 2009). Enforced inactivity can also increase predation risk: some predators such as winter-active spiders appear to rely on the immobility of their prey for hunting success and predation (e.g. de Roince *et al.*, 2013). Since these predators rely on having a CT_{min} that is lower than that of their prey, an increase in variability has the potential to increase the duration and frequency of periods during which predation can occur – cascading to affect community dynamics (see also Section V).

Another threshold effect of cold exposure can be the initiation or activation of immune systems. This has been observed in organisms as diverse as mammals – including humans – (Jansky *et al.*, 1996), amphibians (Maniero & Carey, 1997), reptiles (Tait, 1969), birds (Dabbert *et al.*, 1997) and insects (Sinclair *et al.*, 2013a). It is possible that this cold-induced immune upregulation is a response to a mismatch between cold-active pathogens (Carr *et al.*, 1976) and reduced performance of the immune system at low temperatures (this is thought to be an underlying explanation for the energetically expensive arousal periods during mammalian hibernation; Prendergast *et al.*, 2002; Luis & Hudson, 2006). Alternately, immune activation could be non-adaptive (see

Sinclair *et al.*, 2013a for a discussion of adaptive and non-adaptive hypotheses explaining cold-activation of immunity in insects). Regardless, immune upregulation is expensive (Moret & Schmid-Hempel, 2000; French, Moore & Demas, 2009), so a change in the frequency and nature of activation over winter would be expected to carry energetic costs that might yield fitness consequences, or alter host–parasite and host–pathogen dynamics (see Section V).

(c) *Impacts of the amplitude of thermal cycles*

Increases in daily thermal variability can increase rates of metabolism and photosynthesis in poikilotherms (Fig. 3), because of the curvilinear relationship between temperature and most biological rate processes. Jensen's inequality is a mathematical property of nonlinear functions, which states that the mean of a nonlinear response variable cannot be predicted based on the mean of the driver variable alone, but requires knowledge of the variability of the driver variable and the shape of the response function (Ruel & Ayres, 1999). For example, if the response function is accelerating over the range of temperature fluctuations (as is frequently the case with metabolic rate in ectotherms), the mean of the response variable will be elevated compared to its value at the mean temperature, and increasing thermal variability will further increase the mean of the response variable, even without a corresponding increase in the mean temperature. Thus, increases in thermal variability have the potential to exacerbate the impacts of an increase in mean temperature on metabolism (Ruel & Ayres, 1999). Additionally, thermal performance curves are asymmetric (fitness rapidly declines above the thermal optimum; Angilletta, 2009), and thus Jensen's inequality means that the impact of changes in temperature will also be asymmetric: temperatures above the thermal optimum will reduce fitness far more than temperatures an equal amount below the thermal optimum.

This effect of Jensen's inequality can be exacerbated or mitigated by modifying the shape of the rate–temperature relationship: a steeper curve (i.e. higher temperature sensitivity) will lead to a more pronounced impact (Ruel & Ayres, 1999), suggesting that organisms with high temperature sensitivity or thermal optima that are close to environmental temperatures will experience greater impacts of changes in thermal variability (Table 1; Foden *et al.*, 2013). Exacerbated thermal variability will therefore allow potentially-active ectotherms to take better advantage of warm spells during winter fluctuations. However, lower thermal sensitivity will reduce vulnerability to thermal variation, for example in energy-conserving overwintering ectotherms (Williams *et al.*, 2012b). Thus, short-term (e.g. daily) thermal variability likely exerts a strong selective pressure on temperature–rate relationships in ectotherms and plants, however, few studies to date have examined the impacts of daily thermal variability on overwintering organisms.

For dormant organisms, thermal variability will thus be an important determinant of overwintering energy use, particularly at winter's peripheries when temperatures are

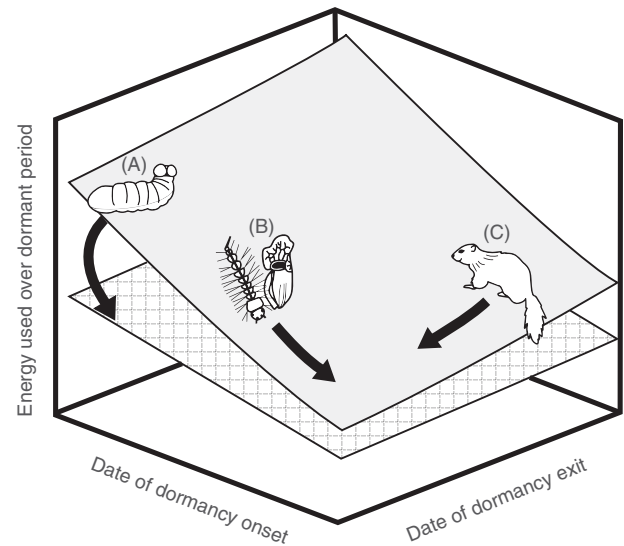


Fig. 4. The relationship between winter energy use and phenology for dormant organisms. A longer winter (early onset of or later exit from dormancy) results in higher energy use. Winter climate change is increasing total energy use through increases in means or variability of temperatures (effectively elevating the entire surface, not shown), and organisms have responded to this in three ways: (A) increasing the degree of metabolic suppression over winter, and thus lowering energy costs (e.g. the duskywing caterpillar *Erynnis propertius*; Williams *et al.*, 2012b); (B) delaying the onset of entry into dormancy, thus reducing the period of pre-winter energy drain (e.g. the pitcher plant mosquito *Wyeomyia smithii*; Bradshaw & Holzapfel, 2001); and (C) advancing the date of exit from dormancy, to take advantage of opportunities to feed and reduce winter energy drain (e.g. the yellow-bellied marmot, *Marmota flaviventris*; Ozgul *et al.*, 2010).

relatively warm and variable. In this context, seasonal timing will be a critical determinant of a species' susceptibility to overwinter energy drain resulting from alterations to thermal variability. Species that enter dormancy early in the autumn will experience significant energy drain as a result of delayed winter onset, and an increase in thermal variability during autumn will thus exacerbate this energy drain because of Jensen's inequality (e.g. Williams *et al.*, 2012b; Sinclair *et al.*, 2013b). By contrast, species with delayed spring emergence, including insects such as *Rhagoletis pomonella* that infest summer-fruiting trees (Feder, Hunt & Bush, 1993), will likely be more susceptible to earlier, more variable, and warmer springs. By contrast, increased buffering (e.g. due to longer snowpack persistence; Decker *et al.*, 2003) might reduce variability, mitigating the impact of the longer post-winter period.

Flexibility of the thermal sensitivity of biological processes or phenology will therefore be a key determinant of the outcome of changing thermal variability during winter and its associated dormancy (Fig. 4). Suppression of thermal sensitivity of metabolism mitigates the impact of increased thermal variability (Williams *et al.*, 2012b). In herbivores, for which entry into dormancy is likely mediated by a decline

in host plant quality (Prior *et al.*, 2009), such plasticity is essential, but may not compensate fully for increased autumn variability (Williams *et al.*, 2012b). In many species, the onset of dormancy is controlled hormonally and entrained to photoperiod (Tauber *et al.*, 1986), apparently reducing the capacity for flexibility because of the programmed nature of the response. However, evolutionary changes in the induction of dormancy as a result of climate change have been observed in a photoperiod-cued pitcher plant mosquito (Bradshaw & Holzapfel, 2001). Similarly, butterfly larvae show state-dependent responses to photoperiod, allowing facultative shifts in dormancy onset and behaviour both before and after dormancy to buffer the impact of reduced growth capacity at higher latitudes (Gotthard, Nylin & Wiklund, 1999, 2000). It is conceivable that such plasticity could also act to mitigate the impacts of winter energy drain.

Overall, while it is clear that the frequency, timing and amplitude of temperature variability dictate the severity of winter's effects on organisms, the examples presented above derive primarily from studies on insects. For organisms with more resilient or resistant overwintering stages (e.g. plant seeds) these effects may be less severe. The ultimate influence of extreme winter temperature events on populations, communities and ecosystems will be a function of both the severity and frequency of these events, and extremely severe events – by definition – occur infrequently. However, extreme events that lead to threshold changes in community trajectories will remain influential over the longer term (Kreyling, Jentsch & Beierkuhnlein, 2011).

(3) Changing snow cover

The strong influence of snow cover on the soil and subnivean microclimate (Fig. 2; Decker *et al.*, 2003; Henry, 2008; Pauli *et al.*, 2013) has important consequences for the condition and survival of organisms that overwinter in these environments, and as a result, changes in snow cover with climate change can result in many different biological impacts (summarised in Table 2). Because snow is an effective insulator, reduced snow cover can expose soil systems to more extreme low temperatures (Bale & Hayward, 2010; Brown & DeGaetano, 2011), described by Groffman *et al.* (2001) as 'colder soils in a warmer world', which in turn can increase mortality for organisms overwintering in or on the soil. The number of times per month that New Zealand alpine cockroaches were predicted to freeze and thaw ranged from 0 to more than 20, depending on snow cover (Sinclair, 2001). *Aphthona* beetles overwintering in the soil beneath snow in the USA prairies had higher survival than those that overwintered in soil with snow removed, but this difference in survival was only seen in relatively cold winters (Joshi, Olson & Carey, 2009). Nest density of arctic lemmings (*Lemmus* and *Dicrostonyx* spp.) was positively correlated with snow depth when snow cover was experimentally manipulated, presumably because the deep, dry snow layer buffered the small mammals from extreme temperatures (Reid *et al.*, 2012). Snow melt can also play an important role in the synchronicity of emergence and flowering (Inouye, 2008).

Table 2. The range of effects of changes in the quantity and timing of snow cover on overwintering organisms

Quantity of snow	
<i>Reduced snow cover</i>	
	Increased soil frost
	Increased food access for predators/browsers (decreased food access with increased rain-on-snow)
	Increased vulnerability of prey
<i>Increased snow cover</i>	
	Increased foraging and locomotion costs (winter-active organisms)
	Increased energetic maintenance costs (winter-inactive organisms)
Timing of snow cover	
<i>Early snowmelt</i>	
	Earlier warm-season resource gathering
	Potential phenological mismatch for dormant organisms
<i>Delayed snowmelt</i>	
	Delayed warm-season resource gathering
	Increased protection from frost
<i>Mid-winter snowmelt</i>	
	Cold deacclimation followed by frost exposure
	Increased access to liquid water

Thermal buffering by snow leads to a counterintuitive observation: organisms from very cold and snowy regions are frequently less cold-tolerant than those from regions with a shallower and less-persistent snow-pack. For example, despite the expectation that frost tolerance increases with increasing latitude within species, northern (snow-insulated) ecotypes of temperate grasses have low frost tolerance relative to their conspecific, southern ecotypes that experience less snow cover (Dionne *et al.*, 2001). Increased soil freezing as a consequence of decreased snow cover might therefore be particularly damaging for organisms adapted to snowy winters. Mid-winter melts can increase soil exposure to freeze–thaw with consequent damage to plants and soil fauna (Bokhorst *et al.*, 2011, 2012a), and these melts also can lead to ice encasement and subsequent anoxia, further stressing soil organisms (Coulson *et al.*, 2000). Despite the potential benefits of snow cover for frost protection, the mild subnivean microclimate can be energetically costly for organisms, because overwinter temperatures determine their energy consumption (Fig. 3). For example, gall flies overwintering below the snow have increased energy consumption compared to those above the snow (Irwin & Lee, 2003). Snow cover thus strongly influences levels of energy stress and cold injury indirectly, through its effects on temperature (Fig. 3), and changes in local patterns of snow cover therefore have the potential to alter habitat suitability on a very small scale.

Snow also impacts organisms directly by modifying the physical environment: both the quantity and the quality of snow can have profound effects, particularly on the biology of winter-active mammals. While the effects of changing snow cover can be assessed experimentally for sessile or small

organisms (e.g. Groffman *et al.*, 2001; Reid *et al.*, 2012), the limited spatial scale of most snow manipulation experiments makes it difficult to assess snow depth effects on large or highly mobile animals under controlled conditions. Nevertheless, observational studies can be used to correlate biological responses to interannual variation in snow depth. For example, wolves (*Canis lupus*) form larger packs in response to deeper snow (Post *et al.*, 1999), but increased snow depth also reduces mobility of their moose (*Alces alces*) prey (Fuller, 1991). Reduced snow cover may also increase resource availability for winter-active predators and browsers by improving access to food (Fig. 3; Martin & Maron, 2012) – which necessarily means that decreased snow also increases predation risk for small mammals which have less protection from predators and extreme temperatures (Yoccoz & Ims, 1999). However, the impacts of changing snow cover are complex: declining snow cover in Canada is associated with decreased wolverine (*Gulo gulo*) population growth rate; the causal factors for this decline likely include reduced denning sites, decreased prey success and reduced snow-related mortality of the ungulates upon whose carcasses wolverines scavenge (Brodie & Post, 2010). Snow quality, determined more-or-less directly by temperature, also determines the winter performance of many organisms, as changes in the density of snow modifies its insulative properties and affects locomotion, while ice layers can modify access through the snowpack. For example, increased frequency of rain-on-snow events, and subsequent ice-up, blocks access to food for herbivores such as *Rangifer tarandus* reindeer (Hansen *et al.*, 2011) and small mammals (Korslund & Steen, 2006; Kausrud *et al.*, 2008).

The timing of snow lie is also critical for many organisms, but the direction of impact strongly depends on species' traits. Early snowmelt can have positive effects for large browsers such as reindeer, which produce calves with increased body mass in the autumn following an early spring snowmelt (Pettorelli *et al.*, 2005). However, if early snow melt causes the resumption of activity before resources are available or interrupts winter feeding opportunities, the effects can be detrimental: early snowmelt can result in food scarcity for hibernating mammals, such as yellow-bellied marmots (*Marmota flaviventris*), that emerge early in response to warmer air temperatures, but before the spring flush of plant growth (Inouye *et al.*, 2000), and early ice breakup increases mortality in polar bears by reducing the length of the winter feeding season and increasing the length of the summer fast (Regehr *et al.*, 2007). By contrast, increased spring snowstorm activity with climate change in some regions can lead to delayed snowmelt, delaying the emergence of Columbian ground squirrels (*Urocitellus columbianus*) and reducing their fitness by reducing the length of the active season (Lane *et al.*, 2012). However, organisms that overwinter in subnivean spaces in very cold environments may benefit from an extension to the protective insulation of snow. For example, snow cover can minimise frost exposure by delaying flower bud development. In montane plants, delayed snow melt therefore increases peak floral abundance, because of decreased spring frost damage (Inouye, 2008).

Mid-winter snowmelt caused by extreme events (best studied because of their effect on hydrology; e.g. Kurian, Lautz & Mitchell, 2013) will not only affect overwinter soil temperatures and lead to encasement if the water refreezes, but also provide liquid water for plants and animals that might otherwise suffer from a water deficit, such as hibernating mammals (e.g. Ben-Hamo *et al.*, 2013). Conversely, increased free water may increase rates of heat loss and risk of flooding, decreasing survival of small mammals (Kausrud *et al.*, 2008). In Greenland, warmer summers result in the accumulation of cold meltwater, delaying flowering and shortening the flowering period of several angiosperms (Høye *et al.*, 2013). These roles of liquid water in determining winter physiology and spring timing in terrestrial systems during winter have received little attention, so the trade-off of negative and positive effects for organisms remains a matter for speculation.

IV. LINKS BETWEEN WINTER AND SUMMER RESPONSES TO CLIMATE CHANGE

The condition of organisms emerging from the winter will determine their performance during the growing season, and their growing-season performance will determine their condition going into the winter and subsequent winter performance (Fig. 5). Similarly, the timing of seasonal events will have ramifications that extend across seasons. For example, in insects, successful overwintering frequently depends on the progression of the life cycle to a specific life stage in time for winter, which in turn relies on the appropriate accumulation of thermal units during the growing season (Tauber *et al.*, 1986). Taking a cross-seasonal perspective will therefore be necessary to identify negative impacts of climate change. For example, advanced spring development and increased spring abundance of a perennial herb in Britain resulted from winter warming, but this was tempered by a decrease in reproductive output by those plants (Fox *et al.*, 1999). Similarly, early snow melt increased survival in conifers, but at the expense of growth rates (Barbeito *et al.*, 2012). Where data on post-winter performance are lacking, links from winter condition to the growing season may often be inferred. For example, winter energy use can determine adult body size in butterflies (Williams *et al.*, 2012a), and the clear size–fecundity relationship in female butterflies (Boggs & Freeman, 2005) implies a fitness consequence of this winter effect. The resilience of organisms to winter energetic stress can also be determined by post-winter processes (Table 1), with resilience decreased in organisms with limited opportunities for post-winter resource acquisition (Breed, Stichter & Crone, 2013), or for which juvenile-derived reserves are essential for reproduction (Irwin & Lee, 2003).

If responses to climate change improve pre-winter condition, winter performance may be enhanced. For example, yellow-bellied marmots have advanced their spring emergence in response to recent climate change, which

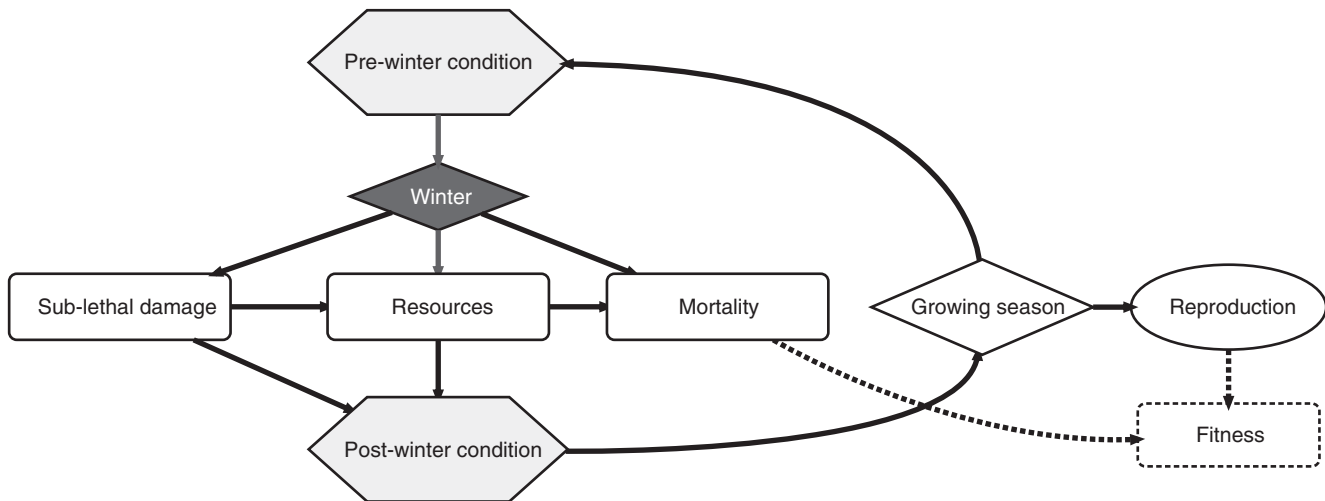


Fig. 5. Integrating winter processes into growing-season biology for a species or population. This assumes that reproduction (which determines fitness) occurs in the growing season, but could be modified for other life histories. The black diamond ‘winter’ represents the abiotic conditions that are experienced during winter, and the three white boxes are the outcomes of biological processes and stresses described in Fig. 3 and Table 1. These processes affect post-winter condition, which affects growing-season performance (all growing-season processes are combined in this framework), which in turn determines the pre-winter condition of organisms. Dashed lines indicate that winter transduces to fitness either directly (*via* mortality) or indirectly (*via* growing-season reproduction). The strength and importance of these links will depend on life history and the extent to which summer and winter stresses exacerbate or negate one another.

allows increased resource accumulation and growth and, consequently, increased overwinter survival and population growth rates (Ozgul *et al.*, 2010). Presumably, such positive impacts of longer growing seasons will help to buffer negative impacts of winter climate change, although few data exist to address this hypothesis. However, some changes to growing-season physiology may have negative effects on winter performance. For example, damselfly larvae (*Ischnura elegans*) that grow rapidly during the growing season do so at the expense of winter cold tolerance (Stoks & De Block, 2011), although this trade-off was not apparent in butterflies (Karl *et al.*, 2013), underlining the likelihood that the relationship between summer and winter will be complex and species-specific.

In Fig. 5, we conceptualise the potential biological impacts of winter climate change on a species (or population) in an inter-seasonal context. We assume that reproduction and growth occur outside of winter; modification will be necessary for species that reproduce in winter. In Fig. 5, the winter variables that affect an organism are represented by ‘Winter’, while ‘Mortality’, ‘Resources’ and ‘Sub-lethal damage’ represent the outcomes of the biological processes and stresses in Fig. 3. Figure 5 can be used in two ways. First, it can be used in conjunction with our framework describing the impacts of winter (Fig. 3, Table 1) to identify areas in which further research is required. Second, if the strength of the causal links shown in Fig. 5 can be determined, it can be used to determine the relative importance of different aspects of winter in determining how a species’ (or population’s) vulnerability to overwinter conditions plays out in the growing season and affects fitness.

The relationships between post-winter condition, growing-season performance (and reproduction) and pre-winter condition are already known for many species, thanks to the preponderance of growing-season studies. Winter mortality has been well explored for many species (Aars & Ims, 2002; Hodges *et al.*, 2006; Stahl *et al.*, 2006; Roland & Matter, 2013), but data are lacking regarding the sub-lethal impacts of winter, mediated through resource consumption and damage, and the effects of these sub-lethal impacts on growing-season performance. Moving forward, the direct relationships between winter conditions and growing-season performance need to be explored further across many taxa [see Kreyling (2010) for a plant-focused discussion of this point], as does the extent to which vulnerability to summer changes may exacerbate or negate vulnerability to winter changes.

V. SCALING FROM INDIVIDUALS TO POPULATIONS, COMMUNITIES, AND ECOSYSTEMS

The direct effects of winter climate change on individual organisms will combine and synergise with competitive interactions to influence demography. Positive impacts of winter climate change, in the form of decreases in winter mortality and/or increased reproductive success, may be balanced or cancelled out by a corresponding increase in intra-specific competition. For example, early snow melt and increased availability of forage decreased overwinter mortality in reindeer, which increased competition

and slowed population growth (Tyler, Forchhammer & Øritsland, 2008). Winter climate change can affect population dynamics both directly and indirectly *via* different mechanisms. In an alpine butterfly, delayed snow melt directly increased population growth by increasing recruitment in the subsequent year, and indirectly increased population growth by increasing the peak abundance of the butterfly's floral resources (Boggs & Inouye, 2012). Climate-change-related shifts in population densities and processes at the leading and retracting range edges (Hill, Griffiths & Thomas, 2011) lead to well-documented poleward range shifts, especially in butterflies (Parmesan *et al.*, 1999; Hill *et al.*, 2002; Chen *et al.*, 2011*b*). In some cases, climate-driven range shifts and expansions have been directly attributed to changes in winter climate (Crozier, 2004; Berger *et al.*, 2007; Cavanaugh *et al.*, 2014). Conversely, differential susceptibility to winter climate change among populations could also reduce performance in peripheral populations (Pelini *et al.*, 2009), leading to range contractions in some species.

At community scales, complex multi-trophic interactions can drive the effects of climate change on individual species. Alterations to the abundance of plants or animals as a result of changes in mortality or phenology can be propagated through communities *via* consumer–resource interactions. For example, in a deciduous forest, increased winter herbivory by elk (*Cervus canadensis*) as a result of decreased snow cover depresses plant and associated bird communities throughout the year (Martin & Maron, 2012). A deeper snow pack in the Great Lakes region of the USA increases hunting success of wolves leading to reduced moose (*Alces alces*) populations, which releases fir trees from heavy browsing and increases the fir understorey (Post *et al.*, 1999). In turn, these changes in understorey composition and browsing could depress soil respiration rates (Persson *et al.*, 2009). Community interactions can modify and even reverse the effects of climate change on individual species. For example, winter-induced changes in herbivory can prevent shrub expansion in Arctic tundra (Olofsson *et al.*, 2009). In ecosystems where predator populations are subject to bottom-up control due to resource limitation, negative effects of winter climate change on prey may extend to higher trophic levels. Winter climate change has decreased plant production and forage quality, leading to declines in herbivore fitness (Awmack & Leather, 2002; Bokhorst *et al.*, 2012*b*), and the collapse of Arctic lemming population cycles has decreased the population growth of several predator species (Gilg, Sittler & Hanski, 2009; Schmidt *et al.*, 2012). Conversely, direct impacts of winter climate change on overwintering carnivores may lessen predation pressure on prey species, with community-wide consequences (Estes *et al.*, 2011), although few examples exist of such climate-induced trophic cascades in a winter context – perhaps because such studies have focused on Arctic and boreal habitats. These multi-trophic interactions make it imperative to predict the direct impacts of winter climate change on species that exert strong top-down or bottom-up control within their

communities, perhaps aiding identification of focal species for winter study.

As we have shown, winter affects different species in different ways. Thus, dissimilar responses to winter climate change by different species can exacerbate phenological mismatches, reconfiguring community interactions (Van der Putten, Macel & Visser, 2010). For example, winter climate change has led to earlier spring leaf-out and caterpillar emergence in European oak forests, decreasing synchrony of (caterpillar) food supply with peak feeding times in passerine birds (Both *et al.*, 2009). Similarly, the plant growing season has advanced faster than the timing of caribou (*Rangifer tarandus*) migration to Arctic breeding grounds, resulting in increased calf mortality and lower calf production (Post & Forchhammer, 2008). By contrast, climate change has actually improved host-plant–herbivore synchrony in a sub-Arctic moth–birch system. Previously, birch bud burst occurred too early for *Agriopis aurantaria* moth larvae to feed on young (palatable) leaves. However, spring development of the moths has advanced more rapidly than birch in response to shorter winters, which has improved synchrony and enabled moth larvae to exploit this new resource (Jepsen *et al.*, 2011). In extreme cases such as irruptive outbreaks of the (winter-limited) mountain pine beetle, winter climate change has contributed to altering landscape-level processes: beetle infestation modifies tree survival and species composition, ultimately converting forests in British Columbia from net carbon sinks to a source of carbon (Kurz *et al.*, 2008).

Species' responses to winter climate change may also be modified by their interactions with pathogens and parasites. Some pathogens, such as the fungus that causes wheat rust (Roelfs *et al.*, 1992), have a range more restricted by low winter temperatures than that of their host; in these cases, milder winters (or reduced instance of extremes) will result in increased prevalence and range expansion of the pathogen, whereas reduced snow cover may prevent such spread due to an increase in extreme low-temperature events. Winter climate change could also significantly affect disease incidence and prevalence indirectly, *via* fitness effects on vectors. For example, the European distribution of the arboviral vector *Aedes albopictus* is currently limited by low temperatures that kill diapausing eggs (Caminade *et al.*, 2012), while mild winters are associated with an increase in fungal disease in beech trees in Maine, largely because of increased survival of the (invasive) scale insect vectors (Kasson & Livingston, 2012). Finally, cold-related immune upregulation or suppression (see Section III.2*b*) could modify host–parasite or host–pathogen interactions, leading to shifts in population dynamics. Changes in these disease-related processes therefore have the potential not only to have single-species effects, but indirectly to mediate larger-scale ecological shifts.

Mutualistic and symbiotic community interactions can also influence the evolutionary response to climate change. Bacterial or viral symbionts can influence thermal tolerances and particular combinations of symbiont and host can be strongly selected against during climate change in the context

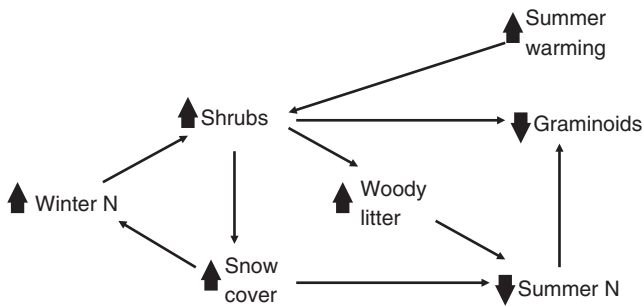


Fig. 6. Example of how adding links to account for species interactions and ecosystem processes that determine seasonal changes in resource availability can extend the integration of winter processes into growing-season biology to the ecosystem scale. This example, simplified from Sturm *et al.* (2005), describes how climate warming may drive potential feedbacks between changes in snow cover, nutrient availability and plant species composition in the Arctic.

of high-temperature tolerance (Harmon, Moran & Ives, 2009). Symbiont–host combinations may change seasonally during hibernation (Carey, Walters & Knight, 2013), and might play a role at low temperatures as well (Sinclair *et al.*, 2013a). Plant–pollinator interactions are at risk of being disrupted by winter climate change, but if this decoupling is incomplete (i.e. there is still overlap between adult flight and flowering periods) and the species involved are generalists, the impacts may be limited (Forrest & Thomson, 2011).

The links addressed in Fig. 5 can be extended to processes that occur at the community or ecosystem scale. In so doing, additional links must be added to account for species interactions such as competition, and ecosystem processes that determine seasonal changes in resource availability. For example, Fig. 6 (based on Sturm *et al.*, 2005) describes potential feedbacks between changes in snow cover, nutrient availability and plant species composition in the Arctic. In this scenario, climate warming is expected to promote shrub expansion into graminoid communities, increasing the trapping of snow. Increased depth and duration of the snowpack can then increase nitrogen availability over winter by increasing soil microbial activity, and because the shrub canopy is above the snow layer, bud-burst and photosynthesis can occur earlier than in the low-statured graminoids, allowing the shrubs to access late-winter nitrogen pulses. Decreased nitrogen availability over summer, enhanced by increases in low-quality, woody shrub litter, coupled with increased shading by shrubs, further reduce the competitive abilities of the graminoids. In contrast to the latter example, extremely low spring snow accumulation is projected to occur over much of the Northern Hemisphere, with >80% of years below the baseline minimum in some areas by 2080–2099 (Diffenbaugh & Field, 2013). The resulting decreases in melt water in spring, coupled with increased evapotranspiration and decreased summer rainfall in some regions, will increase summer drought severity.

As we have demonstrated in this section, understanding the interactions between climate and biotic processes is essential

for predicting how ecosystems will respond to climatic warming (Blois *et al.*, 2013). Moving forward, integrating the responses of organisms across entire ecosystems, while taking into account linkages between winter and summer responses to climate change, and differing capacity to evolve, is a daunting task. This task will be facilitated by *a priori* identification of the key vulnerabilities to winter climate change, a process which is described in the following section.

VI. PREDICTING VULNERABILITY TO WINTER CLIMATE CHANGE

It is clear that winter is an important driver of biological processes and organismal fitness, and that winter climate change has the potential significantly to impact individuals, populations, community interactions and ecosystem processes. However, if a goal of global change research is to offer predictive power to facilitate risk assessments and management decisions, then it is necessary to identify which species and processes will be most vulnerable to changing winters.

Williams *et al.* (2008) proposed an integrative framework to identify and prioritise species that are vulnerable to climate change, where vulnerability was defined as susceptibility of a system to change; in most of our cases, the primary ‘system’ we consider is an individual or population (although in many cases, we and other authors extrapolate the biology of individuals or populations to represent the species, as that is the level at which much conservation thinking is conducted). The authors distinguished between factors determining exposure to a change in climate, and those determining sensitivity to those changes. In their framework, exposure was determined by the degree of regional climate change, filtered through microclimatic buffering due to habitat choice. For example, if temperatures are rising, a species that does not have the capacity to change microhabitat choice or alter thermoregulatory behaviour will be exposed to an increase in temperature, whereas a species that can buffer these regional changes will not (Kearney, Shine & Porter, 2009). In the context of winter, the three primary drivers: changing snow cover, thermal variability, and shifts in mean temperature, interact with overwintering biology to modify the stresses that will be experienced, and information on individual responses is required to predict those stresses. Figure 3 can be used as a framework for determining exposure to stress resulting from winter climate change based on individual responses to those interacting drivers, although such predictions are still dependent on predicting changes in the drivers from climate data and models – a major challenge given the discrepancy between the size of organisms and the scale at which climate data are collected (Potter, Woods & Pincebourde, 2013), and the lack of information about the time frames over which selection will modify winter phenology and physiology.

Assuming that we can accurately assess an organism’s exposure to stress resulting from climate change, the next step is to determine whether it will be sensitive

(i.e. experience negative impacts). Williams *et al.* (2008) suggest that sensitivity is governed by intrinsic ecological, physiological or genetic traits of the focal species (or population) that determine levels of resilience (the ability to survive and recover from a negative impact) and adaptive capacity (the capacity for plastic or evolutionary changes to reduce negative impacts). Related to the capacity for adaptation, we note that estimates of the strength of selection encountered by organisms in winter environments are an essential component of a predictive framework, but to date few studies have measured such selection gradients [Boratynski *et al.* (2010) provide one example of this]. In using Fig. 3 as a framework, it is possible not only to identify the potential exposure to stress resulting from changes in the drivers, but because it makes clear (some of) the causal links between the drivers and organismal fitness, it allows the identification of end traits – and the design of simple experiments – that facilitate an assessment of the susceptibility of organisms to changes in those drivers. For example, there are clear links between overwintering temperature and energy consumption for many overwintering ectotherms. It is thus possible to design a simple experiment (e.g. keep overwintering stages of several species at several temperatures; Williams *et al.*, 2012a) to compare susceptibility of energy use to changes in temperature. Similarly, experimental designs are now well established for determining impacts of repeated stress exposure (Marshall & Sinclair, 2012a), addressing the impacts of shifting variability or snow cover – although the results of such experiments are not necessarily easy to interpret. For example, repeated freezing in overwintering caterpillars saves energy (Marshall & Sinclair, 2012b), but has other sub-lethal impacts (Marshall & Sinclair, 2011). Thus, a reductionist approach can be used to identify or rule out susceptibility to certain drivers of climate change relatively rapidly, but more complex experiments are necessary to understand interactions among drivers.

More generally, it is possible to identify some of the general traits that render individuals or populations of a species vulnerable (or resilient) to winter climate change (Table 1). As with all sensitivity to climate change, species that have high rates of reproduction and short life cycles, large range sizes (but not large spatial scales of operation), and high dispersal will be less vulnerable to change (Williams *et al.*, 2008). However, the links in Fig. 3 allow the identification of winter-specific traits that lead to vulnerability; some of these are outlined in Table 1, and are grouped according to energy balance (e.g. thermoregulatory strategy, metabolism), phenology (e.g. chilling requirements, overwintering stage), cold injury (e.g. cold tolerance, response to repeated stress), water balance and predation (e.g. trophic position, predatory avoidance strategies). Linking changes in community structure to changes in functional processes will be particularly challenging for soil microorganisms, although some combination of experimental and comparative approaches (as proposed by Hodkinson & Wookey, 1999) may provide a deeper understanding of these relationships.

Despite extensive evidence from individual cases for the importance of trophic dynamics in determining overwinter responses, they remain difficult to predict. Community-level experiments are inherently complex and limited in spatial and temporal scope, while the use of population-based data to construct dynamic models of communities is typically inadequate for predicting responses to novel combinations of drivers, even in the growing season (Abrams, 2001). This complexity is intensified when the relative performances of organisms both over summer and winter must be taken into account, but we propose that the species-based *a priori* approach, based on the drivers and vulnerabilities identified in Table 1 and Fig. 3 can be used to identify key impacts of winter. If combined with an understanding of the community interactions in a system, it is possible at least to identify potential responses to winter climate change at the community level.

VII. A CALL TO INTEGRATE WINTER INTO CLIMATE CHANGE RESEARCH

Winter imposes a severe selective pressure that determines fitness, drives many ecological processes, and shapes the evolution of organisms. The pressing need to understand the mechanisms underlying biological responses to climate change, coupled with the rapid changes in winter conditions, together provide a strong imperative to unravel the complexities of responses to winter at the individual, community, and ecosystem scales, and to determine general patterns describing vulnerability to negative impacts. To integrate this information we must combine theoretical and empirical approaches and synthesise across taxa, levels of organisation, and climate drivers.

For theorists, the challenge lies in incorporating winter into models that tend to have forms and parameters associated with growth and assimilation, rather than dormancy and consumption (although there is scope for the latter in Dynamic Energy Budget models; Sousa *et al.*, 2010). Mechanistic models of winter biology exist for some species, and the form of some of these models may be incorporated into existing frameworks, and potentially expanded to include additional aspects of winter climate change. For example, Régnière & Bentz (2007) have provided a robust model of the dynamic shifts in cold tolerance of overwintering mountain pine beetles, although this model does not incorporate any sub-lethal impacts of cold exposure. Because it is likely that the existing relationships between climate variables will be disrupted (Jackson *et al.*, 2009; see also Fig. 2), functional or phylogenetic approaches may be powerful alternatives to existing niche models (Buckley & Kingsolver, 2012) by using existing studies to infer potential impacts of combinations of winter drivers that may be novel for a given species or population. However, data regarding the effects of winter conditions on fitness are sparse and diffuse, cover many non-equivalent metrics of winter performance and impact, and are not necessarily in a model-ready format. Trait databases

such as iPlant (Goff *et al.*, 2011) may provide a source of such information, but theorists and empiricists will need to work together to identify the key traits that will inform vulnerability to winter climate change, using approaches similar to those outlined in Fig. 3 and Table 1.

To inform this theoretical effort, empiricists need to collect more data on the performance and, ultimately, fitness consequences of projected changes in winter climate drivers. Such an understanding requires integration across levels of organisation and from regional to single-organism scales; this integration entails a shift in focus to populations rather than species, metres rather than miles, and minutes rather than months. A lofty goal for mechanistic studies of overwintering biology is the development of general principles that describe how organisms respond to winter, and the ability to predict – *a priori* – which species will be most vulnerable to winter climate change. To accomplish this we must extend more laboratory studies into the field, which will require methodological limitations and biases to be overcome. For example, methods for simulating winter climate change in the field, such as snow fences, snow removal, heated soil cables and overhead heaters, are often plagued by artifacts or scaling limitations (Shen & Harte, 2000). Similarly, there is a need to expand the geographic and taxonomic focus of winter biology. There has been a disproportionate focus on relatively cold environments with long winters (such as the High Arctic) relative to temperate systems (Kreyling, 2010), and there have also been asymmetries in research between the northern and southern hemispheres, which may also bias our understanding of the key aspects of winter (Chown *et al.*, 2004). Throughout this review, it is apparent that the bulk of the literature on some broadly applicable topics is constrained to certain systems; for example, many studies of winter climate change at the community and population levels have been conducted on arctic mammals, but few on temperate insects, whereas a disproportionate amount of research has been conducted on the physiological responses to freezing of temperate insects and crop plants. Finally, there is a need for substantial effort documenting autumn and winter events complementing the successful and ongoing documentation of changes in spring timing and growing-season biology. We particularly encourage a concerted effort to expand existing, well-characterised systems into the winter to develop a more holistic view of how organisms, communities, and ecosystems will respond to climate change.

VIII. CONCLUSIONS

(1) Overwintering is a key component of the biology of organisms that live in temperate, polar and alpine habitats, and has driven the evolution of extreme phenotypes such as dormancy and migration.

(2) The main abiotic drivers of biological responses to winter are the mean and variability of air temperatures and the extent and timing of snow cover. All of these are being affected by climate change in a regionally specific manner.

(3) Understanding the links between abiotic change and organismal performance is important for determining organismal vulnerability to climate change. This will require a mechanistic and integrative approach.

(4) Responses to winter conditions are not isolated from growing-season responses to climate. Therefore it is important to investigate the impacts of winter on performance, fitness and biotic interactions in the context of growing-season biology. We suggest that an opportunity exists to extend existing long-term studies of growing-season biology to incorporate the effects of winter.

(5) At the population and community levels, inter- and intra-specific interactions strongly influence responses to winter climate change. Impacts on individual species will propagate through ecosystems, and the role of winter in modifying these interactions must be considered when predicting the ecological impacts of climate change.

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