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

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5 2 **Cold truths: How winter drives responses of terrestrial organisms to climate**
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23 lethal impacts, energetics, hibernation
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4 20 **Abstract**

5 21 Winter is a key driver of individual performance, community composition, and ecological
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7 22 interactions in terrestrial habitats. Although climate change research tends to focus on
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9 23 performance in the growing season, climate change is also modifying winter conditions rapidly.
10
11 24 Changes to winter temperatures, the variability of winter conditions, and winter snow cover can
12
13 25 interact to induce cold injury, alter energy and water balance, advance or retard phenology, and
14
15 26 modify community interactions. Species vary in their susceptibility to these winter drivers,
16
17 27 hampering efforts to predict biological responses to climate change. Existing frameworks for
18
19 28 predicting the impacts of climate change do not incorporate the complexity of organismal
20
21 29 responses to winter. Here, we synthesise organismal responses to winter climate change, and use
22
23 30 this synthesis to build a framework to predict exposure and sensitivity to negative impacts, and
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25 31 that can be used to estimate the vulnerability of species to winter climate change. We describe
26
27 32 the importance of relationships between winter conditions and performance during the growing
28
29 33 season in determining fitness, and demonstrate how summer and winter processes are linked.
30
31 34 Incorporating winter into current models will require concerted effort from theoreticians and
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33 35 empiricists, and the expansion of current growing season studies to incorporate winter.
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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. 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 the 1997-2000 period are 36.1 °C and 36.7 °C, whereas the respective extreme minimum temperatures at these locations, -37.8 °C and -1.1 °C, differ 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 is 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 the Virginia opossum in eastern North America (Kanda, 2005), the mountain pine beetle in western North America (Stahl, Moore & McKendry, 2006), 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 (Hahn & Denlinger, 2011; Irwin & Lee, 2003), and overwintering energetics constrain some species' distributions (e.g. Humphries, Thomas & Speakman, 2002).

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4 81 In spite of the constraints, many species thrive in places with severe winters, and there
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6 82 are species that might be considered winter-dependent; for example, most Arctic vertebrates
7
8 83 require snow and ice for their reproduction and survival (Gilg et al., 2012), and some
9
10 84 invertebrates disperse and hunt primarily in subnivean (beneath the snow pack) spaces
11
12
13 85 (Addington & Seastedt, 1999; Pauli et al., 2013). Some species that overwinter in a dormant
14
15 86 state have evolved dependence on winter cues for termination of dormancy (Amasino, 2004;
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17
18 87 Tauber, Tauber & Masaki, 1986), and monarch butterflies rely on winter cold to reverse the
19
20 88 direction of their fall migration (Guerra & Reppert, 2013). Many ectotherms and hibernating
21
22 89 mammals rely on low winter temperatures to reduce consumption of energy stores (Humphries et
23
24
25 90 al., 2002; Williams et al., 2012b). At the ecosystem level, freezing of soil in winter can mobilise
26
27 91 nutrients (and/or damage roots), affecting nutrient availability and uptake, and therefore primary
28
29 92 productivity, in the spring (Durán et al., 2013; Groffman et al., 2001). Likewise, winter
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32 93 conditions in many species can define organismal performance in the subsequent summer (Boggs
33
34 94 & Inouye, 2012; Post et al., 1997; Serrano et al., 2011).

35
36
37 95 Repeated glacial/interglacial cycles, coupled with continental drift in and out of the
38
39 96 tropics, mean that physiological and life history adaptations to winter have evolved repeatedly in
40
41 97 multiple lineages of organisms. The evolutionary impact of winter on life histories is significant
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43
44 98 – for example, the northern temperate winter may have been a primary driver of the evolution of
45
46 99 migratory and hibernation phenotypes (Alerstam, Hedenstrom & Akesson, 2003; Turbill, Bieber
47
48 100 & Ruf, 2011). For ectotherms, microbes, and plants, the threat of internal ice formation has
49
50 101 driven the evolution of physiological traits that allow them to resist low temperatures (for
51
52
53 102 example, freeze tolerance in insects and plants; Margesin, Neuner & Storey, 2007).
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55 103 Nevertheless, both endotherms and ectotherms suffer high mortality over winter (Hodges,
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3 104 Boonstra & Krebs, 2006; Roland & Matter, 2013; Stahl et al., 2006), and the population
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6 105 dynamics of diverse fast-reproducing animals including lemmings and moths can be driven
7
8 106 primarily by winter mortality (Callaghan et al., 2004; Virtanen, Neuvonen & Nikula, 1998).

9
10
11 107 Anthropogenic climate change is rapidly altering biological systems, and winter
12
13 108 conditions are changing particularly rapidly (IPCC, 2007). Differential sensitivity of organisms
14
15 109 to climate change is restructuring biological communities due to disparate range and phenology
16
17
18 110 shifts, and altered population dynamics (Chen et al., 2011a; Walther, 2010), and – where the
19
20 111 proximate cause is known – many biological responses to climate change are driven by changes
21
22 112 in winter conditions (e.g. Battisti et al., 2005; Crozier, 2004). To guide mitigation efforts under
23
24
25 113 global climate change, we must identify which species or populations will be “winners” –
26
27 114 benefitting from climate change, and which “losers” will be vulnerable to changes (Somero,
28
29 115 2010). However, the interactions between snow and temperature that determine microclimate
30
31 116 conditions combine with divergent ecological and physiological strategies for dealing with
32
33
34 117 winter stress, leading to variation among species in responses to winter climate change. In some
35
36
37 118 cases, these idiosyncratic responses to winter likely underlie the failure of models to accurately
38
39 119 predict species’ responses to climate change (Cook, Wolkovich & Parmesan, 2012). A limited
40
41 120 understanding of organismal responses to winter climate change (and their cascading effects
42
43
44 121 through communities and ecosystems) thus impedes efforts to predict the biological impacts of
45
46 122 climate change in general.

47
48 123 The interaction between a species’ traits (and the plasticity of those traits; Chown et al.,
49
50 124 2007; Somero, 2010) and changes in the abiotic environment will determine success or failure in
51
52
53 125 a changing world (Foden et al., 2013), so predictions would ideally utilise information on species
54
55 126 traits combined with climate models to output vulnerability. Meta-analyses have shed some light
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3 127 on the relationship between species' traits and their responses to environmental change (e.g.
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6 128 Bokhorst et al., 2012a; Diamond et al., 2011; Jiguet et al., 2007; Thackeray et al., 2010),
7
8 129 however, these analyses have not been in the context of winter, nor have they synthesised across
9
10 130 diverse taxa and abiotic drivers. Thus, we need a framework to identify climate-change-
11
12 131 susceptibility that explicitly includes winter processes and incorporates evolution, ecology and
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14 132 physiology. An essential starting point is a synthesis of the mechanistic bases for the complex
15
16 133 responses to interacting winter climate drivers across terrestrial taxa.
17

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20 134 Here we present a multi-component framework for predicting the impact of change in
21
22 135 abiotic winter drivers on a terrestrial organism. We begin by describing the predicted changes in
23
24 136 winter climate, then synthesise the mechanistic bases for the biological impacts of winter climate
25
26 137 change across terrestrial taxa and regions. We use this synthesis to identify key traits that make
27
28 138 species susceptible to changing winter conditions, and integrate the current state of knowledge
29
30 139 on impacts of winter climate change within the body of knowledge of growing season processes.
31
32 140 We focus on traits influencing exposure and sensitivity to a particular stress, which may arise
33
34 141 from a number of drivers or interactions between drivers, and through both biotic and abiotic
35
36 142 processes. Our review is not meant to be exhaustive in scope, but rather to draw on
37
38 143 representative examples across taxa to illustrate the main biological impacts of winter across a
39
40 144 range of terrestrial organisms, to provide a starting point for readers to access the literature
41
42 145 relevant to their system, and to guide future research in the field of winter-focused global change
43
44 146 biology. This framework is designed to provide researchers with the means to navigate from
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46 147 change in a climate driver to a list of potential biological impacts an organism may experience,
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48 148 and to make a qualitative assessment of the likelihood of any terrestrial organism to suffer a
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50 149 given biological impact.
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151 **II. Winter climate change**

152 Mean winter air temperatures are increasing globally, but the magnitude of
153 predicted winter climate change varies by region (Figure 1A; IPCC, 2007), and is subject to
154 complex feedback mechanisms and interactions between snow- and ice-cover and temperature.
155 While increased temperature alone decreases snow cover, climate models predict that winter
156 precipitation may increase, decrease or change in timing or duration depending on the region
157 (Figure 1B), which means that snow depth may stay the same or even increase in some regions,
158 such as parts of the Arctic (Symon, Arris & Heal, 2005). Many organisms overwinter beneath
159 snow, and snow cover is a critical mediator of soil microclimate; in particular, both reduced
160 precipitation and increased mean air temperatures can increase the frequency and intensity of soil
161 freeze-thaw cycles (Figures 2B, D; Brown & DeGaetano, 2011). Although the Arctic is predicted
162 to experience the most extreme winter warming, changes in snow cover and soil freezing in this
163 region are less sensitive to warming than in northern temperate regions, which feature a
164 shallower snowpack and remain closer to melt temperatures over winter (Henry, 2008). The
165 changing physical conditions of winter can also modify winter length; for example, ‘vanishing
166 winters’ are predicted for low-latitude temperate regions, where persistent snow cover and soil
167 freezing become rare or completely absent (Kreyling & Henry, 2011), and the ‘average’ winter
168 may be getting shorter in temperate North America, where the first autumn frost has been getting
169 later, and the last spring frost earlier, for several decades (Kunkel et al., 2004).

170
171 [Figure 1 here]

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3 173 In addition to changes in mean temperature and precipitation, an increased frequency of
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6 174 extreme weather events can increase the incidence, frequency and intensity of soil freezing,
7
8 175 either as a result of unusually early or late winter frost events, or as a result of mid-winter
9
10 176 warming (or rain) events that reduce snow cover and are followed by freezing temperatures
11
12 177 (Figure 2C). There has been an overall increase in the frequency of extreme thermal events in
13
14 178 both summer and winter, and further increases are predicted over the next century (Easterling et
15
16 179 al., 2000). Increases in extreme minimum and maximum temperatures in recent decades have
17
18 180 varied among seasons and among regions, but overall there has been an increased number of
19
20 181 days of extreme high minimum temperature and a reduced number of days of extreme low
21
22 182 minimum temperature (Caprio, Quamme & Redmond, 2009; Easterling et al., 2000). For
23
24 183 example, across Canada the number of cold nights (minimum temperatures below the 10th
25
26 184 percentile for the 20th century) decreased by 15 per year between 1950 and 2003 (Vincent &
27
28 185 Mekis, 2006). The frequency of both extreme high temperatures and longer mid-winter warm
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30 186 spells is expected to increase with climate change in some regions (Liu et al., 2006).
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39 188 [Figure 2 here]
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44 190 Aside from thermal stress, interactions between temperature and moisture during winter
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46 191 can alter the occurrence of physical stresses such as ice encasement and frost heave (the uplift of
47
48 192 soil when freezing water in soil expands), and increased rainfall over winter will increase the
49
50 193 frequency of rain-on-snow events, which contribute to ice encasement. Rain-on-snow events
51
52 194 have increased in most Arctic regions, in some cases by up to 50% (ACIA, 2005). Furthermore,
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54 195 changes in albedo and permafrost depth can modify water retention by the soil, which can alter
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3 196 the nature of below-ground freeze-thaw (Oztas & Fayetorbay, 2003). Changes in sea or lake ice
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6 197 can also exacerbate terrestrial climate change, for example by increasing moisture availability,
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8 198 leading to increased snow depth in maritime areas, or by modifying albedo and accelerating
9
10 199 spring melt (Deser et al., 2010). With the emphasis on temperature effects in winter research,
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12 200 such interactions with moisture have often been overlooked, and consequently our discussion of
13
14 201 these specific moisture effects remains speculative (and is often absent) throughout much of this
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16 202 review.
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204 **III. Mechanistic bases of the biological impacts of winter climate change**

25 205 The primary abiotic drivers of the biological impacts of winter on terrestrial systems are
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27 206 temperature and snow cover. Temperature determines rates of biological processes, and thermal
28
29 207 variability impacts the likelihood of crossing important biological thresholds (e.g. the freezing
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31 208 point of tissues). Snow strongly modifies both the physical and the thermal environments.
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33 209 Changes in the absolute variability of these factors (as well as their timing and synchrony) can
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35 210 modify the interaction and outcomes of snow cover and temperature. In Figure 3, we describe
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37 211 how these drivers interact to determine biological impacts, and we show the direction of impact
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39 212 of changes in some of these drivers (which we elaborate below). Ultimately, the susceptibility of
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41 213 organisms to winter (see Table 1 for a description of the traits influencing vulnerability to winter
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43 214 changes), and the way these impacts combine and synergise with impacts of climate change
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45 215 during the growing season will determine the winners and losers under global climate change,
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47 216 and understanding these processes will be essential for informed management of biodiversity in a
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49 217 changing world.
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8 221 [Table 1 here]

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13 223 (1) Increased average winter temperatures

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15 224 *(a) Effects on metabolic rate*

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18 225 Increased average temperatures can arise either as a direct result of climate warming, for
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20 226 organisms whose habitats are not buffered from ambient temperatures, or from increased snow
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22 227 cover with associated thermal buffering (Figures 2A-B, Figure 3). Increased average
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24
25 228 temperatures can impact energy stress and phenology by increasing rates of development or
26
27 229 metabolism (Figure 3). Temperature influences metabolism, and thus consumption of stored
28
29 230 energy by 1) directly determining the rates of metabolic processes (such as respiration and
30
31 231 carbon fixation) in poikilotherms and 2) determining the costs of thermoregulation by
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33 232 homeotherms. Thus, increased average temperatures will increase rates of metabolism of
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35
36 233 poikilotherms, while for homeotherms below the thermoneutral zone, metabolic rates will
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38 234 decrease with increased average temperature due to the decreased cost of thermoregulation
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40
41 235 (Table 1).

42
43
44 236 A higher metabolic rate will increase the rate of use of stored energy reserves, which can
45
46 237 expose non-feeding organisms to energetic stress (Figure 3). For example, hibernating bats
47
48 238 expend more energy when hibernaculum temperatures are above an optimal low temperature
49
50 239 (Humphries et al., 2002), dormant hatchling turtles consume more energetic reserves and emerge
51
52 240 in poorer physiological condition after warm winters (Muir et al., 2013), and energy drain means
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54
55 241 that goldenrod gall flies that overwinter in relatively warm subnivean microclimates have
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3 242 reduced survival and fecundity compared to conspecifics overwintering in exposed, colder sites,
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5 243 because their metabolic rates increase exponentially with temperature (Irwin & Lee, 2003). All
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8 244 else being equal, this energy drain is likely to be more pronounced in organisms with high
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10 245 baseline metabolic costs, and less pronounced in organisms, such as diapausing butterfly pupae,
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12 246 that substantially suppress their metabolism during winter (Table 1; e.g. Williams, Hellmann &
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15 247 Sinclair, 2012a).

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18 248 Increased rates of biological processes may permit energy gain for organisms that can
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20 249 take up nutrients during the winter. For example, increased winter temperatures increase
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22 250 photosynthetic rates and thus carbon gain in non-dormant plants as long as water is available,
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24
25 251 although this effect is more pronounced in woody than in herbaceous species (Ensminger, Busch
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27 252 & Hüner, 2006). Similarly, the mineralization of limiting nutrients such as nitrogen increases
28
29 253 with soil temperature over winter (Sturm et al., 2005), which can increase primary productivity,
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31 254 assuming that nutrient release and uptake are synchronised (Groffman et al., 2001).

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33
34 255 For homeotherms, the energetic costs of thermoregulation during winter can rival or
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36 256 exceed energetic costs of the breeding season, yet occur at a time when food availability may be
37
38 257 low (Sgueo et al., 2012). An increase in average winter temperatures will thus lower metabolic
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40 258 costs of thermoregulation in homeotherms that would normally experience winter temperatures
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42
43 259 below the thermoneutral zone, which may alleviate energetic stress (Figure 3; Sears et al., 2009).
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45
46 260 A release from energetic stress as a result of winter climate change may have led to recent
47
48 261 increases in body size of American martens, either via decreased thermoregulatory costs or
49
50 262 increased prey availability (which will reduce energetic stress by increasing nutrient uptake;
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52
53 263 Yom-Tov, Yom-Tov & Jarrell, 2008). Increased body size and/or condition will likely translate
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55 264 into fitness benefits by decreasing overwinter mortality (Hodges et al., 2006), or improving
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3 265 condition at the onset of the breeding season (e.g. Guillemain et al., 2008). Alternately,
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6 266 decreased thermoregulatory costs may increase fitness by reducing the need for pre-winter
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8 267 energy accumulation, which could mitigate trade-offs and predation risk associated with resource
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10 268 acquisition (Gentle & Gosler, 2001). By contrast, warmer winters may lead to summer energy
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13 269 drain for species such as polar bears that feed primarily during winter and fast in the summer.
14
15 270 Warmer winters reduce the length of sea ice stability, resulting in a shorter period in which polar
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17
18 271 bears can acquire their year's nutrients, offsetting any thermoregulatory benefits (Robbins et al.,
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20 272 2012).

21
22 273 However, direct evidence for energetic and performance consequences of winter
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24
25 274 warming in homeotherms is scarce. Changes in variables correlated with increased temperatures
26
27 275 – such as snow cover, resource availability, and precipitation – make it difficult to isolate the
28
29 276 impacts of temperature in observational studies, which form the majority of published work to
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31
32 277 date. For example, although they presumably provide a thermoregulatory advantage, warm
33
34 278 winters reduced maternal investment in reproduction in red deer resulting in smaller offspring.
35
36
37 279 This effect was probably driven by increased costs of locomotion in the deeper snow
38
39 280 characteristic of warm winters, rather than increased temperature *per se* (Post et al., 1997). Thus,
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41 281 the impact in this case was driven by an interaction among abiotic drivers (Figure 3).

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44 282 *(b) Effects on development and phenology*

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46 283 In addition to altering energy balance, increased average temperatures during winter
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48 284 generally promote development at times of year when it would traditionally be arrested, leading
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50 285 to earlier spring, and later autumn, phenology for the majority of terrestrial taxa (Figure 3; Jeong
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52 286 et al., 2011; Walther, 2010). These phenological shifts have been particularly pronounced in cold
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54
55 287 regions such as the Arctic (Høye et al., 2007). However, significant variation exists in
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3 288 phenological plasticity within communities; for example, phenological shifts have been faster at
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6 289 lower trophic levels (Table 1; Both et al., 2009; Thackeray et al., 2010), and within the insects,
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8 290 these shifts are less pronounced in species with specialised diets or that overwinter at earlier life
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10 291 stages (Table 1; Diamond et al., 2011).

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12
13 292 For primary producers, or animals that are not limited by resource availability,
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15 293 performance is likely to be enhanced by maximally-advanced spring phenology and maximally-
16
17 294 delayed autumn phenology (Table 1). Shortening the period of dormancy will allow greater
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19 295 resource accumulation during the growing season, and less energetic stress during winter. If this
20
21 296 hypothesis is correct, performance will be enhanced in organisms whose phenology is strongly
22
23 297 temperature-sensitive and which can therefore respond to increases in average temperatures by
24
25 298 rapid shifts in their growing season. Indeed, the ability to respond to climate change by
26
27 299 advancing spring phenology strongly enhances fitness and persistence in plants (e.g. Fridley,
28
29 300 2012), presumably by lengthening the growing season and increasing resource accumulation
30
31 301 (Pigliucci & Marlow, 2001). A recent evolutionary shift towards later autumn phenology has
32
33 302 also been recorded in pitcher plant mosquitoes, implying fitness gains from an extension of the
34
35 303 length of the growing season (Bradshaw & Holzapfel, 2001), perhaps because resources are not
36
37 304 temporally limited for mosquito larvae feeding on microbes in the contained pitcher plant
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39 305 ecosystem.

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44 306 By contrast, phenological synchrony with crucial resources will likely be more important
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46 307 than growing season or winter length in determining fitness of organisms at higher trophic levels
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48 308 whose resources are temporally limited. This means that the optimal phenotype will depend on
49
50 309 the phenology of the neighbouring trophic levels (Table 1). This dependence occurs because
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52 310 variation in phenological shifts can cause community mismatches, wherein resources for higher
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3 311 trophic levels are no longer synchronised with periods of demand. We will discuss the
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6 312 community-level implications in more detail below (section V), but the salient point at the
7
8 313 organismal level is that a mismatch between food demand and availability is likely to apply
9
10 314 strong selective pressure on higher trophic levels to maintain synchrony with the trophic levels
11
12 315 below. Supporting the hypothesis that phenology may evolve to enhance synchrony with the
13
14 316 trophic level below, winter moth caterpillars have evolved a later spring hatching date in
15
16 317 response to warming, which has increased synchrony with budburst of its host plant (oak), and
17
18 318 presumably imparted higher fitness despite a shorter growing season (van Asch et al., 2013).
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23 319 Thus, the pattern of selection on phenology likely differs among trophic levels, with
24
25 320 producers or animals for which resources are available year-round experiencing consistent
26
27 321 selection for maximal spring advances and autumn delays, while higher trophic levels experience
28
29 322 divergent selection pressures that depend on the responses of the trophic level immediately
30
31 323 below. This differential selection across trophic levels could explain why the responses of plant
32
33 324 phenology to climate change show a strong phylogenetic signal (Willis et al., 2008), while the
34
35 325 responses of insect phenology do not (Diamond et al., 2011): consistent selection on phenology
36
37 326 in producers preserves the phylogenetic signal, while divergent selection on phenology at higher
38
39 327 trophic levels reduces similarities across the phylogeny. Therefore, although it is likely that
40
41 328 phenological shifts will alter resource availability and thus energy stress for consumers whose
42
43 329 resources are temporally restricted, determining whether the impact will be positive or negative
44
45 330 requires consideration of the phenological responses of organisms at lower trophic levels (Figure
46
47 331 3, Table 1). Organisms for which seasonal timing is physiologically fixed, and that therefore
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49 332 have inflexible phenology, may suffer the most pronounced negative impacts of changing winter
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51 333 length and timing with climate change (Post & Forchhammer, 2008).
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3 334 Many plants and insects have chilling or vernalisation thresholds that must be met before
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6 335 post-winter development can resume. In these cases, warmer winters can slow development,
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8 336 leading to phenological delays (rather than advancement) in spring (e.g. Forrest & Thomson,
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10 337 2011; Luedeling et al., 2011). Most studies report an advance in spring phenology, although
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12 338 these are also intermixed with delays or lack of responses in many systems (Thackeray et al.,
13
14 339 2010); these delays are consistent with widespread effects of a reduction in chilling units (Cook
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16 340 et al., 2012). Phenological delays have been well-documented in meadow and steppe plant
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18 341 communities on the Tibetan Plateau, where the beginning of the growing season advanced in
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20 342 response to climate warming for the first half of a 20-year warming period, but was subsequently
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22 343 delayed despite continued climate warming (Yu, Luedeling & Xu, 2010; but see Zhang et al.,
23
24 344 2013). These phenological delays are consistent with insufficient vernalisation (too little
25
26 345 accumulated cold exposure to end dormancy). However, these observations could also arise
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28 346 from the observed decrease in snow depth over this period, which may have reduced the
29
30 347 insulation of the roots and, counter-intuitively, resulted in colder conditions despite warming air
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32 348 temperatures (Yu et al., 2013). There is no way to separate these proximal mechanisms from the
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34 349 available data, although this could be achieved through either autecological experiments on
35
36 350 chilling requirements (e.g. Santiago et al., 2013) or experimental snow manipulation (e.g.
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38 351 Groffman et al., 2001).

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41 352 Average temperatures will thus affect energy balance in two ways – directly, through
42
43 353 rates of metabolism, and indirectly, through phenology and the resulting length of winter (Figure
44
45 354 3). This introduces an important dichotomy in responses to winter climate change among
46
47 355 dormant plants and insects: for cold-adapted species with high chilling or vernalisation
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49 356 requirements, increases in winter temperature will increase both overwinter energy use (by
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3 357 increasing metabolic rates) and winter length (by increasing development time). These changes
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6 358 will amplify the deleterious effects of warming for cold-adapted species. If failure to meet
7
8 359 chilling requirements decreases the viability of populations, it may prove to be a proximate
9
10 360 driver of range contractions at the equatorial range limit in some species. By contrast, for warm-
11
12 361 adapted species that do not have chilling or vernalisation requirements, although warming will
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14 362 still increase overwinter energy use, it will also shorten the period of dormancy by advancing
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16
17 363 spring phenology. This could mitigate the direct negative effects of winter warming on
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20 364 energetics of warm-adapted species.
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23 24 366 (2) Altered thermal variability

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26 367 Winter temperatures fluctuate on multiple temporal scales, ranging from diel temperature
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28 368 fluctuations, through short term cycles associated with weather fronts, to seasonal changes
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31 369 (Deere & Chown, 2006; Gaines & Denny, 1993; Marshall & Sinclair, 2012a; Marshall &
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33 370 Sinclair, 2012b). The magnitude of these fluctuations varies spatially both with microhabitat
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35 371 (Marshall & Sinclair, 2012b), and across larger scales influenced by continentality, latitude and
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38 372 topography. Snow cover will drive much of this variability, so snow cover predictions must be
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40 373 taken into account to determine likely trends in variability in each of these components (Figure
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42
43 374 2). Changes in the seasonal timing of snow cover will exacerbate altered timing of extreme low
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45 375 temperatures (Figure 2). Changes in thermal variability will impact energy balance, phenology,
46
47 376 and cold injury through effects on metabolism, development, and freeze/thaw cycles as described
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49
50 377 below (Figure 3). Species-specific sensitivity to changes in this variability may be particularly
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52 378 important in determining organisms' responses to winter climate change, although we note that
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55 379 changes in variability are extremely difficult to predict, even when only extreme events are
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3 380 considered (Easterling et al., 2000). There are three salient components of fluctuations in winter
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6 381 thermal conditions: a) the intensity and regularity of extreme high and low winter temperatures;
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8 382 b) the frequency with which temperatures cross important physical thresholds (e.g. the freezing
9
10 383 point of water) or biological thresholds (e.g. thresholds for cold-induced damage); and c) the
11
12 384 amplitude of thermal cycles on both diel and short-term scales (such as during storm events).

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14
15 385 *(a) Intensity and regularity of winter extremes*

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18 386 Extreme low temperature events can cause cold injury, and winter mortality or injury is
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20 387 an important component of demographics for many species (e.g. Aukema et al., 2008; Kanda,
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22 388 2005; Spiegel-Roy & Goldschmidt, 2008; Sutherst & Maywald, 2005). Thus, a reduction in the
23
24 389 intensity or duration of extreme winter low temperatures could increase winter and post-winter
25
26 390 survivorship (Table 1; e.g. Tran et al., 2007; Trotter & Shields, 2009), directly influencing the
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28 391 poleward or upper altitudinal range limit of a species (e.g. Crozier, 2004; Neuvonen, Niemelä &
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30 392 Virtanen, 1999). However, there are cases where extreme low temperatures do not directly limit
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32 393 population persistence or geographic range. For example, the monophagous holly-leaf miner (an
33
34 394 agromyzid fly) is more cold tolerant than its host plant (holly, *Ilex aquifolium*), and its northern
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36 395 range limit in Europe is therefore likely set by the factors that set the host range, rather than
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38 396 directly by extreme low temperatures (Klok, Chown & Gaston, 2003). In such cases,
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40 397 amelioration of extreme low temperatures will not directly affect survival, but could still
41
42 398 indirectly lead to range expansion if low temperatures are the primary determinant of resource
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44 399 availability.

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46 400 Changes in thermal variability can modify the timing, predictability and sequence of
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48 401 extreme events over winter. Because many species have life stage-specific tolerance to winter
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50 402 conditions (e.g. diapause-linked cold tolerance in insects, Leather, Walters & Bale, 1993; and
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3 403 aquatic overwintering in adult frogs, Tattersall & Ultsch, 2008), there is potential for changes in
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5
6 404 the seasonality of extremes to lead to mismatches between the occurrence of extreme events and
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8 405 the behavioural or physiological mechanisms that allow organisms to tolerate them. In
9
10 406 particular, organisms with seasonally-programmed responses, or those which irreversibly lose
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12 407 cold tolerance during winter warm spells, will be more vulnerable to unseasonable temperature
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15 408 extremes than those with constitutively high or rapidly-modified tolerances (Table 1). For
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17
18 409 example, extremely warm mid-winter temperatures cause an irreversible loss of winter
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20 410 acclimatisation and the resumption of development in the emerald ash borer (*Agrilus*
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22 411 *planipennis*, Coleoptera, Buprestidae), making them susceptible to subsequent cold snaps
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24
25 412 (Sobek-Swant et al., 2012). Extreme warm periods in spring can also lead to breaking of
26
27 413 dormancy in plants, with subsequent extreme events killing buds and preventing reproduction or
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29 414 growth the following season, as occurred in the unusual North American springs of 2007
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32 415 (Augspurger, 2009; Gu et al., 2008) and 2010 (Hufkens et al., 2012). Indeed, a 124-year
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34 416 temperature dataset combined with observations of frost susceptibility in Illinois, USA shows
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37 417 that the frequency of damaging spring frost events has increased in recent decades (Augspurger,
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39 418 2013). At the beginning of winter, unusual extreme events before organisms have accumulated
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41 419 programmed physiological protection can also lead to damage. For example, the grass *Bromus*
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44 420 *rubens* may be excluded from the intermountain steppe biome of western North America as a
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46 421 consequence of sudden freeze events in late autumn before the onset of (programmed) winter
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48 422 cold tolerance (Bykova & Sage, 2012). Thus, organisms that develop low temperature tolerance
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51 423 in a programmed fashion (e.g. in response to photoperiod), or that have delayed the onset of
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53 424 winter hardening as part of a phenological shift, may be more vulnerable to changes in the
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3 425 occurrence of extreme events in autumn than organisms that can use temperature as a cue to
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6 426 rapidly increase early winter cold hardiness (Table 1).

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8 427 *(b) Frequency of threshold-crossing events*

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10 428 Changes in the frequency, intensity, or duration of extreme events could modify the
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12 429 frequency with which biologically-important thresholds are crossed. For example, the 0 °C
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14 430 threshold delineates the availability of liquid water and the beginning of soil freezing. Similarly,
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16 431 species-specific physiological thresholds exist, such as the temperatures at which ice formation
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18 432 and melting occur; crossing these thresholds can determine sub-lethal impacts (e.g. Marshall &
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20 433 Sinclair, 2010), survival (e.g. Régnière & Bentz, 2007) and overwinter energetics (e.g. Sinclair et
21
22 434 al., 2013) In some regions (e.g. maritime-buffered habitats in the southern hemisphere; Chown
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24 435 et al., 2004), temperatures already hover near the 0 °C threshold: increases in mean temperatures
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26 436 will likely reduce the occurrence of freeze-thaw cycles in such environments, reducing the stress
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28 437 of threshold-crossing events. By contrast, increasing mean temperatures (or decreasing snow
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30 438 cover, see below) may increase the incidence of freeze-thaw in northern temperate habitats, and
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32 439 thus may increase the frequency of such transitions.

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39 440 The implications of repeated freeze-thaw are not well-understood, but the impacts appear
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41 441 to be largely negative. In invertebrates, repeated freeze-thaw can lead to a variety of deleterious
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43 442 consequences, due to both cold injury from the repeated cold exposure, and increased energy
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45 443 expenditure during repair and recovery in thaw periods (Marshall & Sinclair, 2012a). In freeze-
46
47 444 tolerant *Rana sylvatica* frogs, carbohydrate energy reserves provide both fuel for the energy
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49 445 expended during freezing and the cryoprotectants for survival of freezing itself. In this species,
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51 446 repeated freeze-thaw both depletes energy reserves and reduces cold tolerance, suggesting the
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53 447 possibility for substantial fitness reductions with increased freeze-thaw (Sinclair et al., 2013).

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3 448 Repeated freeze-thaw cycles increase the risk of xylem embolism in conifers due to the
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6 449 expansion of gas bubbles during thawing that were formed upon freezing (Mayr, Gruber &
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8 450 Bauer, 2003). Increased intensity or frequency of soil freeze-thaw cycles can increase the lysis of
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10 451 soil microorganisms and damage to plant roots, intensifying leaching and trace gas losses of soil
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12 452 nutrients (Groffman et al., 2001).

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14 453 In some cases, the impacts of repeated events such as freezing may not be cumulative.
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18 454 For example, elevated losses of soil nutrients may only occur in response to exceptionally severe
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20 455 frost soil events, and pools of frost-vulnerable materials in the soil are finite. Once the bulk of
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22 456 soil nutrients in these frost-vulnerable pools have been released, subsequent events may not
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25 457 result in further loss (Matzner & Borken, 2008). Thus, increased frequency of freeze-thaw can
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27 458 have detrimental effects in organisms for which the responses are cumulative, but for organisms
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29 459 or systems where the impact of repeated cold exposure reaches an asymptote (e.g. nutrient
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31 460 leaching), the impacts of repeated events may be less important (Table 1). However, at this point
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33 461 too little is known about the impacts of repeated stress (or about interactions among multiple
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35 462 stressors) to allow generalities to be constructed.

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39 463 *(c) Impacts of the amplitude of thermal cycles*

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41 464 Increases in daily thermal variability can increase rates of metabolism and photosynthesis
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44 465 in poikilotherms (Figure 3), because of the curvilinear relationship between temperature and
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46 466 most biological rate processes. Jensen's inequality is a mathematical property of nonlinear
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48 467 functions, which states that the mean of a nonlinear response variable cannot be predicted based
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50 468 on the mean of the driver variable alone, but requires knowledge of the variability of the driver
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52 469 variable and the shape of the response function (Ruel & Ayres, 1999). For example, if the
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54 470 response function is accelerating over the range of temperature fluctuations (as is frequently the
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3 471 case with metabolic rate in ectotherms), the mean of the response variable will be elevated
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6 472 compared to its value at the mean temperature, and increasing thermal variability will further
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8 473 increase the mean of the response variable, even without a corresponding increase in the mean
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10 474 temperature. Thus, increases in thermal variability have the potential to exacerbate the impacts of
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12 475 an increase in mean temperature on metabolism (Ruel & Ayres, 1999). Additionally, thermal
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14 476 performance curves are asymmetric (fitness rapidly declines above the thermal optimum;
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16 477 Angilletta, 2009), and thus Jensen's inequality means that the impact of changes in temperature
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18 478 will also be asymmetric: temperatures above the thermal optimum will reduce fitness far more
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20 479 than temperatures an equal amount below the thermal optimum.
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25 480 This effect of Jensen's inequality can be exacerbated or mitigated by modifying the shape
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27 481 of the rate-temperature relationship: a steeper curve (i.e. higher temperature sensitivity) will lead
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29 482 to a more pronounced impact (Ruel & Ayres, 1999), suggesting that organisms with high
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31 483 temperature sensitivity or thermal optima that are close to environmental temperatures will
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33 484 experience greater impacts of changes in thermal variability (Table 1; Foden et al., 2013).
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37 485 Exacerbated thermal variability will therefore allow potentially-active ectotherms to take better
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39 486 advantage of warm spells during winter fluctuations. However, lower thermal sensitivity will
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41 487 reduce vulnerability to thermal variation, for example in energy-conserving overwintering
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43 488 ectotherms (Williams et al., 2012b). Thus, short-term (e.g. daily) thermal variability likely
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45 489 exerts a strong selective pressure on temperature-rate relationships in ectotherms and plants,
46
47 490 however, few studies to date have examined the impacts of daily thermal variability on
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49 491 overwintering organisms.
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53 492 For dormant organisms, thermal variability will thus be an important determinant of
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55 493 overwintering energy use, particularly at winter's peripheries when temperatures are relatively
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3 494 warm and variable. In this context, seasonal timing will be a critical determinant of a species'
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6 495 susceptibility to overwinter energy drain resulting from alterations to thermal variability.
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8 496 Species that enter dormancy early in the autumn will experience significant energy drain as a
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10 497 result of delayed winter onset, and an increase in thermal variability during autumn will thus
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12 498 exacerbate this energy drain because of Jensen's inequality (e.g. Sinclair et al., 2013; Williams et
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14 499 al., 2012b). By contrast, species with delayed spring emergence, including insects such as
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16 500 *Rhagoletis pomonella* that infest summer-fruiting trees (Feder, Hunt & Bush, 1993), will likely
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18 501 be more susceptible to earlier, more variable, and warmer springs. By contrast, increased
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20 502 buffering (e.g. due to longer snowpack persistence; Decker et al., 2003) might reduce variability,
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22 503 mitigating the impact of the longer post-winter period.
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27 504 Flexibility of the thermal sensitivity of biological processes or phenology will therefore
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29 505 be a key determinant of the outcome of changing thermal variability during winter and its
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31 506 associated dormancy (Figure 4). Suppression of thermal sensitivity of metabolism mitigates the
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33 507 impact of increased thermal variability (Williams et al., 2012b). In herbivores, for which entry
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35 508 into dormancy is likely mediated by a decline in host plant quality (Prior et al., 2009), such
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37 509 plasticity is essential, but may not fully compensate for increased autumn variability (Williams et
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39 510 al., 2012b). In many species, the onset of dormancy is controlled hormonally and entrained to
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41 511 photoperiod (Tauber et al., 1986), apparently reducing the capacity for flexibility because of the
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43 512 programmed nature of the response. However, evolutionary changes in the induction of
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45 513 dormancy as a result of climate change have been observed in a photoperiod-cued pitcher plant
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47 514 mosquito (Bradshaw & Holzapfel, 2001). Similarly, butterfly larvae show state-dependent
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49 515 responses to photoperiod, allowing facultative shifts in dormancy onset and behaviour both
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51 516 before and after dormancy to buffer the impact of reduced growth capacity at higher latitudes
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3 517 (Gotthard, Nylin & Wiklund, 1999; Gotthard, Nylin & Wiklund, 2000). It is conceivable that
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6 518 such plasticity could also act to mitigate the impacts of winter energy drain.
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10 520 [Figure 4 here]
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15 522 Overall, while it is clear that the frequency, timing and amplitude of temperature
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18 523 variability dictate the severity of winter's effects on organisms, the examples presented above
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20 524 derive primarily from studies on insects. For organisms with more resilient or resistant
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22 525 overwintering stages (e.g. plant seeds) these effects may be less severe. The ultimate influence
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25 526 of extreme winter temperature events on populations, communities and ecosystems will be a
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27 527 function of both the severity and frequency of these events, and extremely severe events may
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29 528 only occur infrequently. However, extreme events that lead to threshold changes in community
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32 529 trajectories will remain influential over the longer term (Kreyling, Jentsch & Beierkuhnlein,
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34 530 2011).
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39 532 (3) Changing snow cover
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41 533 The strong influence of snow cover on the soil and subnivean microclimate (Figure 2;
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43
44 534 Decker et al., 2003; Henry, 2008; Pauli et al., 2013) has important consequences for the
45
46 535 condition and survival of organisms that overwinter in these environments, and as a result,
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48 536 changes in snow cover with climate change can result in many different biological impacts
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50 537 (summarised in Table 2). Because snow is an effective insulator, reduced snow cover can
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53 538 expose soil systems to more extreme low temperatures (Brown & DeGaetano, 2011), described
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55 539 by Groffman et al. (2001) as 'colder soils in a warmer world', which in turn can increase
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3 540 mortality for organisms overwintering in or on the soil. Beetles overwintering in the soil beneath
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6 541 snow in the US prairies had higher survival than those that overwintered in soil with snow
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8 542 removed, but this difference in survival was only seen in relatively cold winters (Joshi, Olson &
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10 543 Carey, 2009), and the number of times per month that New Zealand alpine cockroaches were
11
12 544 predicted to freeze and thaw ranged from zero to more than 20, depending on snow cover
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14 545 (Sinclair, 2001). Lemming nest density was positively correlated with snow depth when snow
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16 546 cover was experimentally manipulated, presumably because the deep, dry snow layer buffered
17
18 547 the small mammals from extreme temperatures (Reid et al., 2012).

548

549 [Table 2 here]

550

551 Thermal buffering by snow leads to a counterintuitive observation – organisms from very
552 cold and snowy regions are frequently less cold tolerant than those from regions with a shallower
553 and less-persistent snow-pack. For example, despite the expectation that frost tolerance increases
554 with increasing latitude within species, northern (snow-insulated) ecotypes of temperate grasses
555 have low frost tolerance relative to their conspecific, southern ecotypes that experience less snow
556 cover (Dionne et al., 2001). Increased soil freezing as a consequence of decreased snow cover
557 might therefore be particularly damaging for organisms adapted to snowy winters. Mid-winter
558 melts can increase soil exposure to freeze-thaw with consequent damage to plants and soil fauna
559 (Bokhorst et al., 2011; Bokhorst et al., 2012a), and these melts also can lead to ice encasement
560 and subsequent anoxia, further stressing soil organisms (Coulson et al., 2000). Despite the
561 potential benefits of snow cover for frost protection, the mild subnivean microclimate can be
562 energetically costly for organisms, because overwinter temperatures determines their energy

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3 563 consumption (Figure 3). For example, gall flies overwintering below the snow have increased
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5 564 energy consumption compared to those above the snow (Irwin & Lee, 2003). Snow cover thus
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7 565 strongly influences levels of energy stress and cold injury indirectly, through its effects on
8
9 566 temperature (Figure 3), and changes in local patterns of snow cover therefore have the potential
10
11 567 to alter habitat suitability on a very small scale.
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14 568 Snow also impacts organisms directly by modifying the physical environment: both the
15
16 569 quantity and the quality of snow can have profound effects, particularly on the biology of winter-
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18 570 active mammals. While the effects of changing snow cover can be assessed experimentally for
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20 571 sessile or small organisms (e.g. Groffman et al., 2001; Reid et al., 2012), the limited spatial scale
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22 572 of most snow manipulation experiments makes it difficult to assess snow depth effects on large
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24 573 or highly mobile animals under controlled conditions. Nevertheless, observational studies can be
25
26 574 used to correlate biological responses to interannual variation in snow depth. For example,
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28 575 wolves form larger packs in response to deeper snow (Post et al., 1999), but increased snow
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30 576 depth also reduces mobility of their deer prey (Fuller, 1991). Reduced snow cover may also
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32 577 increase resource availability for winter-active predators and browsers by improving access to
33
34 578 food (Figure 3; Martin & Maron, 2012) – which necessarily means that decreased snow also
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36 579 increases predation risk for small mammals which have less protection from predators and
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38 580 extreme temperatures (Yoccoz & Ims, 1999). However, the impacts of changing snow cover are
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40 581 complex: declining snow cover in Canada is associated with decreased wolverine population
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42 582 growth rate; the causal factors for this decline likely include reduced denning sites, decreased
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44 583 prey success and reduced snow-related mortality of the ungulates upon whose carcasses
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46 584 wolverines scavenge (Brodie & Post, 2010). Snow quality, determined more-or-less directly by
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48 585 temperature, also determines the winter performance of many organisms, as changes in the
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3 586 density of snow modifies its insulative properties and affect locomotion, while ice layers can
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5 587 modify access through the snowpack. For example, increased frequency of rain on snow events,
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8 588 and subsequent ice-up, blocks access to food for herbivores such as reindeer (Hansen et al.,
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10 589 2011) and small mammals (Kausrud et al., 2008; Korslund & Steen, 2006).

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13 590 The timing of snow lie is also critical for many organisms, but the direction of impact
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15 591 strongly depends on species' traits. Early snowmelt can have positive effects for large browsers
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18 592 such as reindeer, which produce calves with increased body mass in the autumn following an
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20 593 early spring snowmelt (Pettorelli et al., 2005). However, if early snow melt causes the
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22 594 resumption of activity before resources are available or interrupts winter feeding opportunities,
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25 595 the effects can be detrimental: early snowmelt can result in food scarcity for hibernating
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27 596 mammals, such as marmots, that emerge early in response to warmer air temperatures, but before
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29 597 the spring flush of plant growth (Inouye et al., 2000), and early ice breakup increases mortality in
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32 598 polar bear by reducing the length of the winter feeding season and increasing the length of the
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34 599 summer fast (Regehr et al., 2007). By contrast, increased spring snowstorm activity with climate
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37 600 change in some regions can lead to delayed snowmelt, delaying the emergence of ground
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39 601 squirrels and reducing their fitness by reducing the length of the active season (Lane et al.,
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41 602 2012). However, organisms that overwinter in subnivean spaces in very cold environments may
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44 603 benefit from an extension to the protective insulation of snow – for example, peak floral
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46 604 abundance of montane plants is increased after delayed snow melt, due to decreased frost
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48 605 damage in spring (Inouye, 2008).

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50 606 Mid-winter snowmelt caused by extreme events (best-studied because of their effect on
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53 607 hydrology; e.g. Kurian, Lautz & Mitchell, 2013) will not only affect overwinter soil temperatures
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55 608 (see above), but also provide liquid water for plants and animals that might otherwise suffer from
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3 609 a water deficit, such as hibernating mammals (e.g. Ben-Hamo et al., 2013). Conversely,
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6 610 increased free water may increase rates of heat loss and risk of flooding, decreasing survival of
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8 611 small mammals (Kausrud et al., 2008). In Greenland, warmer summers result in the
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10 612 accumulation of cold meltwater, delaying flowering and shortening the flowering period of
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12 613 several angiosperms (Høye et al., 2013). These roles of liquid water in determining winter
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14 614 physiology and spring phenology in terrestrial systems during winter have received little
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16 615 attention, so the trade-off of negative and positive effects for organisms remains a matter for
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18 616 speculation.
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25 618 **IV. Links between winter and summer responses to climate change**

26 619 The condition of organisms emerging from the winter will determine their performance
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28 620 during the growing season, and similarly their growing season performance will determine their
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30 621 condition going into the winter and subsequent winter performance (Figure 5). Taking a cross-
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32 622 seasonal perspective will therefore be necessary to identify negative impacts of climate change.
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34 623 For example, advanced spring phenology and increased spring abundance of a perennial herb in
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36 624 Britain resulted from winter warming, but this was tempered by a decrease in reproductive
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38 625 output by those plants (Fox et al., 1999). Similarly, early snow melt increased survival in
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40 626 conifers, but at the expense of growth rates (Barbeito et al., 2012). Where data on post-winter
41
42 627 performance are lacking, links from winter condition to the growing season may often be
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44 628 inferred. For example, winter energy use can determine adult body size in butterflies (Williams
45
46 629 et al., 2012a), and the clear size-fecundity relationship in female butterflies (Boggs & Freeman,
47
48 630 2005) implies a fitness consequence of this winter effect. The resilience of organisms to winter
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50 631 energetic stress can also be determined by post-winter processes (Table 1), with resilience
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52 632 decreased in organisms with limited opportunities for post-winter resource acquisition (Breed,
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4 633 Stichter & Crone, 2013), or for which juvenile-derived reserves are essential for reproduction
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6 634 (Irwin & Lee, 2003).

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10 636 [Figure 5 here]

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15 638 If responses to climate change improve pre-winter condition, winter performance may be
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17
18 639 enhanced. For example sub-alpine yellow-bellied marmots have advanced their phenology in
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20 640 response to recent climate change, which allows increased resource accumulation and growth
21
22 641 and, consequently, increased overwinter survival and population growth rates (Ozgul et al.,
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24
25 642 2010). Presumably, such positive impacts of longer growing seasons will help to buffer negative
26
27 643 impacts of winter climate change, although few data exist to address this hypothesis. However,
28
29 644 some changes to growing season physiology may have negative effects on winter performance.
30
31 645 For example, damselfly larvae that grow rapidly during the growing season do so at the expense
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33 646 of winter cold tolerance (Stoks & De Block, 2011), although this trade-off was not apparent in
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35
36 647 butterflies (Karl et al., 2013), underlining the likelihood that the relationship between summer
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38
39 648 and winter will be complex and species-specific.

40
41 649 In Figure 5, we conceptualise the potential biological impacts of winter climate change
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43
44 650 on a species in an inter-seasonal context. We assume that reproduction and growth occur outside
45
46 651 of winter – modification will be necessary for species that reproduce in winter. In Figure 5, the
47
48 652 winter variables that affect an organism are represented by ‘Winter’, while ‘Mortality’,
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50 653 ‘Resources’ and ‘Sub-lethal damage’ represent the outcomes of the biological processes and
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52
53 654 stresses in Figure 3. Figure 5 can be used in two ways. First, it can be used in conjunction with
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56 655 our framework describing the impacts of winter on a species’ biology (Figure 3, Table 1) to
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3 656 identify areas in which further research is required. Second, by determining the causal links and
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6 657 strengths of the relationships shown, it can be used to determine the relative importance of
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8 658 different aspects of winter in determining how a species' vulnerability to overwinter conditions
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10
11 659 plays out in the growing season and affects fitness.

12
13 660 The relationships between post-winter condition, growing season performance (and
14
15 661 reproduction) and pre-winter condition are already known for many species, thanks to the
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17
18 662 preponderance of growing-season studies. Winter mortality has been well-explored for many
19
20 663 species (Aars & Ims, 2002; Hodges et al., 2006; Roland & Matter, 2013; Stahl et al., 2006), but
21
22 664 data are lacking regarding the sub-lethal impacts of winter, mediated through resource
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24
25 665 consumption and damage, and the effects of these sub-lethal impacts on growing season
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27 666 performance. Moving forward, the direct relationships between winter conditions and growing
28
29 667 season performance need to be explored further across many taxa (see Kreyling (2010) for a
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31
32 668 plant-focused discussion of this point), as does the extent to which vulnerability to summer
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34 669 changes may exacerbate or negate vulnerability to winter changes.

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38 39 671 **V. Scaling up to populations, communities, and ecosystems**

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41 672 The direct effects of winter climate change on individual organisms will combine and
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43
44 673 synergise with competitive interactions to influence demography. Positive impacts of winter
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46 674 climate change, in the form of decreases in winter mortality, may be balanced or cancelled out by
47
48 675 a corresponding increase in intra-specific competition. For example, early snow-melt and
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51 676 increased availability of forage decreased overwinter mortality in reindeer, which increased
52
53 677 competition and slowed population growth (Tyler, Forchhammer & Øritsland, 2008). Winter
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55 678 climate change can affect population dynamics both directly and indirectly via different
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3 679 mechanisms. For example, in an alpine butterfly, delayed snow melt directly increased
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5 680 population growth by increasing recruitment the subsequent year, and indirectly increased
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8 681 population growth by increasing the peak abundance of the butterfly's floral resources (Boggs &
9
10 682 Inouye, 2012). Climate change-related shifts in population densities and processes at the leading
11
12 683 and retracting range edges (Hill, Griffiths & Thomas, 2011) lead to well-documented poleward
13
14 684 range shifts, especially in butterflies (Chen et al., 2011b; Hill et al., 2002; Parmesan et al., 1999).
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17
18 685 In some cases, climate-driven range shifts have been directly attributed to changes in winter
19
20 686 climate (Berger et al., 2007; Crozier, 2004). Conversely, differential susceptibility to winter
21
22 687 climate change among populations could also reduce performance in peripheral populations
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24
25 688 (Pelini et al., 2009), leading to range contractions in some species.

26
27 689 At community scales, complex multi-trophic interactions can drive the effects of climate
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29 690 change on individual species. Alterations to the abundance of plants or animals as a result of
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31 691 changes in mortality or phenology can be propagated through communities via consumer-
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33
34 692 resource interactions. For example, in a deciduous forest, increased winter herbivory by elk as a
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37 693 result of decreased snow cover depresses plant and associated bird communities throughout the
38
39 694 year (Martin & Maron, 2012). A deeper snow pack in the Great Lakes region of the USA
40
41 695 increases hunting success of wolves leading to reduced moose populations, which releases fir
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44 696 trees from heavy browsing and increases the fir understory (Post et al., 1999). In turn, these
45
46 697 changes in understory composition and browsing could depress soil respiration rates (Persson et
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48 698 al., 2009). Community interactions can modify and even reverse the effects of climate change on
49
50 699 individual species. For example, winter-induced changes in herbivory can prevent shrub
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53 700 expansion in Arctic tundra (Olofsson et al., 2009). In ecosystems where predator populations are
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55 701 subject to bottom-up control due to resource limitation, negative effects of winter climate change
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3 702 on prey may extend to higher trophic levels. Winter climate change has decreased plant
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6 703 production and forage quality, leading to declines in herbivore fitness (Awmack & Leather,
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8 704 2002; Bokhorst et al., 2012b), and the collapse of Arctic lemming population cycles has
9
10 705 decreased the population growth of several predator species (Gilg, Sittler & Hanski, 2009;
11
12 706 Schmidt et al., 2012). Conversely, direct impacts of winter climate change on overwintering
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14 707 carnivores may lessen predation pressure on prey species, with community-wide consequences
15
16 708 (Estes et al., 2011), although few examples of such climate-induced trophic cascades in a winter
17
18 709 context – perhaps because such studies have focused on Arctic and boreal habitats. These multi-
19
20 710 trophic interactions make it imperative to predict the direct impacts of winter climate change on
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22 711 species that exert strong top-down or bottom-up control within their communities, perhaps aiding
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24 712 to identify focal species for winter study.
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29 713 As we have shown, winter affects different species in different ways. Thus, dissimilar
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31 714 responses to winter climate change by different species can exacerbate phenological mismatches,
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33 715 reconfiguring community interactions (Van der Putten, Macel & Visser, 2010). For example,
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35 716 winter climate change has led to earlier spring leaf-out and caterpillar emergence in European
36
37 717 oak forests, decreasing synchrony of (caterpillar) food supply with peak feeding times in
38
39 718 passerine birds (Both et al., 2009). Similarly, the plant growing season has advanced faster than
40
41 719 the timing of the caribou migration to Arctic breeding grounds, resulting in increasing calf
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43 720 mortality and lower calf production (Post & Forchhammer, 2008). By contrast, climate change
44
45 721 has actually improved host plant-herbivore synchrony in a sub-Arctic moth-birch system.
46
47 722 Previously, birch bud burst occurred too early for moth larvae to feed on young (palatable)
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49 723 leaves. However, moth phenology has advanced more rapidly than birch in response to shorter
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51 724 winters, which has improved synchrony and enabled moth larvae to exploit this new resource
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3 725 (Jepsen et al., 2011). In extreme cases such as irruptive outbreaks of the (winter-limited)
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5 726 mountain pine beetle, winter climate change has contributed to altering landscape-level
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8 727 processes: beetle infestation modifies tree survival and species composition, ultimately
9
10 728 converting forests in British Columbia from net carbon sinks to a source of carbon (Kurz et al.,
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12
13 729 2008).

14 730 The links addressed in Figure 5 can be extended to processes that occur at the community
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17
18 731 or ecosystem scale. In doing so, additional links must be added to account for species
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20 732 interactions such as competition, and ecosystem processes that determine seasonal changes in
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22 733 resource availability. For example, Figure 6 (based on Sturm et al., 2005) describes potential
23
24 734 feedbacks between changes in snow cover, nutrient availability and plant species composition in
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26 735 the Arctic. In this scenario, climate warming is expected to promote shrub expansion into
27
28 736 graminoid communities, increasing the trapping of snow. Increased depth and duration of the
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30 737 snowpack can then increase nitrogen availability over winter by increasing soil microbial
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32 738 activity, and because the shrub canopy is above the snow layer, bud-burst and photosynthesis can
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34 739 occur earlier than in the low-statured graminoids, allowing the shrubs to access late-winter
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36 740 nitrogen pulses. Decreased nitrogen availability over summer, enhanced by increases in low
37
38 741 quality, woody shrub litter, coupled with increased shading by shrubs, further reduce the
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40 742 competitive abilities of the graminoids. In contrast to the latter example, extremely low spring
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42 743 snow accumulation is projected to occur over much of the Northern Hemisphere, with >80 % of
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44 744 years below the baseline minimum in some areas by 2080–2099 (Diffenbaugh & Field, 2013).
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46 745 The resulting decreases in melt water in spring, coupled with increased evapotranspiration and
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48 746 decreased summer rainfall in some regions, will increase summer drought severity.
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3 747 As we have demonstrated in this section, understanding the interactions between climate
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6 748 and biotic processes is essential for predicting how ecosystems will respond to climatic warming
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8 749 (Blois et al., 2013). Moving forward, integrating the responses of organisms across entire
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10 750 ecosystems, while taking into account linkages between winter and summer responses to climate
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12 751 change, and differing capacity to evolve, is a daunting task. This task will be facilitated by *a*
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14 752 *priori* identification of the key vulnerabilities to winter climate change, a process which is
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16 753 described in the following section.
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20 754 21 755 **VI. Predicting vulnerability to winter climate change**

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24 756 It is clear that winter is an important driver of biological processes and organismal
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26 757 fitness, and that winter climate change has the potential to significantly impact individuals,
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28 758 populations, community interactions and ecosystem processes. However, if a goal of global
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30 759 change research is to offer predictive power to facilitate risk assessments and management
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32 760 decisions, then it is necessary to identify which species and processes will be vulnerable to
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34 761 changing winters.
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38 762 Williams et al. (2008) proposed an integrative framework to identify and prioritise
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40 763 species that are vulnerable to climate change, where vulnerability was defined as susceptibility of
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42 764 a system to change – in most of our cases, the primary ‘system’ we consider is an individual or
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44 765 population. The authors distinguished between factors determining exposure to a change in
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46 766 climate, and those determining sensitivity to those changes. In their framework, exposure was
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48 767 determined by the degree of regional climate change, filtered through microclimatic buffering
49
50 768 due to habitat choice. For example, if temperatures are rising, a species that does not have the
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52 769 capacity to change microhabitat choice or alter thermoregulatory behaviour will be exposed to an
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54 770 increase in temperature, whereas a species that can buffer these regional changes will not
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3 771 (Kearney, Shine & Porter, 2009). In the context of winter, the three primary drivers of changing
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5 772 snow cover, thermal variability, and shifts in mean temperature interact with overwintering
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8 773 biology to modify the stresses that will be experienced: thus we must understand the causal
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10 774 relationships between the drivers that determine exposure to winter climate change. Figure 3 can
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12
13 775 be used as a framework for determining exposure to stress resulting from winter climate change,
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15 776 although such predictions are still dependent on predicting changes in the drivers from climate
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18 777 data and models – a major challenge given the discrepancy between the size of organisms and
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20 778 the scale at which climate data are collected (Potter, Woods & Pincebourde, 2013), and the lack
21
22 779 of information about the timeframes over which selection will modify winter phenology and
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25 780 physiology.

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27 781 Assuming that we can accurately assess an organism's exposure to climate change, the
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29 782 next step is to determine whether it will be sensitive (i.e. experience negative impacts). Williams
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31 783 et al. (2008) suggest that sensitivity is governed by intrinsic ecological, physiological or genetic
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33 784 traits of the focal species that determine levels of resilience (the ability of a species to survive
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35 785 and recover from a negative impact) and adaptive capacity (the capacity for plastic or
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38 786 evolutionary changes to reduce negative impacts). Related to the capacity for adaptation, we
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40 787 note that estimates of the strength of selection encountered by organisms in winter environments
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42
43 788 are an essential component of a predictive framework, but to date few studies have measured
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45 789 such selection gradients (Boratynski et al. (2010) provide one example of this). In using Figure 3
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48 790 as a framework, it is possible not only to identify the potential exposure to stress resulting from
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50 791 changes in the drivers, but because it makes clear (some of) the causal links between the drivers
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52 792 and organismal fitness, it allows the identification of end traits – and the design of simple
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55 793 experiments – that facilitate an assessment of the susceptibility of organisms to changes in those
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3 794 drivers. For example, there are clear links between overwintering temperature and energy
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6 795 consumption for many overwintering ectotherms. It is thus possible to design a simple
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8 796 experiment (e.g. keep overwintering stages of several species at several temperatures; Williams
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10 797 et al., 2012a) to compare susceptibility of energy use to changes in temperature. Similarly,
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12 798 experimental designs are now well established for determining impacts of repeated stress
13
14 799 exposure (Marshall & Sinclair, 2012a), addressing the impacts of shifting variability or snow
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16 800 cover – although the results of such experiments are not necessarily easy to interpret. For
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18 801 example, repeated freezing in overwintering caterpillars saves energy (Marshall & Sinclair,
19
20 802 2012b) but has other sub-lethal impacts (Marshall & Sinclair, 2011). Thus, a reductionist
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22 803 approach can be used to identify or rule out susceptibility to certain drivers of climate change
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24 804 relatively rapidly, but more complex experiments are necessary to understand interactions among
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26 805 drivers.
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32 806 More generally, it is possible to identify some of the general traits that render individuals
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34 807 or populations of a species vulnerable (or resilient) to winter climate change (Table 1). As with
35
36 808 all sensitivity to climate change, species that have high rates of reproduction and short lifecycles,
37
38 809 large range sizes (but not large spatial scales of operation), and high dispersal will be less
39
40 810 vulnerable to change (Williams et al., 2008). However, the links in Figure 3 allow the
41
42 811 identification of winter-specific traits that lead to vulnerability; some of these are outlined in
43
44 812 Table 1, and are grouped according to energy balance (e.g. thermoregulatory strategy,
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46 813 metabolism), phenology (e.g. chilling requirements, overwintering stage), cold injury (e.g. cold
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48 814 tolerance, response to repeated stress), water balance and predation (e.g. trophic position,
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50 815 predatory avoidance strategies).
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3 816 Despite extensive evidence from individual cases for the importance of trophic dynamics
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6 817 in determining overwinter responses, they remain difficult to predict. Community-level
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8 818 experiments are inherently complex and limited in spatial and temporal scope, while the use of
9
10 819 population-based data to construct dynamic models of communities is typically inadequate for
11
12 820 predicting responses to novel combinations of drivers, even in the growing season (Abrams,
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14 821 2001). This complexity is intensified when the relative performances of organisms both over
15
16 822 summer and winter must be taken into account, but we propose that the species-based *a priori*
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18 823 approach, based on the drivers and vulnerabilities identified in Table 1 and Figure 3 can be used
19
20 824 to identify key impacts of winter. If combined with an understanding of the community
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22 825 interactions in a system, it is possible to at least identify potential responses to winter climate
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24 826 change at the community level.
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30 31 32 828 **VII. A call to further integrate winter into climate change research**

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34 829 Winter imposes a severe selective pressure that determines fitness, drives many
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36 830 ecological processes, and shapes the evolution of organisms. The pressing need to understand
37
38 831 the mechanisms underlying biological responses to climate change, coupled with the rapid
39
40 832 changes in winter conditions, together provide a strong imperative to unravel the complexities of
41
42 833 responses to winter at the individual, community, and ecosystem scales, and to determine general
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44 834 patterns describing vulnerability to negative impacts. To integrate this information we must
45
46 835 combine theoretical and empirical approaches and synthesise across taxa, levels of organisation,
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48 836 and climate drivers.
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53 837 For theorists, the challenge lies in incorporating winter into models that tend to have
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55 838 forms and parameters associated with growth and assimilation, rather than dormancy and
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57 839 consumption (although there is scope for the latter in Dynamic Energy Budget models; Sousa et
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3 840 al., 2010). Mechanistic models of winter biology exist for some species, and the form of some of
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6 841 these models may be incorporated into existing frameworks, and potentially expanded to include
7
8 842 additional aspects of winter climate change. For example, Régnière and Bentz (2007) have
9
10 843 provided a robust model of the dynamic shifts in cold tolerance of overwintering mountain pine
11
12 844 beetles, although this model does not incorporate any sub-lethal impacts of cold exposure.
13
14 845 Because it is likely that the existing relationships between climate variables will be disrupted
15
16 846 (Jackson et al., 2009; see also Figure 2), functional or phylogenetic approaches may be powerful
17
18 847 alternatives to existing niche models (Buckley & Kingsolver, 2012) by using existing studies to
19
20 848 infer potential impacts of combinations of winter drivers that may be novel for a given species or
21
22 849 population. However, data regarding the effects of winter conditions on fitness is sparse and
23
24 850 diffuse, and not necessarily in a model-ready format. Trait databases such as iPlant (Goff et al.,
25
26 851 2011) may provide a source of such information, but theorists and empiricists will need to work
27
28 852 together to identify the key traits that will inform vulnerability to winter climate change, using
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30 853 approaches similar to those outlined in Figure 3 and Table 1.
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37 854 To inform this theoretical effort, empiricists need to collect more data on the performance
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39 855 and, ultimately, fitness consequences of projected changes in winter climate drivers. Such an
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41 856 understanding requires integration across levels of organisation and from regional to single-
42
43 857 organism scales; this entails a shift in focus to populations rather than species, metres rather than
44
45 858 miles, and minutes rather than months. A lofty goal for mechanistic studies of overwintering
46
47 859 biology is the development of general principles that describe how organisms respond to winter,
48
49 860 and the ability to predict – *a priori* – which species will be most vulnerable to winter climate
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51 861 change. To accomplish this we must extend more laboratory studies into the field, which will
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53 862 require methodological limitations and biases to be overcome. For example, methods for
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3 863 simulating winter climate change in the field, such as snow fences, snow removal, heated soil
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6 864 cables and overhead heaters, are often plagued by artifacts or scaling limitations (Shen & Harte,
7
8 865 2000). Similarly, there is a need to expand the geographic and taxonomic focus of winter
9
10 866 biology. There has been a disproportionate focus on relatively cold environments with long
11
12 867 winters (such as the high arctic) relative to temperate systems (Kreyling, 2010), and there have
13
14 868 also been asymmetries in research between the northern and southern hemispheres, which may
15
16 869 also bias our understanding of the key aspects of winter (Chown et al., 2004). Throughout this
17
18 870 review, it is apparent that the bulk of the literature on some broadly-applicable topics is
19
20 871 constrained to certain systems; for example, many studies of winter climate change at the
21
22 872 community and population levels have been conducted on arctic mammals, but few on temperate
23
24 873 insects, whereas a disproportionate amount of research has been conducted on the physiological
25
26 874 responses to freezing of temperate insects and crop plants. Finally, there is a need for substantial
27
28 875 effort documenting fall and winter events complementing the successful and ongoing
29
30 876 documentation of changes in spring phenology and growing season biology. We particularly
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32 877 encourage a concerted effort to expand existing, well-characterised, systems into the winter to
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34 878 develop a more holistic view of how organisms, communities, and ecosystems will respond to
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36 879 climate change.
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881 **VIII. Conclusions**

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

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3 885 (2) The main abiotic drivers of biological responses to winter are the mean and
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6 886 variability of air temperatures and the extent and timing of snow cover. All of these
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8 887 are being affected by climate change in a regionally-specific manner.
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10 888 (3) Understanding the links between abiotic change and organismal performance is
11
12 889 important for determining organismal vulnerability to climate change. This will
13
14 890 require a mechanistic and integrative approach.
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16 891 (4) Responses to winter conditions are not isolated from growing season responses to
17
18 892 climate. Therefore it is important to investigate the impacts of winter on
19
20 893 performance, fitness and biotic interactions in the context of growing season biology.
21
22 894 We suggest that an opportunity exists to extend existing long-term studies of growing
23
24 895 season biology to incorporate the effects of winter.
25
26 896 (5) At the population and community levels, inter- and intra-specific interactions strongly
27
28 897 influence responses to winter climate change. Impacts on individual species will
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30 898 propagate through ecosystems, and the role of winter in modifying these interactions
31
32 899 must be considered when predicting the ecological impacts of climate change.
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50 906 **X. References**

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3 1384 **Figure Captions**

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6 1385 **Figure 1** - Projected winter climate change in terrestrial systems over the next century. Predicted
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8 1386 January (northern hemisphere) or July (southern hemisphere) differences between 2090-2099
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10 1387 and 2000-2009 in (A) mean surface air temperature and (B) total precipitation. Tropical regions
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12 1388 (23°S to 23°N) that do not experience winter are in grey. Predictions are from the HADCM3
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14 1389 model, A2 scenario (Lowe, 2005); means for each cell over the early time period were subtracted
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16 1390 from the means for the late time period to give projected changes.
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22 1392 **Figure 2** – Examples of the effects of changes in air temperature and snowfall on snow depth
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24 1393 and soil temperature during winter. (A) Current climate. Note that snow cover buffers soil
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26 1394 temperatures. (B) increased mean air temperature results in increased soil freeze-thaw cycles
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28 1395 during a mid-winter melt because the soils become exposed to warm air temperatures during the
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30 1396 day and freezing air temperatures at night. (C) scenarios whereby increased air temperature
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32 1397 variability modifies soil freezing. In late fall, an early frost exposes soil to cold air prior to
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34 1398 development of the snowpack. Warm spells in either mid-winter or early spring melt the
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36 1399 snowpack, leaving soils vulnerable to subsequent drops in air temperature. Finally, snow melt
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38 1400 can be accelerated by increased diel air temperature variability. (D) reduced winter precipitation
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40 1401 leads to increased soil freeze-thaw cycles following a mid-winter melt and during spring melt as
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42 1402 a result of reduced snow cover at these times.
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51 1404 **Figure 3** - A blueprint for predicting the biological impacts of winter climate change on
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53 1405 terrestrial organisms. Abiotic drivers of winter climate change (black circles) alter physiological,
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55 1406 biotic or abiotic processes (white, light grey and white rectangles respectively) leading to
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3 1407 biological impacts (white hexagons). Signs on arrows indicate the direction of the relationship,
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6 1408 and can be navigated with reference to Table 1 and examples in the text. The dotted line
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8 1409 indicates that decreases in snow and ice occur in response to increased macroclimatic
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10 1410 temperatures; all other relationships occur within organisms' microclimates.
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15 1412 **Figure 4** - The relationship between winter energy use and phenology for dormant organisms. A
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17 1413 longer winter (early onset of or later exit from dormancy) results in higher energy use. Winter
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19 1414 climate change is increasing total energy use through increases in means or variability of
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21 1415 temperatures (effectively elevating the entire surface, not shown), and organisms have responded
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23 1416 to this in three ways: A) increasing the degree of metabolic suppression over winter, and thus
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25 1417 lowering energy costs (e.g. the duskywing caterpillar *Erynnis propertius*; Williams et al., 2012b);
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27 1418 B) delaying the onset of entry into dormancy, thus reducing the period of pre-winter energy drain
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29 1419 (e.g. the pitcher plant mosquito *Wyeomyia smithii*; Bradshaw & Holzapfel, 2001); and C)
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31 1420 advancing the date of exit from dormancy, to take advantage of opportunities to feed and reduce
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33 1421 winter energy drain (e.g. the yellow-bellied marmot, *Marmota flaviventris*; Ozgul et al., 2010).
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41 1423 **Figure 5** – Integrating winter processes into growing season biology. This assumes that
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43 1424 reproduction (which determines fitness) occurs in the growing season, but could be modified for
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45 1425 other life histories. The black diamond 'winter' represents the abiotic conditions that are
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47 1426 experienced during winter, and the three white boxes are the outcomes of biological processes
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49 1427 and stresses described in Figure 1 and Table 1. These processes affect post-winter condition,
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51 1428 which affects growing season performance (all growing season processes are combined in this
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53 1429 framework), which in turn determines the pre-winter condition of organisms. The strength and
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4 1430 importance of these links will depend on life history and the extent to which summer and winter
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6 1431 stresses exacerbate or negate one another.

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10 1433 **Figure 6** – Example of how adding links to account for species interactions and ecosystem

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12 1434 processes that determine seasonal changes in resource availability can extend the integration of

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14 1435 winter processes into growing season biology to the ecosystem scale. This example, simplified

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16 1436 from(based on Sturm et al., 2005), describes how climate warming may drive potential feedbacks

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18 1437 between changes in snow cover, nutrient availability and plant species composition in the Arctic.

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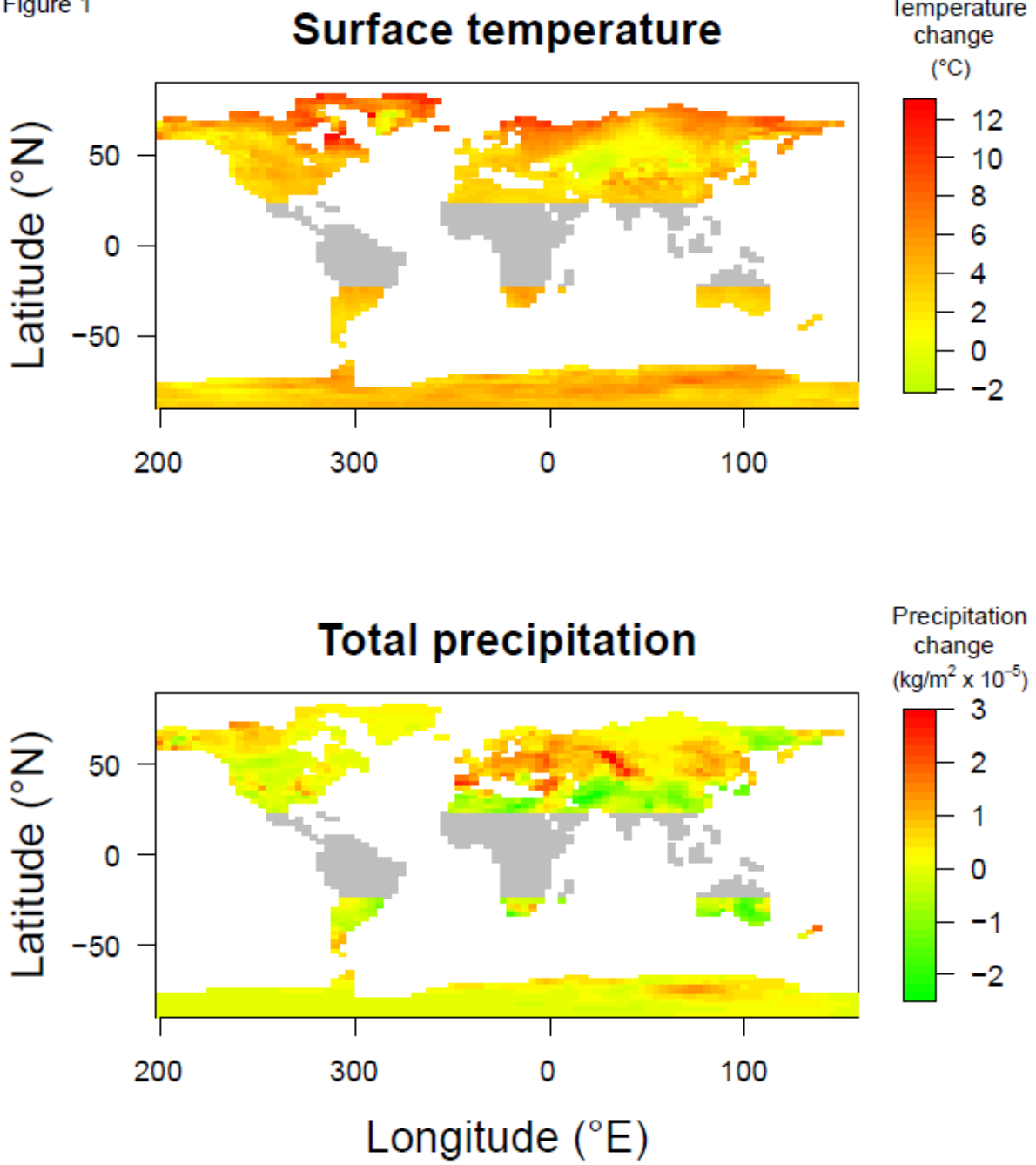
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1441 Figure 1

1442 Figure 1



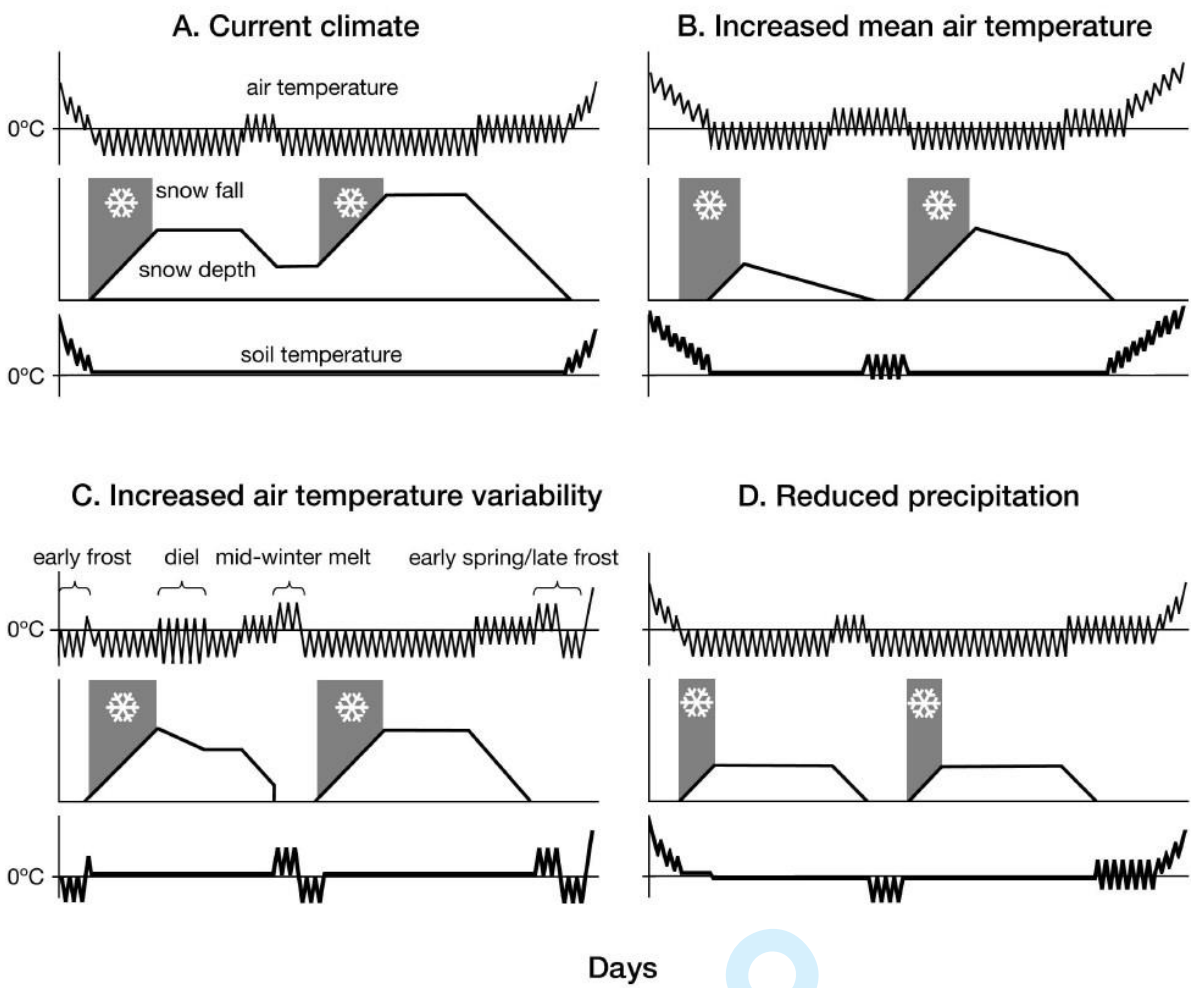
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1445 Figure 2

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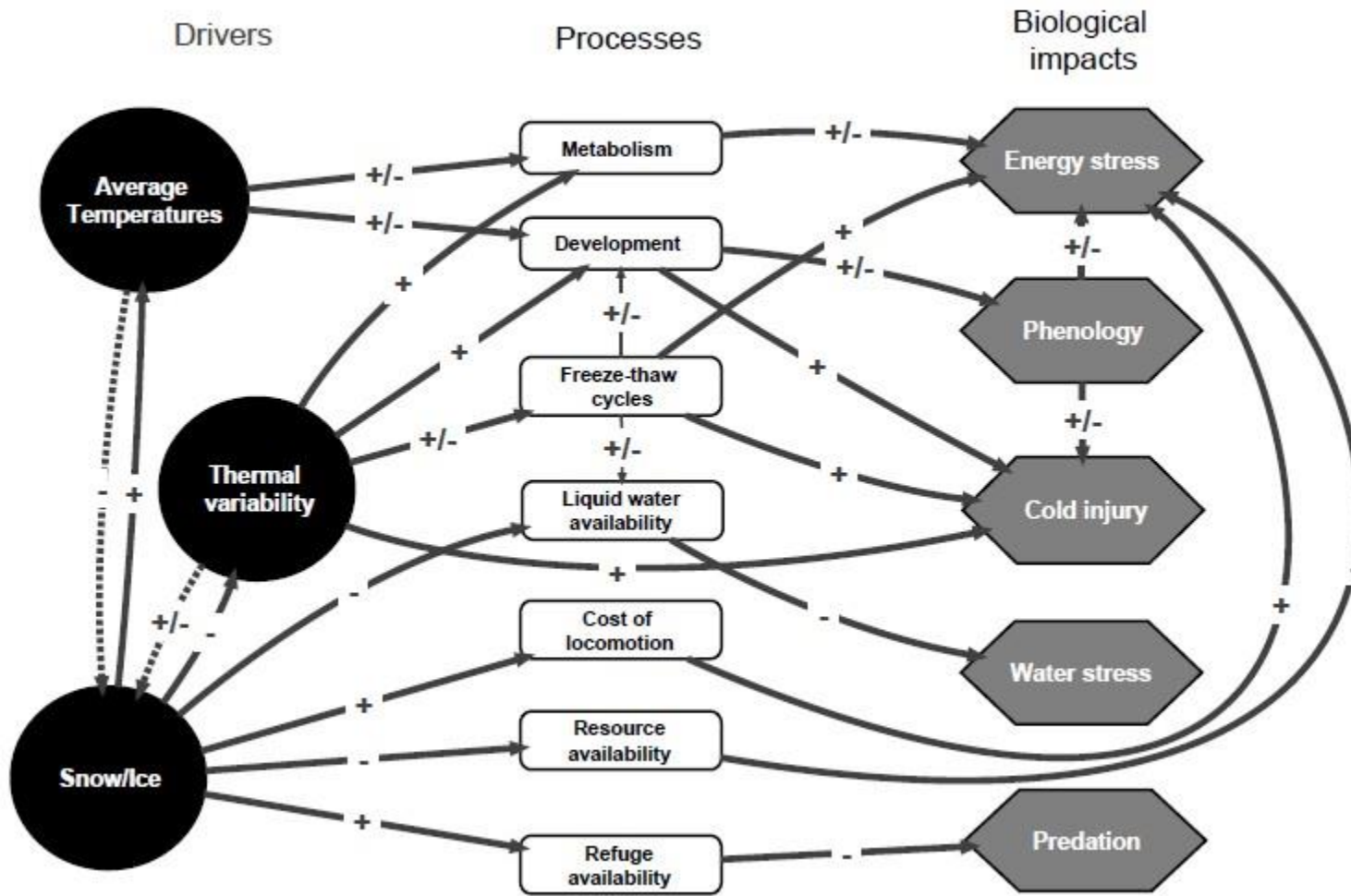


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Figure 3

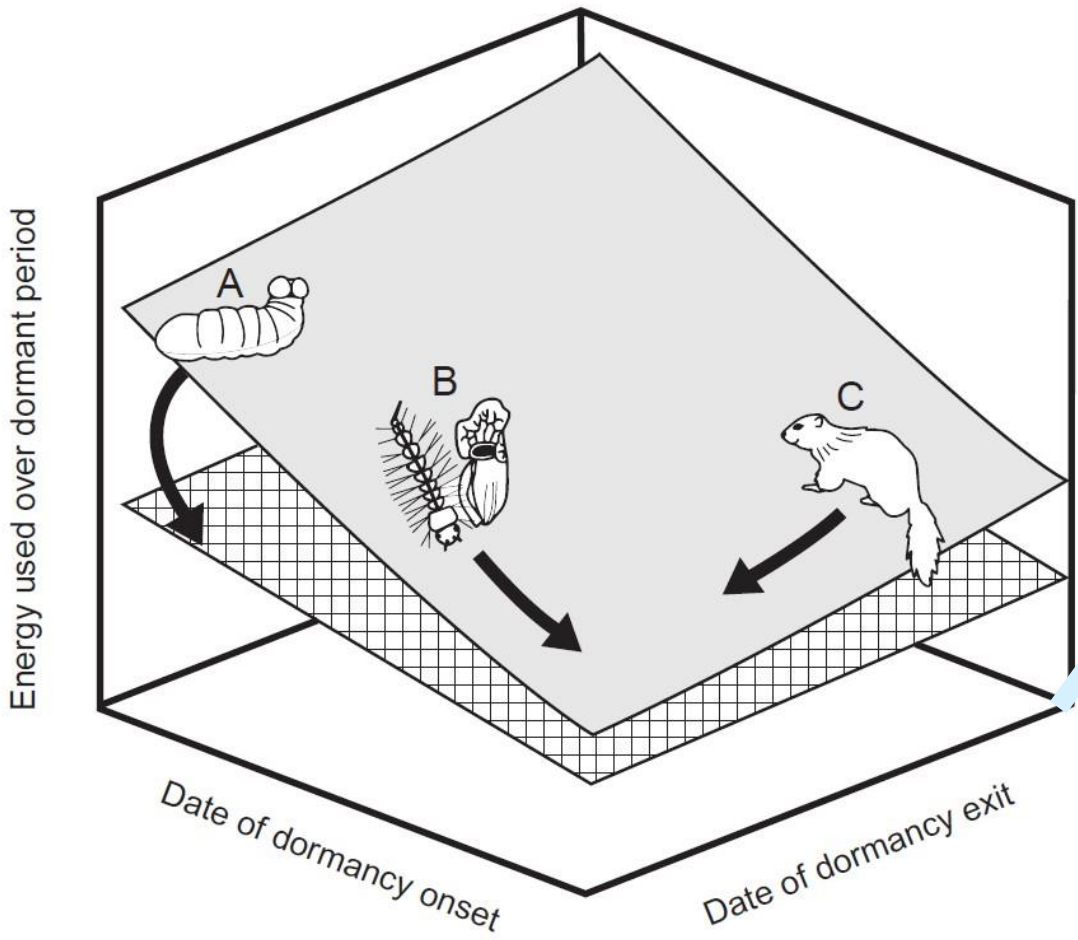


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1455 Figure 4

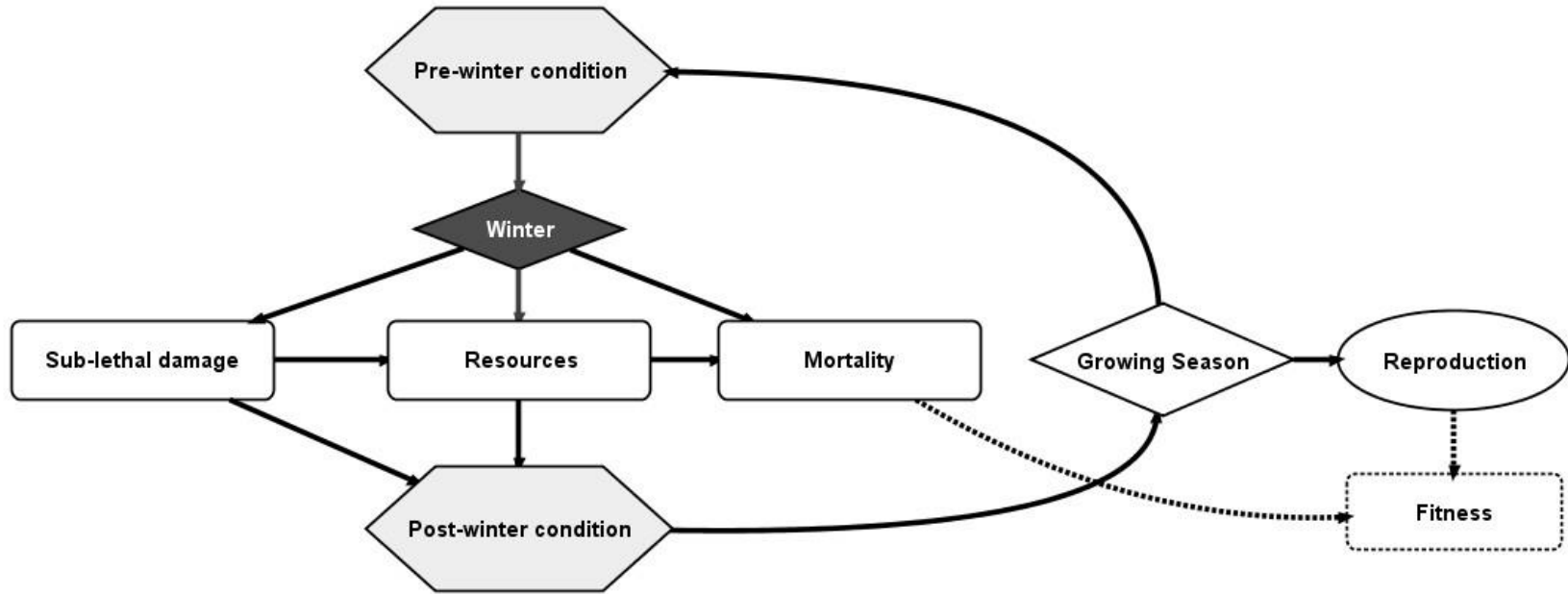
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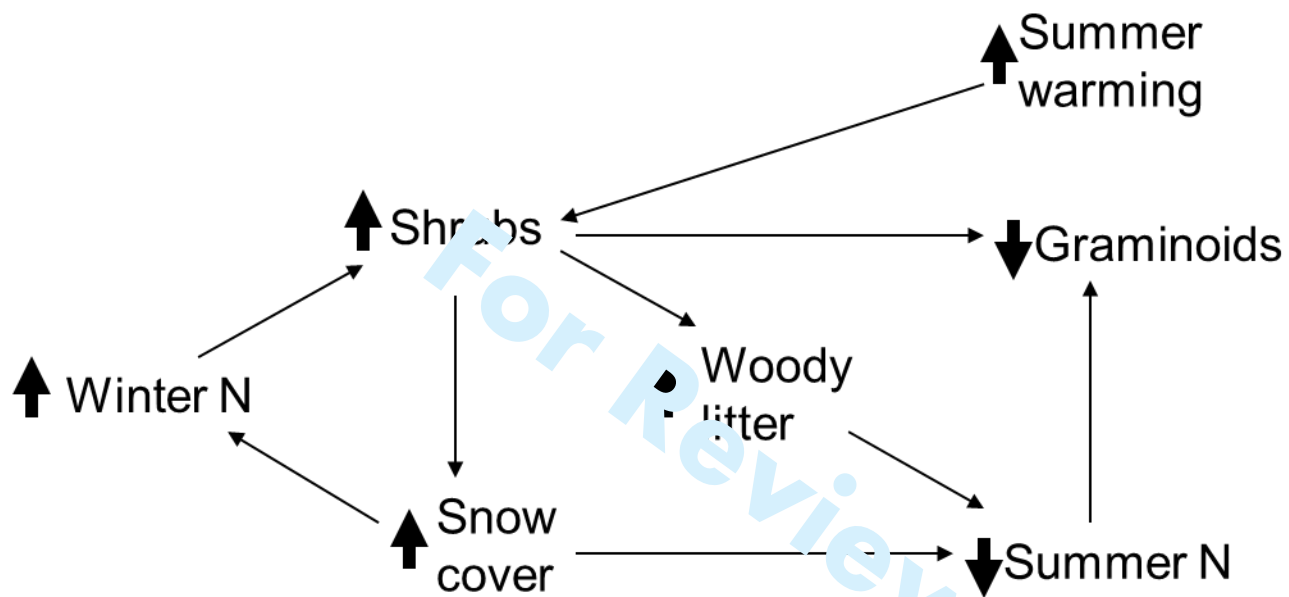
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1465 Figure 6



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4 1468 **Table 1** – Organismal traits influencing vulnerability to winter climate change. Vulnerability is a product of traits that increase stress
5 1469 exposure in response to a climate driver and traits that increase sensitivity to this stress, with sensitivity determined by a lack of either
6 1470 resilience or adaptive potential. Climate drivers (indicated in italics, and with reference to the text and Figure 3) are increased average
7 1471 temperatures (*AvT*), thermal variability (subdivided here into increased daily thermal variability (*DV*), extreme temperatures (*ExT*) and
8 1472 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
<u>Energy balance</u>		
Thermoregulatory strategy (<i>AvT</i> , <i>DV</i>) <ul style="list-style-type: none"> poikilotherms > homeotherms 	Reproductive strategy (<i>AvT</i> , <i>DV</i>) <ul style="list-style-type: none"> capital breeding > income 	<ul style="list-style-type: none"> Consumption of finite energy reserves (<i>AvT</i>, <i>DV</i>)
Energy intake and availability (<i>AvT</i> , <i>DV</i> , <i>S+</i>) <ul style="list-style-type: none"> no energy intake/limited food available > winter energy uptake 	Energy storage(<i>AvT</i> , <i>DV</i>) <ul style="list-style-type: none"> low > high pre-winter energy stores Energetic recovery (<i>AvT</i> , <i>DV</i>) <ul style="list-style-type: none"> no post-winter feeding > feeds post-winter 	
Metabolic suppression (<i>AvT</i> , <i>DV</i> , <i>S+</i>) <ul style="list-style-type: none"> low > high suppression 		<ul style="list-style-type: none"> Increased cost of locomotion (<i>S+</i>)
Metabolic plasticity (<i>AvT</i> , <i>DV</i>) <ul style="list-style-type: none"> low > high plasticity 	Feeding strategy (<i>S+</i> , <i>S-</i>) <ul style="list-style-type: none"> specialist > generalist 	<ul style="list-style-type: none"> Decreased food access (<i>S+</i>)
Trophic position (<i>S+</i>) <ul style="list-style-type: none"> predator > prey heterotroph > autotroph 		
Habitat (<i>S-</i>) <ul style="list-style-type: none"> subnivean > supranivean 		

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Table 1 (continued)

Traits determining stress exposure	Traits determining sensitivity to stress	Proximal cause of vulnerability
<u>Phenology</u>		
Chilling or vernalization requirements (<i>AvT</i>)	Trophic level (<i>AvT</i>)	<ul style="list-style-type: none"> • Reduction in length of growing season (<i>AvT</i>)
<ul style="list-style-type: none"> • obligate > facultative dormancy • chilling requirement > non-thermal cues 	<ul style="list-style-type: none"> • consumers > primary producers Diet breadth (<i>AvT</i>) <ul style="list-style-type: none"> • low > high 	<ul style="list-style-type: none"> • Trophic mismatches (<i>AvT</i>)
Habitat requirements (<i>S-</i>)	Overwintering stage (<i>AvT</i>)	<ul style="list-style-type: none"> • habitat not available for reproduction (<i>S-</i>)
<ul style="list-style-type: none"> • snow dependent > not snow dependent 	<ul style="list-style-type: none"> • early in lifecycle > late in lifecycle Genetic variation in reaction norms (<i>AvT</i>) <ul style="list-style-type: none"> • low variation > high 	

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Table 1 (continued)

Cold injuryCold hardiness (*ExT*)

- cold-susceptible > cold-hardy

Cold tolerance strategy (*ExT*)

- seasonally programmed but readily deacclimate > constitutive protection

Position of biological thresholds (*ExT*, *F/T*)

- lower/higher than current conditions > near current conditions

Habitat (*S-*)

- subnivean > supranivean

Water Balance

Susceptibility to waterlogging and ice encasement

- hypoxia intolerant > hypoxia tolerant

Rapid cold hardening (*ExT*)

- none > effective rapid hardening response

Thermal plasticity (*ExT*)

- no reacclimation > reacclimation

Cumulative impact of repeated stress (*F/T*)

- cumulative > no cumulative impact/impact reaches asymptote

Water balance strategy

- no winter water consumption > water consumption over winter

- Direct injury from cold (*ExT*)

- Cumulative cold injury (*F/T*)

- Energetic costs of repairing cold injury (*F/T*, *S-*)

- Hypoxia from waterlogging/ice encasement

- Unavailability of liquid water when frozen

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Table 1 (continued)

Traits determining stress exposure	Traits determining sensitivity to stress	Proximal cause of vulnerability
<u>Predation</u>		
Trophic position (<i>S</i> -)	Predator avoidance (<i>S</i> -)	Increased mortality
<ul style="list-style-type: none"> • prey > predator 	<ul style="list-style-type: none"> • low camouflage plasticity > low 	
Habitat (<i>S</i> -)	<ul style="list-style-type: none"> • low defenses > high 	
<ul style="list-style-type: none"> • subnivian > supranivean 	<ul style="list-style-type: none"> • high palatability > low • low alertness > high 	

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For Review Only

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4 1478 **Table 2** – The range of effects of changes in the quantity and timing of snow cover on overwintering organisms.

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6 **Quantity of snow**

7 *Reduced snow cover*

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9 increased soil frost
10 increased food access for predators/browsers
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12 (decreased food access with increased rain-on-snow)
13 increased vulnerability of prey

14 *Increased snow cover*

- 15
16 increased foraging and locomotion costs (winter-active organisms)
17 increased energetic maintenance costs (winter-inactive organisms)
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19 **Timing of snow cover**

20 *early snowmelt*

- 21
22 earlier warm-season resource gathering
23 potential phenological mismatch for dormant organisms
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25 *delayed snowmelt*

- 26 delayed warm-season resource gathering
27 increased protection from frost
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29 *mid-winter snowmelt*

- 30 cold deacclimation followed by frost exposure
31 increased access to liquid water
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