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

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3 **change**

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9 **Running Title:** Organismal responses to winter climate change

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12 **Key words:** Snow, frost, cold, extreme events, average temperatures, freeze-thaw cycles, sub-

13 lethal impacts, energetics, hibernation

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Abstract

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

Contents

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).

81   In spite of the constraints, many species thrive in places with severe winters, and there

82 are species that might be considered winter-dependent; for example, most Arctic vertebrates

83 require snow and ice for their reproduction and survival (Gilg et al., 2012), and some

84 invertebrates disperse and hunt primarily in subnivean (beneath the snow pack) spaces

85 (Addington & Seastedt, 1999; Pauli et al., 2013). Some species that overwinter in a dormant

86 state have evolved dependence on winter cues for termination of dormancy (Amasino, 2004;

87 Tauber, Tauber & Masaki, 1986), and monarch butterflies rely on winter cold to reverse the

88 direction of their fall migration (Guerra & Reppert, 2013). Many ectotherms and hibernating

89 mammals rely on low winter temperatures to reduce consumption of energy stores (Humphries et

90 al., 2002; Williams et al., 2012b). At the ecosystem level, freezing of soil in winter can mobilise

91 nutrients (and/or damage roots), affecting nutrient availability and uptake, and therefore primary

92 productivity, in the spring (Durán et al., 2013; Groffman et al., 2001). Likewise, winter

93 conditions in many species can define organismal performance in the subsequent summer (Boggs

94 & Inouye, 2012; Post et al., 1997; Serrano et al., 2011).

95   Repeated glacial/interglacial cycles, coupled with continental drift in and out of the

96 tropics, mean that physiological and life history adaptations to winter have evolved repeatedly in

97 multiple lineages of organisms. The evolutionary impact of winter on life histories is significant

98 – for example, the northern temperate winter may have been a primary driver of the evolution of

99 migratory and hibernation phenotypes (Alerstam, Hedenstrom & Akesson, 2003; Turbill, Bieber

100 & Ruf, 2011). For ectotherms, microbes, and plants, the threat of internal ice formation has

101 driven the evolution of physiological traits that allow them to resist low temperatures (for

102 example, freeze tolerance in insects and plants; Margesin, Neuner & Storey, 2007).

103 Nevertheless, both endotherms and ectotherms suffer high mortality over winter (Hodges,

104 Boonstra & Krebs, 2006; Roland & Matter, 2013; Stahl et al., 2006), and the population

105 dynamics of diverse fast-reproducing animals including lemmings and moths can be driven

106 primarily by winter mortality (Callaghan et al., 2004; Virtanen, Neuvonen & Nikula, 1998).

107   Anthropogenic climate change is rapidly altering biological systems, and winter

108 conditions are changing particularly rapidly (IPCC, 2007). Differential sensitivity of organisms

109 to climate change is restructuring biological communities due to disparate range and phenology

110 shifts, and altered population dynamics (Chen et al., 2011a; Walther, 2010), and – where the

111 proximate cause is known – many biological responses to climate change are driven by changes

112 in winter conditions (e.g. Battisti et al., 2005; Crozier, 2004). To guide mitigation efforts under

113 global climate change, we must identify which species or populations will be "winners" –

114 benefitting from climate change, and which "losers" will be vulnerable to changes (Somero,

115 2010). However, the interactions between snow and temperature that determine microclimate

116 conditions combine with divergent ecological and physiological strategies for dealing with

117 winter stress, leading to variation among species in responses to winter climate change. In some

118 cases, these idiosyncratic responses to winter likely underlie the failure of models to accurately

119 predict species' responses to climate change (Cook, Wolkovich & Parmesan, 2012). A limited

120 understanding of organismal responses to winter climate change (and their cascading effects

121 through communities and ecosystems) thus impedes efforts to predict the biological impacts of

122 climate change in general.

123   The interaction between a species' traits (and the plasticity of those traits; Chown et al.,

124 2007; Somero, 2010) and changes in the abiotic environment will determine success or failure in

125 a changing world (Foden et al., 2013), so predictions would ideally utilise information on species

126 traits combined with climate models to output vulnerability. Meta-analyses have shed some light

127 on the relationship between species' traits and their responses to environmental change (e.g.

128 Bokhorst et al., 2012a; Diamond et al., 2011; Jiguet et al., 2007; Thackeray et al., 2010),

129 however, these analyses have not been in the context of winter, nor have they synthesised across

130 diverse taxa and abiotic drivers. Thus, we need a framework to identify climate-change-

131 susceptibility that explicitly includes winter processes and incorporates evolution, ecology and

132 physiology. An essential starting point is a synthesis of the mechanistic bases for the complex

133 responses to interacting winter climate drivers across terrestrial taxa.

134   Here we present a multi-component framework for predicting the impact of change in

135 abiotic winter drivers on a terrestrial organism. We begin by describing the predicted changes in

136 winter climate, then synthesise the mechanistic bases for the biological impacts of winter climate

137 change across terrestrial taxa and regions. We use this synthesis to identify key traits that make

138 species susceptible to changing winter conditions, and integrate the current state of knowledge

139 on impacts of winter climate change within the body of knowledge of growing season processes.

140 We focus on traits influencing exposure and sensitivity to a particular stress, which may arise

141 from a number of drivers or interactions between drivers, and through both biotic and abiotic

142 processes. Our review is not meant to be exhaustive in scope, but rather to draw on

143 representative examples across taxa to illustrate the main biological impacts of winter across a

144 range of terrestrial organisms, to provide a starting point for readers to access the literature

145 relevant to their system, and to guide future research in the field of winter-focused global change

146 biology. This framework is designed to provide researchers with the means to navigate from

147 change in a climate driver to a list of potential biological impacts an organism may experience,

148 and to make a qualitative assessment of the likelihood of any terrestrial organism to suffer a

149 given biological impact.

150

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]

172

173   In addition to changes in mean temperature and precipitation, an increased frequency of

174 extreme weather events can increase the incidence, frequency and intensity of soil freezing,

175 either as a result of unusually early or late winter frost events, or as a result of mid-winter

176 warming (or rain) events that reduce snow cover and are followed by freezing temperatures

177 (Figure 2C). There has been an overall increase in the frequency of extreme thermal events in

178 both summer and winter, and further increases are predicted over the next century (Easterling et

179 al., 2000). Increases in extreme minimum and maximum temperatures in recent decades have

180 varied among seasons and among regions, but overall there has been an increased number of

181 days of extreme high minimum temperature and a reduced number of days of extreme low

182 minimum temperature (Caprio, Quamme & Redmond, 2009; Easterling et al., 2000). For

183 example, across Canada the number of cold nights (minimum temperatures below the 10th

184 percentile for the 20th century) decreased by 15 per year between 1950 and 2003 (Vincent &

185 Mekis, 2006). The frequency of both extreme high temperatures and longer mid-winter warm

186 spells is expected to increase with climate change in some regions (Liu et al., 2006).

187

188 [Figure 2 here]

189

190   Aside from thermal stress, interactions between temperature and moisture during winter

191 can alter the occurrence of physical stresses such as ice encasement and frost heave (the uplift of

192 soil when freezing water in soil expands), and increased rainfall over winter will increase the

193 frequency of rain-on-snow events, which contribute to ice encasement. Rain-on-snow events

194 have increased in most Arctic regions, in some cases by up to 50% (ACIA, 2005). Furthermore,

195 changes in albedo and permafrost depth can modify water retention by the soil, which can alter

196   the nature of below-ground freeze-thaw (Oztas & Fayetorbay, 2003). Changes in sea or lake ice

197   can also exacerbate terrestrial climate change, for example by increasing moisture availability,

198   leading to increased snow depth in maritime areas, or by modifying albedo and accelerating

199   spring melt (Deser et al., 2010). With the emphasis on temperature effects in winter research,

200   such interactions with moisture have often been overlooked, and consequently our discussion of

201   these specific moisture effects remains speculative (and is often absent) throughout much of this

202   review.

203

204   **III. Mechanistic bases of the biological impacts of winter climate change**

205   The primary abiotic drivers of the biological impacts of winter on terrestrial systems are

206   temperature and snow cover. Temperature determines rates of biological processes, and thermal

207   variability impacts the likelihood of crossing important biological thresholds (e.g. the freezing

208   point of tissues). Snow strongly modifies both the physical and the thermal environments.

209   Changes in the absolute variability of these factors (as well as their timing and synchrony) can

210   modify the interaction and outcomes of snow cover and temperature. In Figure 3, we describe

211   how these drivers interact to determine biological impacts, and we show the direction of impact

212   of changes in some of these drivers (which we elaborate below). Ultimately, the susceptibility of

213   organisms to winter (see Table 1 for a description of the traits influencing vulnerability to winter

214   changes), and the way these impacts combine and synergise with impacts of climate change

215   during the growing season will determine the winners and losers under global climate change,

216   and understanding these processes will be essential for informed management of biodiversity in a

217   changing world.

218

219   [Figure 3 here]

220

221   [Table 1 here]

222

223   (1) Increased average winter temperatures

224   *(a) Effects on metabolic rate*

225   Increased average temperatures can arise either as a direct result of climate warming, for

226   organisms whose habitats are not buffered from ambient temperatures, or from increased snow

227   cover with associated thermal buffering (Figures 2A-B, Figure 3). Increased average

228   temperatures can impact energy stress and phenology by increasing rates of development or

229   metabolism (Figure 3). Temperature influences metabolism, and thus consumption of stored

230   energy by 1) directly determining the rates of metabolic processes (such as respiration and

231   carbon fixation) in poikilotherms and 2) determining the costs of thermoregulation by

232   homeotherms. Thus, increased average temperatures will increase rates of metabolism of

233   poikilotherms, while for homeotherms below the thermoneutral zone, metabolic rates will

234   decrease with increased average temperature due to the decreased cost of thermoregulation

235   (Table 1).

236   A higher metabolic rate will increase the rate of use of stored energy reserves, which can

237   expose non-feeding organisms to energetic stress (Figure 3). For example, hibernating bats

238   expend more energy when hibernaculum temperatures are above an optimal low temperature

239   (Humphries et al., 2002), dormant hatchling turtles consume more energetic reserves and emerge

240   in poorer physiological condition after warm winters (Muir et al., 2013), and energy drain means

241   that goldenrod gall flies that overwinter in relatively warm subnivean microclimates have

242 reduced survival and fecundity compared to conspecifics overwintering in exposed, colder sites,

243 because their metabolic rates increase exponentially with temperature (Irwin & Lee, 2003). All

244 else being equal, this energy drain is likely to be more pronounced in organisms with high

245 baseline metabolic costs, and less pronounced in organisms, such as diapausing butterfly pupae,

246 that substantially suppress their metabolism during winter (Table 1; e.g. Williams, Hellmann &

247 Sinclair, 2012a).

248   Increased rates of biological processes may permit energy gain for organisms that can

249 take up nutrients during the winter. For example, increased winter temperatures increase

250 photosynthetic rates and thus carbon gain in non-dormant plants as long as water is available,

251 although this effect is more pronounced in woody than in herbaceous species (Ensminger, Busch

252 & Hüner, 2006). Similarly, the mineralization of limiting nutrients such as nitrogen increases

253 with soil temperature over winter (Sturm et al., 2005), which can increase primary productivity,

254 assuming that nutrient release and uptake are synchronised (Groffman et al., 2001).

255   For homeotherms, the energetic costs of thermoregulation during winter can rival or

256 exceed energetic costs of the breeding season, yet occur at a time when food availability may be

257 low (Sgueo et al., 2012). An increase in average winter temperatures will thus lower metabolic

258 costs of thermoregulation in homeotherms that would normally experience winter temperatures

259 below the thermoneutral zone, which may alleviate energetic stress (Figure 3; Sears et al., 2009).

260 A release from energetic stress as a result of winter climate change may have led to recent

261 increases in body size of American martens, either via decreased thermoregulatory costs or

262 increased prey availability (which will reduce energetic stress by increasing nutrient uptake;

263 Yom-Tov, Yom-Tov & Jarrell, 2008). Increased body size and/or condition will likely translate

264 into fitness benefits by decreasing overwinter mortality (Hodges et al., 2006), or improving

265   condition at the onset of the breeding season (e.g. Guillemain et al., 2008). Alternately,

266   decreased thermoregulatory costs may increase fitness by reducing the need for pre-winter

267   energy accumulation, which could mitigate trade-offs and predation risk associated with resource

268   acquisition (Gentle & Gosler, 2001). By contrast, warmer winters may lead to summer energy

269   drain for species such as polar bears that feed primarily during winter and fast in the summer.

270   Warmer winters reduce the length of sea ice stability, resulting in a shorter period in which polar

271   bears can acquire their year's nutrients, offsetting any thermoregulatory benefits (Robbins et al.,

272   2012).

273   However, direct evidence for energetic and performance consequences of winter

274   warming in homeotherms is scarce. Changes in variables correlated with increased temperatures

275   – such as snow cover, resource availability, and precipitation – make it difficult to isolate the

276   impacts of temperature in observational studies, which form the majority of published work to

277   date. For example, although they presumably provide a thermoregulatory advantage, warm

278   winters reduced maternal investment in reproduction in red deer resulting in smaller offspring.

279   This effect was probably driven by increased costs of locomotion in the deeper snow

280   characteristic of warm winters, rather than increased temperature *per se* (Post et al., 1997). Thus,

281   the impact in this case was driven by an interaction among abiotic drivers (Figure 3).

282   *(b) Effects on development and phenology*

283   In addition to altering energy balance, increased average temperatures during winter

284   generally promote development at times of year when it would traditionally be arrested, leading

285   to earlier spring, and later autumn, phenology for the majority of terrestrial taxa (Figure 3; Jeong

286   et al., 2011; Walther, 2010). These phenological shifts have been particularly pronounced in cold

287   regions such as the Arctic (Høye et al., 2007). However, significant variation exists in

288 phenological plasticity within communities; for example, phenological shifts have been faster at

289 lower trophic levels (Table 1; Both et al., 2009; Thackeray et al., 2010), and within the insects,

290 these shifts are less pronounced in species with specialised diets or that overwinter at earlier life

291 stages (Table 1; Diamond et al., 2011).

292 For primary producers, or animals that are not limited by resource availability,

293 performance is likely to be enhanced by maximally-advanced spring phenology and maximally-

294 delayed autumn phenology (Table 1). Shortening the period of dormancy will allow greater

295 resource accumulation during the growing season, and less energetic stress during winter. If this

296 hypothesis is correct, performance will be enhanced in organisms whose phenology is strongly

297 temperature-sensitive and which can therefore respond to increases in average temperatures by

298 rapid shifts in their growing season. Indeed, the ability to respond to climate change by

299 advancing spring phenology strongly enhances fitness and persistence in plants (e.g. Fridley,

300 2012), presumably by lengthening the growing season and increasing resource accumulation

301 (Pigliucci & Marlow, 2001). A recent evolutionary shift towards later autumn phenology has

302 also been recorded in pitcher plant mosquitoes, implying fitness gains from an extension of the

303 length of the growing season (Bradshaw & Holzapfel, 2001), perhaps because resources are not

304 temporally limited for mosquito larvae feeding on microbes in the contained pitcher plant

305 ecosystem.

306 By contrast, phenological synchrony with crucial resources will likely be more important

307 than growing season or winter length in determining fitness of organisms at higher trophic levels

308 whose resources are temporally limited. This means that the optimal phenotype will depend on

309 the phenology of the neighbouring trophic levels (Table 1). This dependence occurs because

310 variation in phenological shifts can cause community mismatches, wherein resources for higher

311 trophic levels are no longer synchronised with periods of demand. We will discuss the

312 community-level implications in more detail below (section V), but the salient point at the

313 organismal level is that a mismatch between food demand and availability is likely to apply

314 strong selective pressure on higher trophic levels to maintain synchrony with the trophic levels

315 below. Supporting the hypothesis that phenology may evolve to enhance synchrony with the

316 trophic level below, winter moth caterpillars have evolved a later spring hatching date in

317 response to warming, which has increased synchrony with budburst of its host plant (oak), and

318 presumably imparted higher fitness despite a shorter growing season (van Asch et al., 2013).

319   Thus, the pattern of selection on phenology likely differs among trophic levels, with

320 producers or animals for which resources are available year-round experiencing consistent

321 selection for maximal spring advances and autumn delays, while higher trophic levels experience

322 divergent selection pressures that depend on the responses of the trophic level immediately

323 below. This differential selection across trophic levels could explain why the responses of plant

324 phenology to climate change show a strong phylogenetic signal (Willis et al., 2008), while the

325 responses of insect phenology do not (Diamond et al., 2011): consistent selection on phenology

326 in producers preserves the phylogenetic signal, while divergent selection on phenology at higher

327 trophic levels reduces similarities across the phylogeny. Therefore, although it is likely that

328 phenological shifts will alter resource availability and thus energy stress for consumers whose

329 resources are temporally restricted, determining whether the impact will be positive or negative

330 requires consideration of the phenological responses of organisms at lower trophic levels (Figure

331 3, Table 1). Organisms for which seasonal timing is physiologically fixed, and that therefore

332 have inflexible phenology, may suffer the most pronounced negative impacts of changing winter

333 length and timing with climate change (Post & Forchhammer, 2008).

15

334   Many plants and insects have chilling or vernalisation thresholds that must be met before

335   post-winter development can resume. In these cases, warmer winters can slow development,

336   leading to phenological delays (rather than advancement) in spring (e.g. Forrest & Thomson,

337   2011; Luedeling et al., 2011). Most studies report an advance in spring phenology, although

338   these are also intermixed with delays or lack of responses in many systems (Thackeray et al.,

339   2010); these delays are consistent with widespread effects of a reduction in chilling units (Cook

340   et al., 2012). Phenological delays have been well-documented in meadow and steppe plant

341   communities on the Tibetan Plateau, where the beginning of the growing season advanced in

342   response to climate warming for the first half of a 20-year warming period, but was subsequently

343   delayed despite continued climate warming (Yu, Luedeling & Xu, 2010; but see Zhang et al.,

344   2013). These phenological delays are consistent with insufficient vernalisation (too little

345   accumulated cold exposure to end dormancy). However, these observations could also arise

346   from the observed decrease in snow depth over this period, which may have reduced the

347   insulation of the roots and, counter-intuitively, resulted in colder conditions despite warming air

348   temperatures (Yu et al., 2013). There is no way to separate these proximal mechanisms from the

349   available data, although this could be achieved through either autecological experiments on

350   chilling requirements (e.g. Santiago et al., 2013) or experimental snow manipulation (e.g.

351   Groffman et al., 2001).

352   Average temperatures will thus affect energy balance in two ways – directly, through

353   rates of metabolism, and indirectly, through phenology and the resulting length of winter (Figure

354   3). This introduces an important dichotomy in responses to winter climate change among

355   dormant plants and insects: for cold-adapted species with high chilling or vernalisation

356   requirements, increases in winter temperature will increase both overwinter energy use (by

357 increasing metabolic rates) and winter length (by increasing development time). These changes

358 will amplify the deleterious effects of warming for cold-adapted species. If failure to meet

359 chilling requirements decreases the viability of populations, it may prove to be a proximate

360 driver of range contractions at the equatorial range limit in some species. By contrast, for warm-

361 adapted species that do not have chilling or vernalisation requirements, although warming will

362 still increase overwinter energy use, it will also shorten the period of dormancy by advancing

363 spring phenology. This could mitigate the direct negative effects of winter warming on

364 energetics of warm-adapted species.

365

366 (2) Altered thermal variability

367 Winter temperatures fluctuate on multiple temporal scales, ranging from diel temperature

368 fluctuations, through short term cycles associated with weather fronts, to seasonal changes

369 (Deere & Chown, 2006; Gaines & Denny, 1993; Marshall & Sinclair, 2012a; Marshall &

370 Sinclair, 2012b). The magnitude of these fluctuations varies spatially both with microhabitat

371 (Marshall & Sinclair, 2012b), and across larger scales influenced by continentality, latitude and

372 topography. Snow cover will drive much of this variability, so snow cover predictions must be

373 taken into account to determine likely trends in variability in each of these components (Figure

374 2). Changes in the seasonal timing of snow cover will exacerbate altered timing of extreme low

375 temperatures (Figure 2). Changes in thermal variability will impact energy balance, phenology,

376 and cold injury through effects on metabolism, development, and freeze/thaw cycles as described

377 below (Figure 3). Species-specific sensitivity to changes in this variability may be particularly

378 important in determining organisms' responses to winter climate change, although we note that

379 changes in variability are extremely difficult to predict, even when only extreme events are

380   considered (Easterling et al., 2000). There are three salient components of fluctuations in winter

381   thermal conditions: a) the intensity and regularity of extreme high and low winter temperatures;

382   b) the frequency with which temperatures cross important physical thresholds (e.g. the freezing

383   point of water) or biological thresholds (e.g. thresholds for cold-induced damage); and c) the

384   amplitude of thermal cycles on both diel and short-term scales (such as during storm events).

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

386   Extreme low temperature events can cause cold injury, and winter mortality or injury is

387   an important component of demographics for many species (e.g. Aukema et al., 2008; Kanda,

388   2005; Spiegel-Roy & Goldschmidt, 2008; Sutherst & Maywald, 2005). Thus, a reduction in the

389   intensity or duration of extreme winter low temperatures could increase winter and post-winter

390   survivorship (Table 1; e.g. Tran et al., 2007; Trotter & Shields, 2009), directly influencing the

391   poleward or upper altitudinal range limit of a species (e.g. Crozier, 2004; Neuvonen, Niemelä &

392   Virtanen, 1999). However, there are cases where extreme low temperatures do not directly limit

393   population persistence or geographic range. For example, the monophagous holly-leaf miner (an

394   agromyzid fly) is more cold tolerant than its host plant (holly, *Ilex aquifolium*), and its northern

395   range limit in Europe is therefore likely set by the factors that set the host range, rather than

396   directly by extreme low temperatures (Klok, Chown & Gaston, 2003). In such cases,

397   amelioration of extreme low temperatures will not directly affect survival, but could still

398   indirectly lead to range expansion if low temperatures are the primary determinant of resource

399   availability.

400   Changes in thermal variability can modify the timing, predictability and sequence of

401   extreme events over winter. Because many species have life stage-specific tolerance to winter

402   conditions (e.g. diapause-linked cold tolerance in insects, Leather, Walters & Bale, 1993; and

403   aquatic overwintering in adult frogs, Tattersall & Ultsch, 2008), there is potential for changes in

404   the seasonality of extremes to lead to mismatches between the occurrence of extreme events and

405   the behavioural or physiological mechanisms that allow organisms to tolerate them. In

406   particular, organisms with seasonally-programmed responses, or those which irreversibly lose

407   cold tolerance during winter warm spells, will be more vulnerable to unseasonable temperature

408   extremes than those with constitutively high or rapidly-modified tolerances (Table 1). For

409   example, extremely warm mid-winter temperatures cause an irreversible loss of winter

410   acclimatisation and the resumption of development in the emerald ash borer (*Agrilus*

411   *planipennis*, Coleoptera, Buprestidae), making them susceptible to subsequent cold snaps

412   (Sobek-Swant et al., 2012). Extreme warm periods in spring can also lead to breaking of

413   dormancy in plants, with subsequent extreme events killing buds and preventing reproduction or

414   growth the following season, as occurred in the unusual North American springs of 2007

415   (Augspurger, 2009; Gu et al., 2008) and 2010 (Hufkens et al., 2012). Indeed, a 124-year

416   temperature dataset combined with observations of frost susceptibility in Illinois, USA shows

417   that the frequency of damaging spring frost events has increased in recent decades (Augspurger,

418   2013). At the beginning of winter, unusual extreme events before organisms have accumulated

419   programmed physiological protection can also lead to damage. For example, the grass *Bromus*

420   *rubens* may be excluded from the intermountain steppe biome of western North America as a

421   consequence of sudden freeze events in late autumn before the onset of (programmed) winter

422   cold tolerance (Bykova & Sage, 2012). Thus, organisms that develop low temperature tolerance

423   in a programmed fashion (e.g. in response to photoperiod), or that have delayed the onset of

424   winter hardening as part of a phenological shift, may be more vulnerable to changes in the

425   occurrence of extreme events in autumn than organisms that can use temperature as a cue to

426   rapidly increase early winter cold hardiness (Table 1).

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

428   Changes in the frequency, intensity, or duration of extreme events could modify the

429   frequency with which biologically-important thresholds are crossed. For example, the 0 °C

430   threshold delineates the availability of liquid water and the beginning of soil freezing. Similarly,

431   species-specific physiological thresholds exist, such as the temperatures at which ice formation

432   and melting occur; crossing these thresholds can determine sub-lethal impacts (e.g. Marshall &

433   Sinclair, 2010), survival (e.g. Régnière & Bentz, 2007) and overwinter energetics (e.g. Sinclair et

434   al., 2013) In some regions (e.g. maritime-buffered habitats in the southern hemisphere; Chown

435   et al., 2004), temperatures already hover near the 0 °C threshold: increases in mean temperatures

436   will likely reduce the occurrence of freeze-thaw cycles in such environments, reducing the stress

437   of threshold-crossing events. By contrast, increasing mean temperatures (or decreasing snow

438   cover, see below) may increase the incidence of freeze-thaw in northern temperate habitats, and

439   thus may increase the frequency of such transitions.

440   The implications of repeated freeze-thaw are not well-understood, but the impacts appear

441   to be largely negative. In invertebrates, repeated freeze-thaw can lead to a variety of deleterious

442   consequences, due to both cold injury from the repeated cold exposure, and increased energy

443   expenditure during repair and recovery in thaw periods (Marshall & Sinclair, 2012a). In freeze-

444   tolerant *Rana sylvatica* frogs, carbohydrate energy reserves provide both fuel for the energy

445   expended during freezing and the cryoprotectants for survival of freezing itself. In this species,

446   repeated freeze-thaw both depletes energy reserves and reduces cold tolerance, suggesting the

447   possibility for substantial fitness reductions with increased freeze-thaw (Sinclair et al., 2013).

448 Repeated freeze-thaw cycles increase the risk of xylem embolism in conifers due to the

449 expansion of gas bubbles during thawing that were formed upon freezing (Mayr, Gruber &

450 Bauer, 2003). Increased intensity or frequency of soil freeze-thaw cycles can increase the lysis of

451 soil microorganisms and damage to plant roots, intensifying leaching and trace gas losses of soil

452 nutrients (Groffman et al., 2001).

453   In some cases, the impacts of repeated events such as freezing may not be cumulative.

454 For example, elevated losses of soil nutrients may only occur in response to exceptionally severe

455 frost soil events, and pools of frost-vulnerable materials in the soil are finite. Once the bulk of

456 soil nutrients in these frost-vulnerable pools have been released, subsequent events may not

457 result in further loss (Matzner & Borken, 2008). Thus, increased frequency of freeze-thaw can

458 have detrimental effects in organisms for which the responses are cumulative, but for organisms

459 or systems where the impact of repeated cold exposure reaches an asymptote (e.g. nutrient

460 leaching), the impacts of repeated events may be less important (Table 1). However, at this point

461 too little is known about the impacts of repeated stress (or about interactions among multiple

462 stressors) to allow generalities to be constructed.

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

464   Increases in daily thermal variability can increase rates of metabolism and photosynthesis

465 in poikilotherms (Figure 3), because of the curvilinear relationship between temperature and

466 most biological rate processes. Jensen's inequality is a mathematical property of nonlinear

467 functions, which states that the mean of a nonlinear response variable cannot be predicted based

468 on the mean of the driver variable alone, but requires knowledge of the variability of the driver

469 variable and the shape of the response function (Ruel & Ayres, 1999). For example, if the

470 response function is accelerating over the range of temperature fluctuations (as is frequently the

471   case with metabolic rate in ectotherms), the mean of the response variable will be elevated

472   compared to its value at the mean temperature, and increasing thermal variability will further

473   increase the mean of the response variable, even without a corresponding increase in the mean

474   temperature. Thus, increases in thermal variability have the potential to exacerbate the impacts of

475   an increase in mean temperature on metabolism (Ruel & Ayres, 1999). Additionally, thermal

476   performance curves are asymmetric (fitness rapidly declines above the thermal optimum;

477   Angilletta, 2009), and thus Jensen's inequality means that the impact of changes in temperature

478   will also be asymmetric: temperatures above the thermal optimum will reduce fitness far more

479   than temperatures an equal amount below the thermal optimum.

480   This effect of Jensen's inequality can be exacerbated or mitigated by modifying the shape

481   of the rate-temperature relationship: a steeper curve (i.e. higher temperature sensitivity) will lead

482   to a more pronounced impact (Ruel & Ayres, 1999), suggesting that organisms with high

483   temperature sensitivity or thermal optima that are close to environmental temperatures will

484   experience greater impacts of changes in thermal variability (Table 1; Foden et al., 2013).

485   Exacerbated thermal variability will therefore allow potentially-active ectotherms to take better

486   advantage of warm spells during winter fluctuations. However, lower thermal sensitivity will

487   reduce vulnerability to thermal variation, for example in energy-conserving overwintering

488   ectotherms (Williams et al., 2012b). Thus, short-term (e.g. daily) thermal variability likely

489   exerts a strong selective pressure on temperature-rate relationships in ectotherms and plants,

490   however, few studies to date have examined the impacts of daily thermal variability on

491   overwintering organisms.

492   For dormant organisms, thermal variability will thus be an important determinant of

493   overwintering energy use, particularly at winter's peripheries when temperatures are relatively

494 warm and variable. In this context, seasonal timing will be a critical determinant of a species'

495 susceptibility to overwinter energy drain resulting from alterations to thermal variability.

496 Species that enter dormancy early in the autumn will experience significant energy drain as a

497 result of delayed winter onset, and an increase in thermal variability during autumn will thus

498 exacerbate this energy drain because of Jensen's inequality (e.g. Sinclair et al., 2013; Williams et

499 al., 2012b). By contrast, species with delayed spring emergence, including insects such as

500 *Rhagoletis pomonella* that infest summer-fruiting trees (Feder, Hunt & Bush, 1993), will likely

501 be more susceptible to earlier, more variable, and warmer springs. By contrast, increased

502 buffering (e.g. due to longer snowpack persistence; Decker et al., 2003) might reduce variability,

503 mitigating the impact of the longer post-winter period.

504   Flexibility of the thermal sensitivity of biological processes or phenology will therefore

505 be a key determinant of the outcome of changing thermal variability during winter and its

506 associated dormancy (Figure 4). Suppression of thermal sensitivity of metabolism mitigates the

507 impact of increased thermal variability (Williams et al., 2012b). In herbivores, for which entry

508 into dormancy is likely mediated by a decline in host plant quality (Prior et al., 2009), such

509 plasticity is essential, but may not fully compensate for increased autumn variability (Williams et

510 al., 2012b). In many species, the onset of dormancy is controlled hormonally and entrained to

511 photoperiod (Tauber et al., 1986), apparently reducing the capacity for flexibility because of the

512 programmed nature of the response. However, evolutionary changes in the induction of

513 dormancy as a result of climate change have been observed in a photoperiod-cued pitcher plant

514 mosquito (Bradshaw & Holzapfel, 2001). Similarly, butterfly larvae show state-dependent

515 responses to photoperiod, allowing facultative shifts in dormancy onset and behaviour both

516 before and after dormancy to buffer the impact of reduced growth capacity at higher latitudes

517   (Gotthard, Nylin & Wiklund, 1999; Gotthard, Nylin & Wiklund, 2000). It is conceivable that

518   such plasticity could also act to mitigate the impacts of winter energy drain.

519

520   [Figure 4 here]

521

522   Overall, while it is clear that the frequency, timing and amplitude of temperature

523   variability dictate the severity of winter's effects on organisms, the examples presented above

524   derive primarily from studies on insects. For organisms with more resilient or resistant

525   overwintering stages (e.g. plant seeds) these effects may be less severe. The ultimate influence

526   of extreme winter temperature events on populations, communities and ecosystems will be a

527   function of both the severity and frequency of these events, and extremely severe events may

528   only occur infrequently. However, extreme events that lead to threshold changes in community

529   trajectories will remain influential over the longer term (Kreyling, Jentsch & Beierkuhnlein,

530   2011).

531

532   (3) Changing snow cover

533   The strong influence of snow cover on the soil and subnivean microclimate (Figure 2;

534   Decker et al., 2003; Henry, 2008; Pauli et al., 2013) has important consequences for the

535   condition and survival of organisms that overwinter in these environments, and as a result,

536   changes in snow cover with climate change can result in many different biological impacts

537   (summarised in Table 2). Because snow is an effective insulator, reduced snow cover can

538   expose soil systems to more extreme low temperatures (Brown & DeGaetano, 2011), described

539   by Groffman et al. (2001) as 'colder soils in a warmer world', which in turn can increase

540   mortality for organisms overwintering in or on the soil. Beetles overwintering in the soil beneath

541   snow in the US prairies had higher survival than those that overwintered in soil with snow

542   removed, but this difference in survival was only seen in relatively cold winters (Joshi, Olson &

543   Carey, 2009), and the number of times per month that New Zealand alpine cockroaches were

544   predicted to freeze and thaw ranged from zero to more than 20, depending on snow cover

545   (Sinclair, 2001). Lemming nest density was positively correlated with snow depth when snow

546   cover was experimentally manipulated, presumably because the deep, dry snow layer buffered

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

25

563 consumption (Figure 3). For example, gall flies overwintering below the snow have increased

564 energy consumption compared to those above the snow (Irwin & Lee, 2003). Snow cover thus

565 strongly influences levels of energy stress and cold injury indirectly, through its effects on

566 temperature (Figure 3), and changes in local patterns of snow cover therefore have the potential

567 to alter habitat suitability on a very small scale.

568 Snow also impacts organisms directly by modifying the physical environment: both the

569 quantity and the quality of snow can have profound effects, particularly on the biology of winter-

570 active mammals. While the effects of changing snow cover can be assessed experimentally for

571 sessile or small organisms (e.g. Groffman et al., 2001; Reid et al., 2012), the limited spatial scale

572 of most snow manipulation experiments makes it difficult to assess snow depth effects on large

573 or highly mobile animals under controlled conditions. Nevertheless, observational studies can be

574 used to correlate biological responses to interannual variation in snow depth. For example,

575 wolves form larger packs in response to deeper snow (Post et al., 1999), but increased snow

576 depth also reduces mobility of their deer prey (Fuller, 1991). Reduced snow cover may also

577 increase resource availability for winter-active predators and browsers by improving access to

578 food (Figure 3; Martin & Maron, 2012) – which necessarily means that decreased snow also

579 increases predation risk for small mammals which have less protection from predators and

580 extreme temperatures (Yoccoz & Ims, 1999). However, the impacts of changing snow cover are

581 complex: declining snow cover in Canada is associated with decreased wolverine population

582 growth rate; the causal factors for this decline likely include reduced denning sites, decreased

583 prey success and reduced snow-related mortality of the ungulates upon whose carcasses

584 wolverines scavenge (Brodie & Post, 2010). Snow quality, determined more-or-less directly by

585 temperature, also determines the winter performance of many organisms, as changes in the

586 density of snow modifies its insulative properties and affect locomotion, while ice layers can

587 modify access through the snowpack. For example, increased frequency of rain on snow events,

588 and subsequent ice-up, blocks access to food for herbivores such as reindeer (Hansen et al.,

589 2011) and small mammals (Kausrud et al., 2008; Korslund & Steen, 2006).

590   The timing of snow lie is also critical for many organisms, but the direction of impact

591 strongly depends on species' traits. Early snowmelt can have positive effects for large browsers

592 such as reindeer, which produce calves with increased body mass in the autumn following an

593 early spring snowmelt (Pettorelli et al., 2005). However, if early snow melt causes the

594 resumption of activity before resources are available or interrupts winter feeding opportunities,

595 the effects can be detrimental: early snowmelt can result in food scarcity for hibernating

596 mammals, such as marmots, that emerge early in response to warmer air temperatures, but before

597 the spring flush of plant growth (Inouye et al., 2000), and early ice breakup increases mortality in

598 polar bear by reducing the length of the winter feeding season and increasing the length of the

599 summer fast (Regehr et al., 2007). By contrast, increased spring snowstorm activity with climate

600 change in some regions can lead to delayed snowmelt, delaying the emergence of ground

601 squirrels and reducing their fitness by reducing the length of the active season (Lane et al.,

602 2012). However, organisms that overwinter in subnivean spaces in very cold environments may

603 benefit from an extension to the protective insulation of snow – for example, peak floral

604 abundance of montane plants is increased after delayed snow melt, due to decreased frost

605 damage in spring (Inouye, 2008).

606   Mid-winter snowmelt caused by extreme events (best-studied because of their effect on

607 hydrology; e.g. Kurian, Lautz & Mitchell, 2013) will not only affect overwinter soil temperatures

608 (see above), but also provide liquid water for plants and animals that might otherwise suffer from

609   a water deficit, such as hibernating mammals (e.g. Ben-Hamo et al., 2013). Conversely,

610   increased free water may increase rates of heat loss and risk of flooding, decreasing survival of

611   small mammals (Kausrud et al., 2008). In Greenland, warmer summers result in the

612   accumulation of cold meltwater, delaying flowering and shortening the flowering period of

613   several angiosperms (Høye et al., 2013). These roles of liquid water in determining winter

614   physiology and spring phenology in terrestrial systems during winter have received little

615   attention, so the trade-off of negative and positive effects for organisms remains a matter for

616   speculation.

617

IV. Links between winter and summer responses to climate change

619   The condition of organisms emerging from the winter will determine their performance

620   during the growing season, and similarly their growing season performance will determine their

621   condition going into the winter and subsequent winter performance (Figure 5). Taking a cross-

622   seasonal perspective will therefore be necessary to identify negative impacts of climate change.

623   For example, advanced spring phenology and increased spring abundance of a perennial herb in

624   Britain resulted from winter warming, but this was tempered by a decrease in reproductive

625   output by those plants (Fox et al., 1999). Similarly, early snow melt increased survival in

626   conifers, but at the expense of growth rates (Barbeito et al., 2012). Where data on post-winter

627   performance are lacking, links from winter condition to the growing season may often be

628   inferred. For example, winter energy use can determine adult body size in butterflies (Williams

629   et al., 2012a), and the clear size-fecundity relationship in female butterflies (Boggs & Freeman,

630   2005) implies a fitness consequence of this winter effect. The resilience of organisms to winter

631   energetic stress can also be determined by post-winter processes (Table 1), with resilience

632   decreased in organisms with limited opportunities for post-winter resource acquisition (Breed,

633   Stichter & Crone, 2013), or for which juvenile-derived reserves are essential for reproduction

634   (Irwin & Lee, 2003).

635

636   [Figure 5 here]

637

638   If responses to climate change improve pre-winter condition, winter performance may be

639   enhanced. For example sub-alpine yellow-bellied marmots have advanced their phenology in

640   response to recent climate change, which allows increased resource accumulation and growth

641   and, consequently, increased overwinter survival and population growth rates (Ozgul et al.,

642   2010). Presumably, such positive impacts of longer growing seasons will help to buffer negative

643   impacts of winter climate change, although few data exist to address this hypothesis. However,

644   some changes to growing season physiology may have negative effects on winter performance.

645   For example, damselfly larvae that grow rapidly during the growing season do so at the expense

646   of winter cold tolerance (Stoks & De Block, 2011), although this trade-off was not apparent in

647   butterflies (Karl et al., 2013), underlining the likelihood that the relationship between summer

648   and winter will be complex and species-specific.

649   In Figure 5, we conceptualise the potential biological impacts of winter climate change

650   on a species in an inter-seasonal context. We assume that reproduction and growth occur outside

651   of winter – modification will be necessary for species that reproduce in winter. In Figure 5, the

652   winter variables that affect an organism are represented by 'Winter', while 'Mortality',

653   'Resources' and 'Sub-lethal damage' represent the outcomes of the biological processes and

654   stresses in Figure 3. Figure 5 can be used in two ways. First, it can be used in conjunction with

655   our framework describing the impacts of winter on a species' biology (Figure 3, Table 1) to

656   identify areas in which further research is required. Second, by determining the causal links and

657   strengths of the relationships shown, it can be used to determine the relative importance of

658   different aspects of winter in determining how a species' vulnerability to overwinter conditions

659   plays out in the growing season and affects fitness.

660   The relationships between post-winter condition, growing season performance (and

661   reproduction) and pre-winter condition are already known for many species, thanks to the

662   preponderance of growing-season studies. Winter mortality has been well-explored for many

663   species (Aars & Ims, 2002; Hodges et al., 2006; Roland & Matter, 2013; Stahl et al., 2006), but

664   data are lacking regarding the sub-lethal impacts of winter, mediated through resource

665   consumption and damage, and the effects of these sub-lethal impacts on growing season

666   performance. Moving forward, the direct relationships between winter conditions and growing

667   season performance need to be explored further across many taxa (see Kreyling (2010) for a

668   plant-focused discussion of this point), as does the extent to which vulnerability to summer

669   changes may exacerbate or negate vulnerability to winter changes.

670

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

672   The direct effects of winter climate change on individual organisms will combine and

673   synergise with competitive interactions to influence demography. Positive impacts of winter

674   climate change, in the form of decreases in winter mortality, may be balanced or cancelled out by

675   a corresponding increase in intra-specific competition. For example, early snow-melt and

676   increased availability of forage decreased overwinter mortality in reindeer, which increased

677   competition and slowed population growth (Tyler, Forchhammer & Øritsland, 2008). Winter

678   climate change can affect population dynamics both directly and indirectly via different

679   mechanisms. For example, in an alpine butterfly, delayed snow melt directly increased

680   population growth by increasing recruitment the subsequent year, and indirectly increased

681   population growth by increasing the peak abundance of the butterfly's floral resources (Boggs &

682   Inouye, 2012). Climate change-related shifts in population densities and processes at the leading

683   and retracting range edges (Hill, Griffiths & Thomas, 2011) lead to well-documented poleward

684   range shifts, especially in butterflies (Chen et al., 2011b; Hill et al., 2002; Parmesan et al., 1999).

685   In some cases, climate-driven range shifts have been directly attributed to changes in winter

686   climate (Berger et al., 2007; Crozier, 2004). Conversely, differential susceptibility to winter

687   climate change among populations could also reduce performance in peripheral populations

688   (Pelini et al., 2009), leading to range contractions in some species.

689   At community scales, complex multi-trophic interactions can drive the effects of climate

690   change on individual species. Alterations to the abundance of plants or animals as a result of

691   changes in mortality or phenology can be propagated through communities via consumer-

692   resource interactions. For example, in a deciduous forest, increased winter herbivory by elk as a

693   result of decreased snow cover depresses plant and associated bird communities throughout the

694   year (Martin & Maron, 2012). A deeper snow pack in the Great Lakes region of the USA

695   increases hunting success of wolves leading to reduced moose populations, which releases fir

696   trees from heavy browsing and increases the fir understory (Post et al., 1999). In turn, these

697   changes in understory composition and browsing could depress soil respiration rates (Persson et

698   al., 2009). Community interactions can modify and even reverse the effects of climate change on

699   individual species. For example, winter-induced changes in herbivory can prevent shrub

700   expansion in Arctic tundra (Olofsson et al., 2009). In ecosystems where predator populations are

701   subject to bottom-up control due to resource limitation, negative effects of winter climate change

702 on prey may extend to higher trophic levels. Winter climate change has decreased plant

703 production and forage quality, leading to declines in herbivore fitness (Awmack & Leather,

704 2002; Bokhorst et al., 2012b), and the collapse of Arctic lemming population cycles has

705 decreased the population growth of several predator species (Gilg, Sittler & Hanski, 2009;

706 Schmidt et al., 2012). Conversely, direct impacts of winter climate change on overwintering

707 carnivores may lessen predation pressure on prey species, with community-wide consequences

708 (Estes et al., 2011), although few examples of such climate-induced trophic cascades in a winter

709 context – perhaps because such studies have focused on Arctic and boreal habitats. These multi-

710 trophic interactions make it imperative to predict the direct impacts of winter climate change on

711 species that exert strong top-down or bottom-up control within their communities, perhaps aiding

712 to identify focal species for winter study.

713 As we have shown, winter affects different species in different ways. Thus, dissimilar

714 responses to winter climate change by different species can exacerbate phenological mismatches,

715 reconfiguring community interactions (Van der Putten, Macel & Visser, 2010). For example,

716 winter climate change has led to earlier spring leaf-out and caterpillar emergence in European

717 oak forests, decreasing synchrony of (caterpillar) food supply with peak feeding times in

718 passerine birds (Both et al., 2009). Similarly, the plant growing season has advanced faster than

719 the timing of the caribou migration to Arctic breeding grounds, resulting in increasing calf

720 mortality and lower calf production (Post & Forchhammer, 2008). By contrast, climate change

721 has actually improved host plant-herbivore synchrony in a sub-Arctic moth-birch system.

722 Previously, birch bud burst occurred too early for moth larvae to feed on young (palatable)

723 leaves. However, moth phenology has advanced more rapidly than birch in response to shorter

724 winters, which has improved synchrony and enabled moth larvae to exploit this new resource

725   (Jepsen et al., 2011). In extreme cases such as irruptive outbreaks of the (winter-limited)

726   mountain pine beetle, winter climate change has contributed to altering landscape-level

727   processes: beetle infestation modifies tree survival and species composition, ultimately

728   converting forests in British Columbia from net carbon sinks to a source of carbon (Kurz et al.,

729   2008).

730   The links addressed in Figure 5 can be extended to processes that occur at the community

731   or ecosystem scale. In doing so, additional links must be added to account for species

732   interactions such as competition, and ecosystem processes that determine seasonal changes in

733   resource availability. For example, Figure 6 (based on Sturm et al., 2005) describes potential

734   feedbacks between changes in snow cover, nutrient availability and plant species composition in

735   the Arctic. In this scenario, climate warming is expected to promote shrub expansion into

736   graminoid communities, increasing the trapping of snow. Increased depth and duration of the

737   snowpack can then increase nitrogen availability over winter by increasing soil microbial

738   activity, and because the shrub canopy is above the snow layer, bud-burst and photosynthesis can

739   occur earlier than in the low-statured graminoids, allowing the shrubs to access late-winter

740   nitrogen pulses. Decreased nitrogen availability over summer, enhanced by increases in low

741   quality, woody shrub litter, coupled with increased shading by shrubs, further reduce the

742   competitive abilities of the graminoids. In contrast to the latter example, extremely low spring

743   snow accumulation is projected to occur over much of the Northern Hemisphere, with >80 % of

744   years below the baseline minimum in some areas by 2080–2099 (Diffenbaugh & Field, 2013).

745   The resulting decreases in melt water in spring, coupled with increased evapotranspiration and

746   decreased summer rainfall in some regions, will increase summer drought severity.

747   As we have demonstrated in this section, understanding the interactions between climate

748 and biotic processes is essential for predicting how ecosystems will respond to climatic warming

749 (Blois et al., 2013). Moving forward, integrating the responses of organisms across entire

750 ecosystems, while taking into account linkages between winter and summer responses to climate

751 change, and differing capacity to evolve, is a daunting task. This task will be facilitated by *a*

752 *priori* identification of the key vulnerabilities to winter climate change, a process which is

753 described in the following section.

754
755 **VI. Predicting vulnerability to winter climate change**

756   It is clear that winter is an important driver of biological processes and organismal

757 fitness, and that winter climate change has the potential to significantly impact individuals,

758 populations, community interactions and ecosystem processes. However, if a goal of global

759 change research is to offer predictive power to facilitate risk assessments and management

760 decisions, then it is necessary to identify which species and processes will be vulnerable to

761 changing winters.

762   Williams et al. (2008) proposed an integrative framework to identify and prioritise

763 species that are vulnerable to climate change, where vulnerability was defined as susceptibility of

764 a system to change – in most of our cases, the primary 'system' we consider is an individual or

765 population. The authors distinguished between factors determining exposure to a change in

766 climate, and those determining sensitivity to those changes. In their framework, exposure was

767 determined by the degree of regional climate change, filtered through microclimatic buffering

768 due to habitat choice. For example, if temperatures are rising, a species that does not have the

769 capacity to change microhabitat choice or alter thermoregulatory behaviour will be exposed to an

770 increase in temperature, whereas a species that can buffer these regional changes will not

771   (Kearney, Shine & Porter, 2009). In the context of winter, the three primary drivers of changing

772   snow cover, thermal variability, and shifts in mean temperature interact with overwintering

773   biology to modify the stresses that will be experienced: thus we must understand the causal

774   relationships between the drivers that determine exposure to winter climate change. Figure 3 can

775   be used as a framework for determining exposure to stress resulting from winter climate change,

776   although such predictions are still dependent on predicting changes in the drivers from climate

777   data and models – a major challenge given the discrepancy between the size of organisms and

778   the scale at which climate data are collected (Potter, Woods & Pincebourde, 2013), and the lack

779   of information about the timeframes over which selection will modify winter phenology and

780   physiology.

781   Assuming that we can accurately assess an organism's exposure to climate change, the

782   next step is to determine whether it will be sensitive (i.e. experience negative impacts). Williams

783   et al. (2008) suggest that sensitivity is governed by intrinsic ecological, physiological or genetic

784   traits of the focal species that determine levels of resilience (the ability of a species to survive

785   and recover from a negative impact) and adaptive capacity (the capacity for plastic or

786   evolutionary changes to reduce negative impacts). Related to the capacity for adaptation, we

787   note that estimates of the strength of selection encountered by organisms in winter environments

788   are an essential component of a predictive framework, but to date few studies have measured

789   such selection gradients (Boratynski et al. (2010) provide one example of this). In using Figure 3

790   as a framework, it is possible not only to identify the potential exposure to stress resulting from

791   changes in the drivers, but because it makes clear (some of) the causal links between the drivers

792   and organismal fitness, it allows the identification of end traits – and the design of simple

793   experiments – that facilitate an assessment of the susceptibility of organisms to changes in those

794 drivers. For example, there are clear links between overwintering temperature and energy

795 consumption for many overwintering ectotherms. It is thus possible to design a simple

796 experiment (e.g. keep overwintering stages of several species at several temperatures; Williams

797 et al., 2012a) to compare susceptibility of energy use to changes in temperature. Similarly,

798 experimental designs are now well established for determining impacts of repeated stress

799 exposure (Marshall & Sinclair, 2012a), addressing the impacts of shifting variability or snow

800 cover – although the results of such experiments are not necessarily easy to interpret. For

801 example, repeated freezing in overwintering caterpillars saves energy (Marshall & Sinclair,

802 2012b) but has other sub-lethal impacts (Marshall & Sinclair, 2011). Thus, a reductionist

803 approach can be used to identify or rule out susceptibility to certain drivers of climate change

804 relatively rapidly, but more complex experiments are necessary to understand interactions among

805 drivers.

806 More generally, it is possible to identify some of the general traits that render individuals

807 or populations of a species vulnerable (or resilient) to winter climate change (Table 1). As with

808 all sensitivity to climate change, species that have high rates of reproduction and short lifecycles,

809 large range sizes (but not large spatial scales of operation), and high dispersal will be less

810 vulnerable to change (Williams et al., 2008). However, the links in Figure 3 allow the

811 identification of winter-specific traits that lead to vulnerability; some of these are outlined in

812 Table 1, and are grouped according to energy balance (e.g. thermoregulatory strategy,

813 metabolism), phenology (e.g. chilling requirements, overwintering stage), cold injury (e.g. cold

814 tolerance, response to repeated stress), water balance and predation (e.g. trophic position,

815 predatory avoidance strategies).

816   Despite extensive evidence from individual cases for the importance of trophic dynamics

817   in determining overwinter responses, they remain difficult to predict. Community-level

818   experiments are inherently complex and limited in spatial and temporal scope, while the use of

819   population-based data to construct dynamic models of communities is typically inadequate for

820   predicting responses to novel combinations of drivers, even in the growing season (Abrams,

821   2001). This complexity is intensified when the relative performances of organisms both over

822   summer and winter must be taken into account, but we propose that the species-based *a priori*

823   approach, based on the drivers and vulnerabilities identified in Table 1 and Figure 3 can be used

824   to identify key impacts of winter. If combined with an understanding of the community

825   interactions in a system, it is possible to at least identify potential responses to winter climate

826   change at the community level.

827

828   **VII. A call to further integrate winter into climate change research**

829   Winter imposes a severe selective pressure that determines fitness, drives many

830   ecological processes, and shapes the evolution of organisms. The pressing need to understand

831   the mechanisms underlying biological responses to climate change, coupled with the rapid

832   changes in winter conditions, together provide a strong imperative to unravel the complexities of

833   responses to winter at the individual, community, and ecosystem scales, and to determine general

834   patterns describing vulnerability to negative impacts. To integrate this information we must

835   combine theoretical and empirical approaches and synthesise across taxa, levels of organisation,

836   and climate drivers.

837   For theorists, the challenge lies in incorporating winter into models that tend to have

838   forms and parameters associated with growth and assimilation, rather than dormancy and

839   consumption (although there is scope for the latter in Dynamic Energy Budget models; Sousa et

840   al., 2010). Mechanistic models of winter biology exist for some species, and the form of some of

841   these models may be incorporated into existing frameworks, and potentially expanded to include

842   additional aspects of winter climate change. For example, Régnière and Bentz (2007) have

843   provided a robust model of the dynamic shifts in cold tolerance of overwintering mountain pine

844   beetles, although this model does not incorporate any sub-lethal impacts of cold exposure.

845   Because it is likely that the existing relationships between climate variables will be disrupted

846   (Jackson et al., 2009; see also Figure 2), functional or phylogenetic approaches may be powerful

847   alternatives to existing niche models (Buckley & Kingsolver, 2012) by using existing studies to

848   infer potential impacts of combinations of winter drivers that may be novel for a given species or

849   population. However, data regarding the effects of winter conditions on fitness is sparse and

850   diffuse, and not necessarily in a model-ready format. Trait databases such as iPlant (Goff et al.,

851   2011) may provide a source of such information, but theorists and empiricists will need to work

852   together to identify the key traits that will inform vulnerability to winter climate change, using

853   approaches similar to those outlined in Figure 3 and Table 1.

854   To inform this theoretical effort, empiricists need to collect more data on the performance

855   and, ultimately, fitness consequences of projected changes in winter climate drivers. Such an

856   understanding requires integration across levels of organisation and from regional to single-

857   organism scales; this entails a shift in focus to populations rather than species, metres rather than

858   miles, and minutes rather than months. A lofty goal for mechanistic studies of overwintering

859   biology is the development of general principles that describe how organisms respond to winter,

860   and the ability to predict – *a priori* – which species will be most vulnerable to winter climate

861   change. To accomplish this we must extend more laboratory studies into the field, which will

862   require methodological limitations and biases to be overcome. For example, methods for

863   simulating winter climate change in the field, such as snow fences, snow removal, heated soil

864   cables and overhead heaters, are often plagued by artifacts or scaling limitations (Shen & Harte,

865   2000). Similarly, there is a need to expand the geographic and taxonomic focus of winter

866   biology. There has been a disproportionate focus on relatively cold environments with long

867   winters (such as the high arctic) relative to temperate systems (Kreyling, 2010), and there have

868   also been asymmetries in research between the northern and southern hemispheres, which may

869   also bias our understanding of the key aspects of winter (Chown et al., 2004). Throughout this

870   review, it is apparent that the bulk of the literature on some broadly-applicable topics is

871   constrained to certain systems; for example, many studies of winter climate change at the

872   community and population levels have been conducted on arctic mammals, but few on temperate

873   insects, whereas a disproportionate amount of research has been conducted on the physiological

874   responses to freezing of temperate insects and crop plants. Finally, there is a need for substantial

875   effort documenting fall and winter events complementing the successful and ongoing

876   documentation of changes in spring phenology and growing season biology. We particularly

877   encourage a concerted effort to expand existing, well-characterised, systems into the winter to

878   develop a more holistic view of how organisms, communities, and ecosystems will respond to

879   climate change.

880

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.

(2) The main abiotic drivers of biological responses to winter are the mean and

variability of air temperatures and the extent and timing of snow cover. All of these

are being affected by climate change in a regionally-specific manner.

(3) Understanding the links between abiotic change and organismal performance is

important for determining organismal vulnerability to climate change. This will

require a mechanistic and integrative approach.

(4) Responses to winter conditions are not isolated from growing season responses to

climate. Therefore it is important to investigate the impacts of winter on

performance, fitness and biotic interactions in the context of growing season biology.

We suggest that an opportunity exists to extend existing long-term studies of growing

season biology to incorporate the effects of winter.

(5) At the population and community levels, inter- and intra-specific interactions strongly

influence responses to winter climate change. Impacts on individual species will

propagate through ecosystems, and the role of winter in modifying these interactions

must be considered when predicting the ecological impacts of climate change.

IX. Acknowledgements

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1383

1384   **Figure Captions**

1385   **Figure 1** - Projected winter climate change in terrestrial systems over the next century. Predicted

1386   January (northern hemisphere) or July (southern hemisphere) differences between 2090-2099

1387   and 2000-2009 in (A) mean surface air temperature and (B) total precipitation. Tropical regions

1388   (23°S to 23°N) that do not experience winter are in grey. Predictions are from the HADCM3

1389   model, A2 scenario (Lowe, 2005); means for each cell over the early time period were subtracted

1390   from the means for the late time period to give projected changes.

1391

1392   **Figure 2** – Examples of the effects of changes in air temperature and snowfall on snow depth

1393   and soil temperature during winter. (A) Current climate. Note that snow cover buffers soil

1394   temperatures. (B) increased mean air temperature results in increased soil freeze-thaw cycles

1395   during a mid-winter melt because the soils become exposed to warm air temperatures during the

1396   day and freezing air temperatures at night. (C) scenarios whereby increased air temperature

1397   variability modifies soil freezing. In late fall, an early frost exposes soil to cold air prior to

1398   development of the snowpack. Warm spells in either mid-winter or early spring melt the

1399   snowpack, leaving soils vulnerable to subsequent drops in air temperature. Finally, snow melt

1400   can be accelerated by increased diel air temperature variability. (D) reduced winter precipitation

1401   leads to increased soil freeze-thaw cycles following a mid-winter melt and during spring melt as

1402   a result of reduced snow cover at these times.

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1404   **Figure 3** - A blueprint for predicting the biological impacts of winter climate change on

1405   terrestrial organisms. Abiotic drivers of winter climate change (black circles) alter physiological,

1406   biotic or abiotic processes (white, light grey and white rectangles respectively) leading to

1407 biological impacts (white hexagons). Signs on arrows indicate the direction of the relationship,

1408 and can be navigated with reference to Table 1 and examples in the text. The dotted line

1409 indicates that decreases in snow and ice occur in response to increased macroclimatic

1410 temperatures; all other relationships occur within organisms' microclimates.

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1412 **Figure 4** - The relationship between winter energy use and phenology for dormant organisms. A

1413 longer winter (early onset of or later exit from dormancy) results in higher energy use. Winter

1414 climate change is increasing total energy use through increases in means or variability of

1415 temperatures (effectively elevating the entire surface, not shown), and organisms have responded

1416 to this in three ways: A) increasing the degree of metabolic suppression over winter, and thus

1417 lowering energy costs (e.g. the duskywing caterpillar *Erynnis propertius*; Williams et al., 2012b);

1418 B) delaying the onset of entry into dormancy, thus reducing the period of pre-winter energy drain

1419 (e.g. the pitcher plant mosquito *Wyeomyia smithii*; Bradshaw & Holzapfel, 2001); and C)

1420 advancing the date of exit from dormancy, to take advantage of opportunities to feed and reduce

1421 winter energy drain (e.g. the yellow-bellied marmot, *Marmota flaviventris*; Ozgul et al., 2010).

1422

1423 **Figure 5** – Integrating winter processes into growing season biology. This assumes that

1424 reproduction (which determines fitness) occurs in the growing season, but could be modified for

1425 other life histories. The black diamond 'winter' represents the abiotic conditions that are

1426 experienced during winter, and the three white boxes are the outcomes of biological processes

1427 and stresses described in Figure 1 and Table 1. These processes affect post-winter condition,

1428 which affects growing season performance (all growing season processes are combined in this

1429 framework), which in turn determines the pre-winter condition of organisms. The strength and
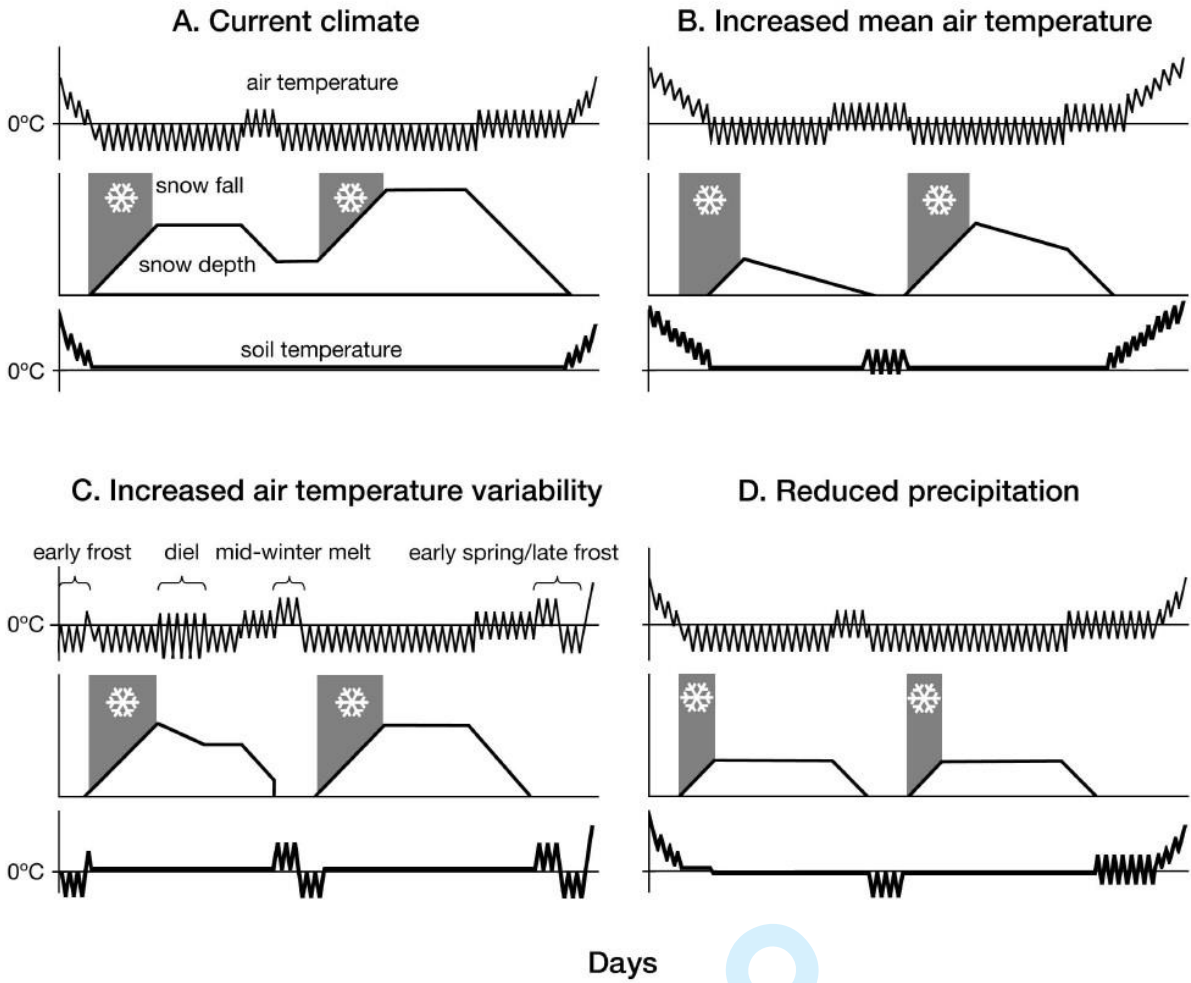
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1430   importance of these links will depend on life history and the extent to which summer and winter

1431   stresses exacerbate or negate one another.

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

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

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

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

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

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1441   Figure 1

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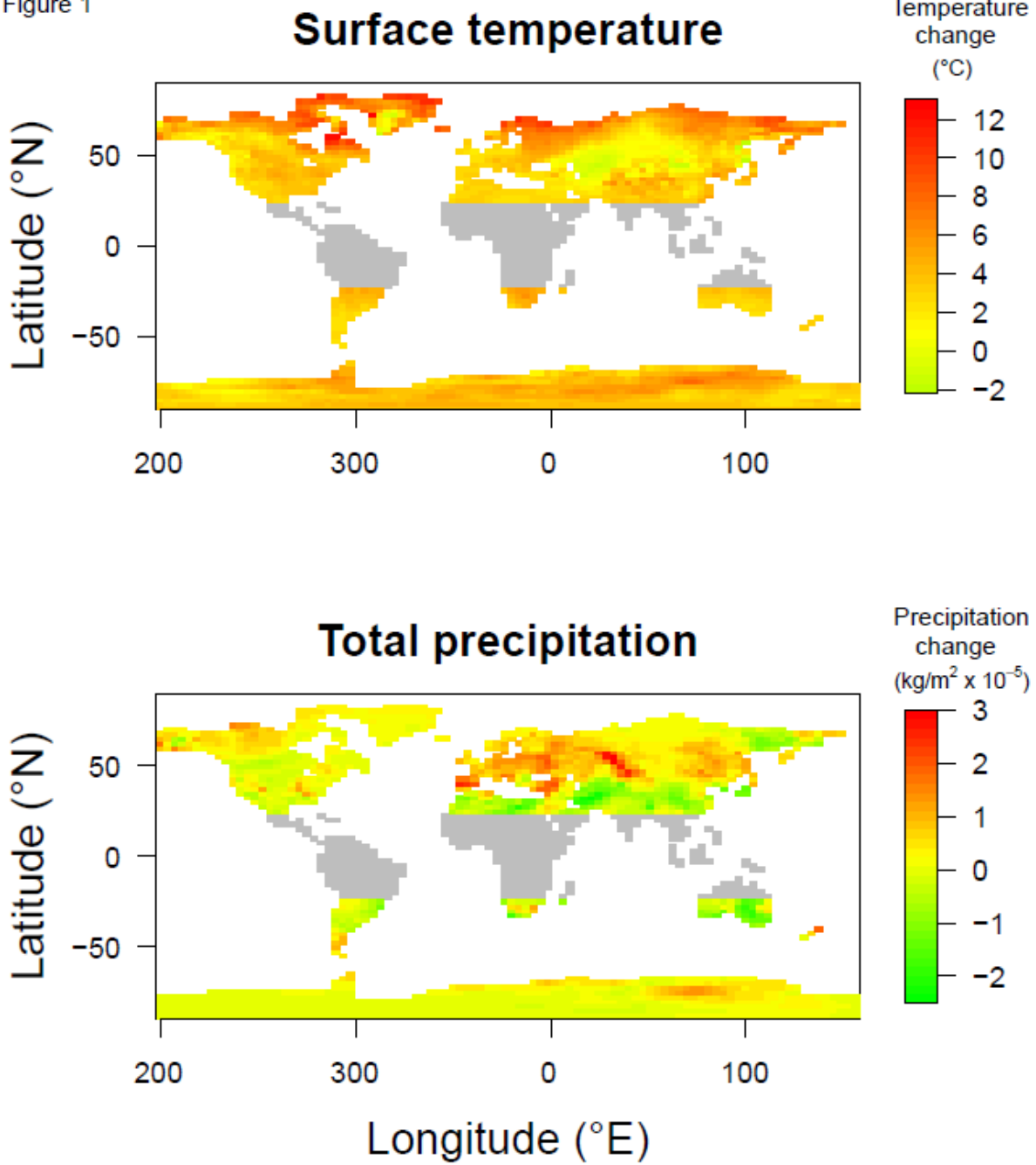
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1445   Figure 2

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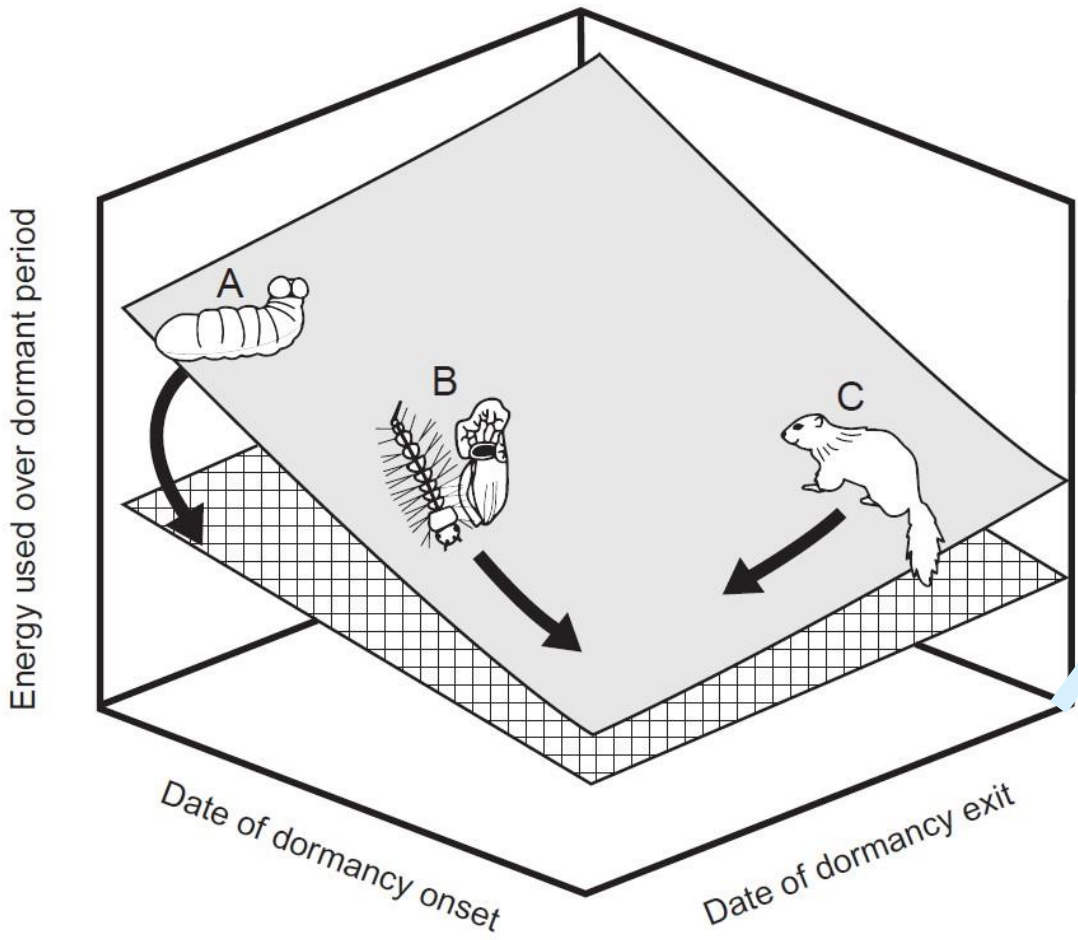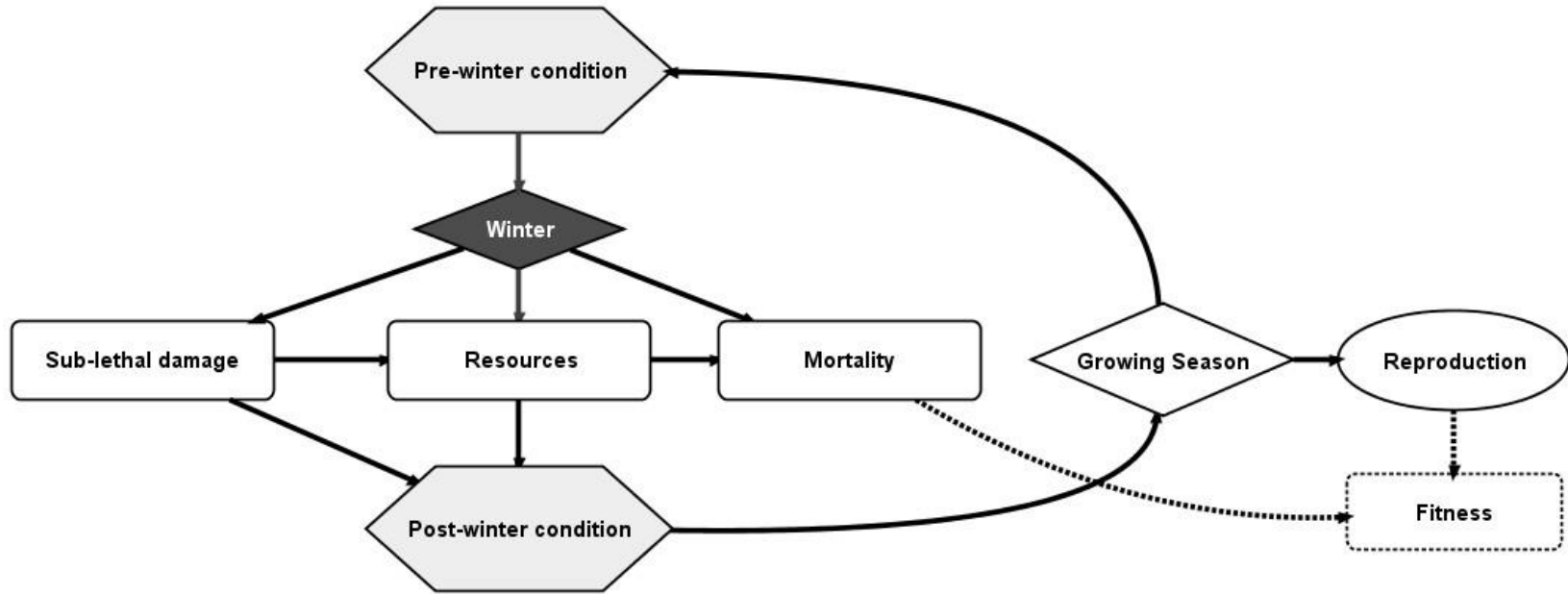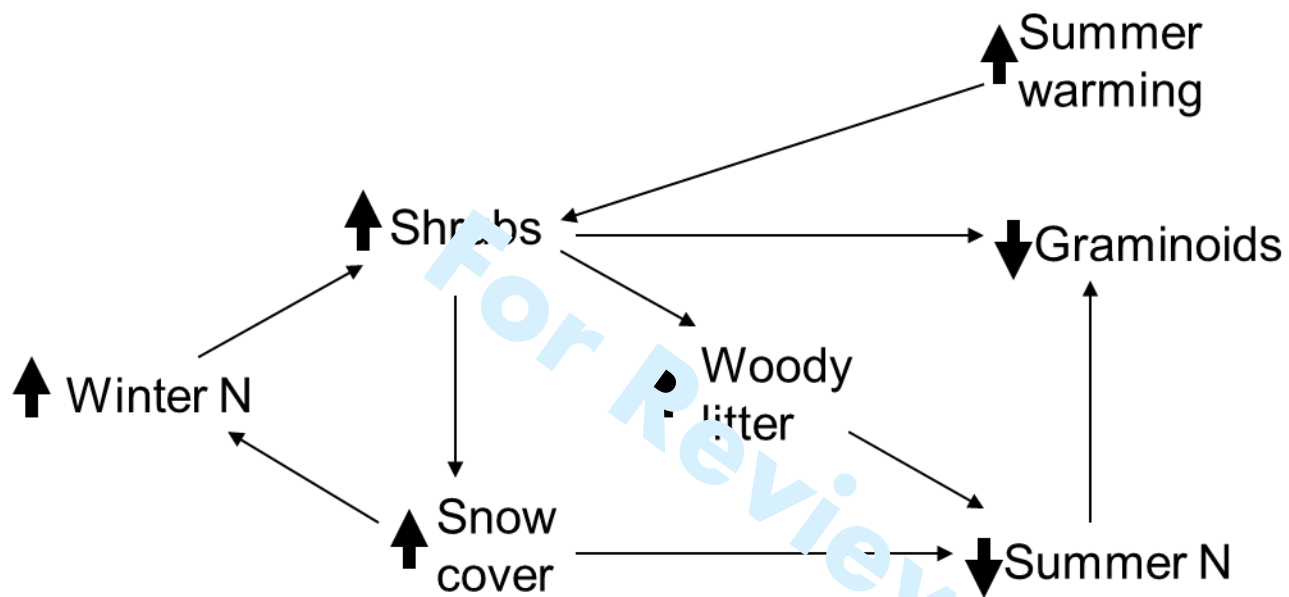6   1451   Figure 3
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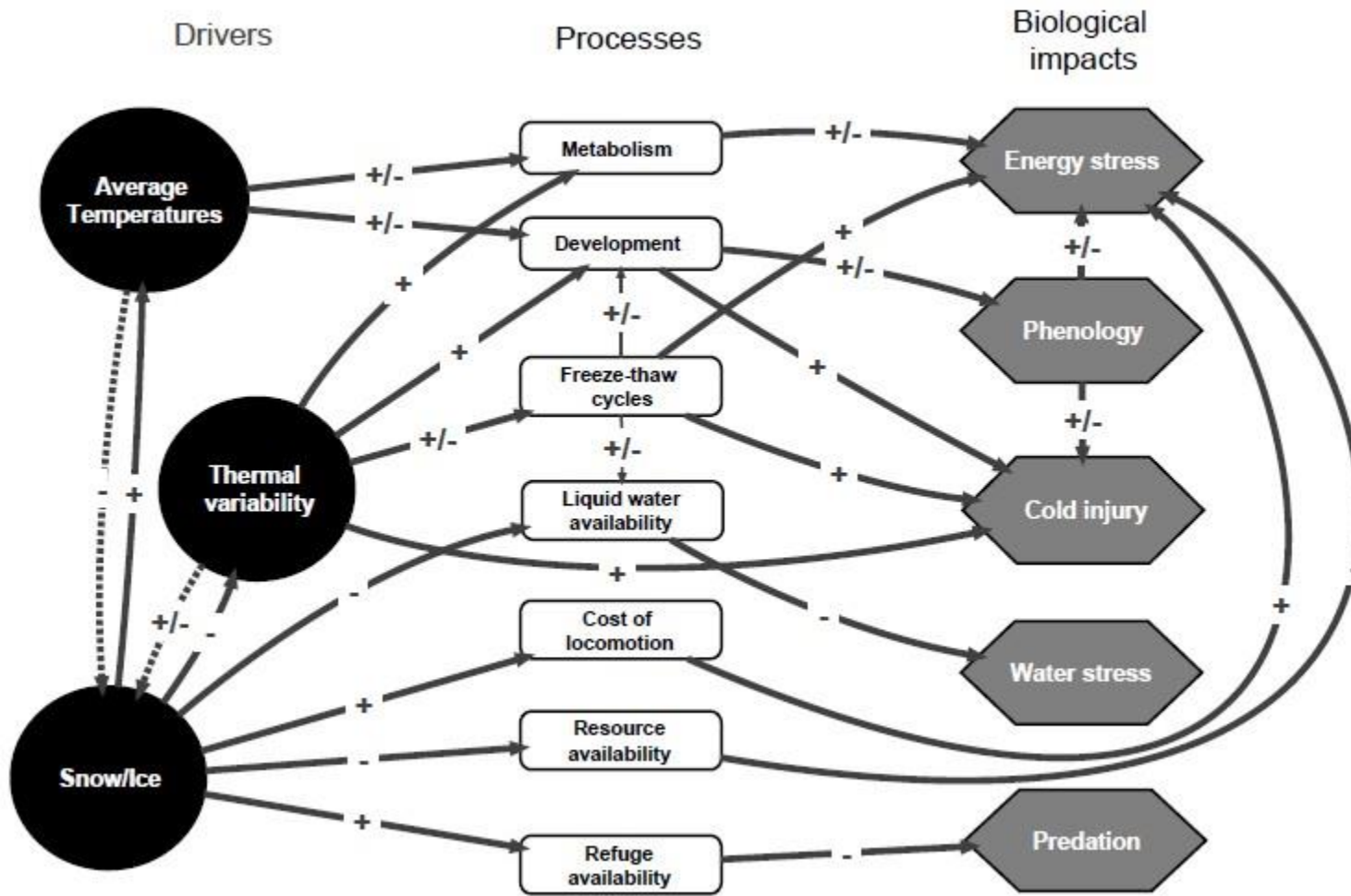
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1455 Figure 4

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1459 Figure 5

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1465   Figure 6

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1468 **Table 1** – Organismal traits influencing vulnerability to winter climate change. Vulnerability is a product of traits that increase stress
1469 exposure in response to a climate driver and traits that increase sensitivity to this stress, with sensitivity determined by a lack of either
1470 resilience or adaptive potential. Climate drivers (indicated in italics, and with reference to the text and Figure 3) are increased average
1471 temperatures *(AvT)*, thermal variability (subdivided here into increased daily thermal variability *(DV)*, extreme temperatures *(ExT)* and
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 *(AvT, DV)* • poikilotherms > homeotherms	Reproductive strategy *(AvT, DV)* • capital breeding > income	• Consumption of finite energy reserves *(AvT, DV)*
Energy intake and availability *(AvT, DV, S+)* • no energy intake/limited food available > winter energy uptake	Energy storage*(AvT, DV)* • low > high pre-winter energy stores	• Decreased resource availability
Metabolic suppression *(AvT, DV, S+)* • low > high suppression	Energetic recovery *(AvT, DV)* • no post-winter feeding > feeds post-winter	• Increased cost of locomotion *(S+)*
Metabolic plasticity *(AvT, DV)* • low > high plasticity	Feeding strategy *(S+, S-)* • specialist > generalist	• Decreased food access *(S+)*
Trophic position *(S+)* • predator > prey • heterotroph > autotroph		
Habitat *(S-)* • subnivean > supranivean		

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Table 1 (continued)

Traits determining stress exposure	Traits determining sensitivity to stress	Proximal cause of vulnerability
Phenology		
Chilling or vernalization requirements *(AvT)*	Trophic level *(AvT)*	• Reduction in length of growing season *(AvT)*
• obligate > facultative dormancy	• consumers > primary producers	• Trophic mismatches *(AvT)*
• chilling requirement > non-thermal cues	Diet breadth *(AvT)*	• habitat not available for reproduction *(S-)*
Habitat requirements *(S-)*	• low > high	
• snow dependent > not snow dependent	Overwintering stage *(AvT)*	
	• early in lifecycle > late in lifecycle	
	Genetic variation in reaction norms *(AvT)*	
	• low variation > high	

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Table 1 (continued)

Cold injury

Cold 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

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

- Direct injury from cold *(ExT)*
- Cumulative cold injury *(F/T)*
- Energetic costs of repairing cold injury *(F/T, S-)*

Water Balance

Susceptibility to waterlogging and ice encasement

- hypoxia intolerant > hypoxia tolerant

Water balance strategy

- no winter water consumption > water consumption over winter

- 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
Predation		
Trophic position *(S-)*	Predator avoidance *(S-)*	Increased mortality
• prey > predator	• low camouflage plasticity > low	
Habitat *(S-)*	• low defenses > high	
• subnivian > supranivean	• high palatability > low	
	• low alertness > high	

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

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Quantity of snow	
Reduced snow cover	
	increased soil frost
	increased food access for predators/browsers
	(decreased food access with increased rain-on-snow)
	increased vulnerability of prey
Increased snow cover	
	increased foraging and locomotion costs (winter-active organisms)
	increased energetic maintenance costs (winter-inactive organisms)
Timing of snow cover	
early snowmelt	
	earlier warm-season resource gathering
	potential phenological mismatch for dormant organisms
delayed snowmelt	
	delayed warm-season resource gathering
	increased protection from frost
mid-winter snowmelt	
	cold deacclimation followed by frost exposure
	increased access to liquid water

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