

Understanding evolutionary impacts of seasonality

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Understanding evolutionary impacts of seasonality

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29 **Abstract**

30 Seasonality is a critically important aspect of environmental variability, and strongly shapes all
31 aspects of life for organisms living in highly seasonal environments. Seasonality has played a
32 key role in generating biodiversity, and has driven the evolution of extreme physiological
33 adaptations and behaviors such as migration and hibernation. Fluctuating selection pressures on
34 survival and fecundity between summer and winter provide a complex selective landscape,
35 which can be met by a combination of three outcomes of adaptive evolution: genetic
36 polymorphism, phenotypic plasticity, and bet-hedging. Here, we have identified four important
37 research questions with the goal of advancing our understanding of evolutionary impacts of
38 seasonality. First, we ask how characteristics of environments and species will determine which
39 adaptive response occurs. Relevant characteristics include costs and limits of plasticity,
40 predictability and reliability of cues, and grain of environmental variation relative to generation
41 time. A second important question is how phenological shifts will amplify or ameliorate
42 selection on physiological hardiness. Shifts in phenology can preserve the thermal niche despite
43 shifts in climate, but may fail to completely conserve the niche or may even expose life stages to
44 conditions that cause mortality. Considering distinct environmental sensitivities of life history
45 stages will be key to refining models that forecast susceptibility to climate change. Third, we
46 must identify critical physiological phenotypes that underlie seasonal adaptation and work
47 towards understanding the genetic architectures of these responses. These architectures are key
48 for predicting evolutionary responses. Pleiotropic genes that regulate multiple responses to
49 changing seasons may facilitate coordination among functionally related traits, or conversely
50 may constrain the expression of optimal phenotypes. Finally, we must advance our
51 understanding of how changes in seasonal fluctuations are impacting ecological interaction

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3 52 networks. We should move beyond simple dyadic interactions, such a predator prey dynamics,
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6 53 and understand how these interactions scale up to affect ecological interaction networks. As
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8 54 global climate change alters many aspects of seasonal variability, including extreme events and
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11 55 changes in mean conditions, organisms must respond appropriately or go extinct. The outcome
12
13 56 of adaptation to seasonality will determine responses to climate change.
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18 58 Keywords: bet-hedging, polymorphism, plasticity, phenology, winter, dormancy
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60 Introduction

61 Seasonality represents the strongest and most ubiquitous source of external variation influencing
62 human and natural systems (Fretwell 1972; Levins 1968; Wingfield and Kenagy 1991). The
63 combined effects of Earth's tilt and rotation result in annual sine wave variations in day-length,
64 with downstream effects on temperature, rainfall and resource availability (Lisovski et al. this
65 issue). In the temperate and polar zones, winters are characterized by short days, cold air
66 temperatures, moisture in the form of ice and snow, and reduced or suspended primary
67 production and activity (Williams et al. 2015). Summers are characterized by long days and
68 conditions that are permissive for growth and development, including warm air temperatures,
69 elevated primary production, and increased animal activity often including reproduction. In the
70 tropics, seasonality consists of wet and dry seasons, which drive changes in morphology
71 (including leaf senescence), physiology and behavior that contribute to seasonal shifts in
72 operative temperatures (e.g. Christian and Bedford 1995). Seasonal changes thus impact
73 organisms both directly, through the effects of light, temperature, precipitation, and other abiotic
74 variables on their physiology, and indirectly, via biotic interactions.

75 Seasonal environments impose fluctuating selection on life history traits that can elicit adaptive
76 responses (Rajpurohit et al. this issue; Varpe this issue). Morphological and physiological traits
77 are frequently plastic, described by functions termed reaction norms that relate a trait value to an
78 environmental variable (Kingsolver et al. 2015). The shape and intercept of these functions may
79 evolve in response to changing seasonality, for example, the shape of the temperature vs.
80 survivorship curve. Alternatively, organism may evolve life cycles with distinct life stages, each
81 with different reaction norms 'tuned' to the seasons in which they occur (McNamara and
82 Houston 2008; Wingfield 2008). This strategy is also an evolutionary solution to constraints

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3 83 caused by trade-offs among life history traits that compete for resources (Zera and Harshman
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5 84 2001). For example, selection may favor high reproductive investment during favorable periods
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8 85 associated with population growth (e.g., summer), but reduced reproductive (and increased
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10 86 somatic) investment during unfavorable periods characterized by stress (e.g., winter) (Betini et
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12 87 al. 2017; Schluter et al. 1991). Organisms often evolve distinct reproductive and dormant or
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14 88 migratory life history stages in response to these contrasting selection pressures (Varpe this
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16 89 issue).

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20 90 Organisms in seasonal environments must integrate information from multiple environmental
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22 91 cues to time transitions between life-history stages. Phenology, the timing of biological events,
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24 92 must synchronize both with environmental conditions, and with interacting organisms from the
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26 93 same and other species. Synchronizing cues must predict future selective environments, and are
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28 94 most reliable when cues are themselves drivers of selection (e.g. temperature, precipitation, food
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30 95 resources). However, drivers of selection are frequently not used as cues, when there is a long
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32 96 time lag between cue sensing and readiness to respond (Levins 1968; Visser et al. 2010). For
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34 97 example, many organisms need to complete development, undergo morphological changes, or
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36 98 migrate before beginning feeding and reproduction (Košťál 2006; Tombre et al. 2008). Such time
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38 99 lags can reduce the adaptive value of plastic responses (Padilla and Adolph 1996). Therefore,
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43 100 many organisms use cues, frequently day-length, that are not themselves drivers of selection to
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45 101 provide advance notice of seasonal transitions.

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48 102 Global climate change is shifting the relationship between day-length and drivers of selection,
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50 103 fundamentally altering seasonal cycles. Spring is coming earlier, and fall later, extending the
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52 104 growing season and causing many organisms to alter their phenology (Parmesan 2006). Earlier
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54 105 spring phenology is exposing organisms to increased risk of damaging cold snaps on vulnerable
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3 106 life stages in spring. Environmentally cued phenology and physiological reaction norms exhibit
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5 107 predictable genetic variation that responds rapidly to selection (Bradshaw and Holzapfel 2001;
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8 108 Diamond et al. 2017; Menzel et al. 2006; Parmesan 2006). Thus, the legacy of past adaptation to
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10 109 seasonal environments will impact future responses to global climate change, making it a high
11
12 110 priority to understand the evolutionary impacts of seasonality.
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112 **Outstanding questions**

113 The ecological and evolutionary impacts of seasonality on organisms have long been a topic of
114 interest to biologists (Dobzhansky and Ayala 1973; Fretwell 1972; Levins 1968), but our
115 understanding of these impacts is still incomplete. We have identified four pressing questions
116 that together promise to advance our understanding of evolutionary impacts of seasonality. In the
117 following sections, we give background on each question, outline gaps in knowledge, and
118 suggest how these gaps can be addressed.

119 ***1) How does seasonally fluctuating selection impact evolutionary*** 120 ***trajectories?***

121 *“If large body size is an adaptation to cold (...), what size is optimum in an*
122 *environment which is sometimes hot and sometimes cold?” (Levins 1968).*

123 **1.1 Background**

124 Seasonally fluctuating selective pressures complicate the selective environment in comparison to
125 stable or weakly seasonal environments. Evolutionary responses to seasonality include 1) the
126 maintenance of genetic polymorphism, 2) phenotypic plasticity, and 3) bet-hedging (Fig. 1).

127 Genetic polymorphism refers to the presence of two or more distinct gene variants (alleles) at a

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3 128 single locus within a population. When the selective drivers change across generations, natural
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5 129 selection can cause cyclic changes in allele frequencies in genes associated with adaptation to
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8 130 distinct seasons (Dobzhansky and Ayala 1973). “Winter” alleles rise throughout the winter and
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10 131 reach a peak in spring due to differential survival of individuals with those alleles, which are
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12 132 then gradually replaced by individuals bearing “summer” alleles during the growing season
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14 133 (Fig.1B; Bergland et al. 2014; Carvalho and Crisp 1987; Cogni et al. 2014). Seasonal variation is
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16 134 thus one class of temporal variation that can maintain genetic variation within populations
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18 135 (Haldane and Jayakar 1963), potentially maintaining polymorphisms at many loci across the
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20 136 genome (Wittmann et al. 2017). Seasonal changes in frequency at polymorphic loci may be
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22 137 generated by life history trade-offs in resource allocation or acquisition (Betini et al. 2017;
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24 138 Schluter et al. 1991). Poleward phenotypes and genotypes tend to resemble winter phenotypes
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26 139 and genotypes, suggesting that seasons can in some ways be considered the time-analog of
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28 140 spatial environmental clines. Variation in the extent and magnitude of seasonality can also be
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30 141 one mechanism by which spatial clines are generated (e.g., the seasonal phase cline model,
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32 142 Rhomberg and Singh 1988). For example, populations of *Drosophila melanogaster* collected in
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34 143 Pennsylvania orchards at the end of the growing season are similar genetically and
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36 144 phenotypically to southern populations, while populations emerging after winter are similar to
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38 145 northern populations (Behrman et al. 2015; Cogni et al. 2014; Cogni et al. 2015). Adaptation to
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40 146 seasonal fluctuations therefore contributes to adaptation across a geographic range (Conover
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42 147 1992).

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46 149 Phenotypic plasticity enables genotypes to express diverse phenotypes in response to
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48 150 environmental variation, which are adaptive when they improve fitness in a given environment
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3 151 (Fig.1C; Schlichting and Pigliucci 1998; Van Tienderen 1991). Plasticity is heritable and
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6 152 responds to selection (Scheiner and Lyman 1991). Seasonality influences the evolution of
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8 153 adaptive plasticity, which is determined by genetic and physiological properties of the organism
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10 154 (e.g., costs and limits to plasticity, genetic architecture of plastic responses) and characteristics of
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12 155 the environment (e.g. predictability and reliability of cues, grain of environmental variation
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15 156 relative to generation time) (DeWitt et al. 1998; Levins 1968; Schlichting and Pigliucci 1998;
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17 157 Van Tienderen 1991).

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22 159 Two leading hypotheses for the evolution of plasticity of thermal hardiness in seasonal
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24 160 environments make opposing predictions: the latitudinal hypothesis predicts that plasticity will
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27 161 increase with increasing seasonality due to increased environmental variation (Janzen 1967),
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29 162 while the trade-off hypothesis predicts that plasticity will be lower in seasonal environments due
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31 163 to a trade-off between inherent and inducible hardiness (Cavicchi et al. 1995; Overgaard et al.
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33 164 2011; Stillman 2003). Support for both hypotheses is mixed. The latitudinal hypothesis is most
34
35 165 often supported in situations where behavioral thermoregulation is limited (thus increasing
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37 166 selection on physiological sensitivity), such as for dormant life stages or aquatic habitats where
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39 167 spatial thermal heterogeneity is reduced (Gunderson and Stillman 2015; Shah and Ghalambor
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41
42 168 this issue). The trade-off hypothesis is supported in some groups of animals and not others,
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45 169 suggesting that our knowledge of the costs and mechanisms of thermal plasticity are incomplete
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48 170 (Stillman 2003).

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53 172 Phenotypic plasticity can be expressed within a single generation (at timescales ranging from
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55 173 rapid hardening responses through developmental acclimatization) or across generations (aka

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3 174 parental environmental effects, Mousseau and Fox 1998); the rate of environmental change
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5 175 compared to the generation time of organisms is pertinent to which evolves more readily
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8 176 (Gilchrist 1995). Within- and across- generation plasticity can sometimes evolve in concert, with
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10 177 one sometimes influencing the adaptive value and evolution of the other (Ezard et al. 2014;
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12 178 Kuijper and Hoyle 2015). Phenological plasticity is an important class of plasticity, and will be
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15 179 discussed further in Q2.

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17 180 Some aspects of seasonal fluctuations are unpredictable, such as frequency of extreme events,
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20 181 which can favor the evolution of bet-hedging (Seeger and Brockman 1987; Van Tienderen 1991).
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22 182 Bet-hedging describes a form of risk-spreading, whereby the fitness in benign environments is
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24 183 decreased in order to increase fitness across all environments (formally, the mean arithmetic
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26 184 fitness of a strategy is reduced in order to decrease variance in fitness, thus increasing geometric
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28 185 mean fitness). For example, variation in insect diapause or seed dormancy may diversify the
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30 186 environments experienced by individuals (Hopper 1999; Venable 2007). Bet-hedging can occur
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32 187 through genotypes producing variable phenotypes (e.g., variation in germination time; Venable
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34 188 2007), or genotypes producing a single generalist phenotype (Fig. 1D; Van Tienderen 1991).

35 36 37 38 39 189 **1.2 Gaps in knowledge**

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41 190 The specific ecological and genetic conditions that maintain seasonal polymorphisms over long
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43 191 periods of time is unclear, as is the extent to which polymorphisms that are maintained by
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45 192 seasonal fluctuations in turn contribute to adaptation to geographically variable environments.
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47 193 Regarding plasticity, how do within and across-generational plasticity jointly evolve in response
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49 194 to seasonality? How does the interaction of predictable seasonal variation and unpredictable
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51 195 extreme events influence the evolution of plasticity versus bet-hedging? How will intrinsic and
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53 196 extrinsic factors influence the evolution of each strategy? At the ecophysiological level, the
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3 197 presence of seasonally fluctuating polymorphisms are a tantalizing hint of genetic trade-offs
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6 198 between stress hardiness and reproduction. Functionally characterizing the physiological
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8 199 pathways linking specific environmental drivers to selection on these loci will further our
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10 200 understanding of the pathways and processes underlying seasonal adaptation.
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13 201 **1.3 Significance and future prospects**

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15 202 Contemporary climate change is pushing environmental variation beyond the boundaries of past
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17 203 selection in a variety of ways: altering seasonal amplitude, shifting means and variation and
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19 204 changing the onset of seasonal events. Adaptation to highly seasonal environments potentially
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21 205 impacts responses to environmental change in two ways: 1) if seasonality increases genetic
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23 206 polymorphisms in populations, the increased genetic variation may increase the adaptive
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25 207 response to climate change (Schmidt and Conde 2006); and 2) adaptive phenotypic plasticity and
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27 208 bet-hedging could promote population persistence during periods of rapid environmental change,
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29 209 potentially altering selective gradients (Bay et al. 2017). Determining more broadly the relative
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31 210 contributions of these three outcomes of adaptation in the response to seasonal environments in
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33 211 diverse animal and plant populations will enable broad-scale insights into the potential for
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35 212 adaptive responses to climate change. These outcomes will also affect how population dynamics
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37 213 respond to environmental change, and thus how ecological feedbacks will shape evolutionary
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39 214 processes, promoting adaptation or increasing risk of extinction (Betini et al. 2017; Kokko and
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41 215 Lopez-Sepulcre 2007; Schoener 2011; Winder and Schindler 2004).
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49 216 An increase in extreme weather events (Easterling et al. 2000) may alter the predictability of
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51 217 seasonal environments and shift the outcome of adaptation towards bet-hedging or a fixed
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53 218 generalist strategy. Similarly, phenotypic plasticity may become less reliable if the relationship
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55 219 between cues and environmental drivers of selection become decoupled, which will lead to
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3 220 directional selection on cue sensitivity. Plasticity may either promote or impede adaptation to
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5 221 sustained environmental change, depending on the magnitude and direction of the plastic
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8 222 response compared to the optimal phenotype (Bay et al. 2017; Chevin et al. 2010; Lynch and
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10 223 Lande 1993). Including seasonality in models for organisms with multiple generations per season
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12 224 suggests that phenotypic plasticity (including the evolution of plasticity) will contribute
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15 225 relatively more than genetic evolution to climate change responses in more seasonal
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17 226 environments, and that plasticity can facilitate evolution by buffering seasonal variation in
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20 227 selection (Kingsolver and Buckley in review).
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23 228 ***2) How do selection on phenology and the physiological niche interact?***

24 229 **2.1 Background**

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29 230 When a single organism experiences seasonal fluctuation within its lifetime, that organism must
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31 231 be able to withstand the full range of seasonal environmental variation. Despite the fitness
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33 232 disadvantages associated with delaying reproduction, organisms often respond to temporal
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36 233 variation by limiting reproduction to specific seasons (Tuljapurkar 1990). Environmentally cued
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38 234 phenology is critical to matching each life stage to seasonal environments within the limits of
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41 235 physiological performance. Conversely, variation in physiological traits underlie phenology
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43 236 (Hereford this issue). Differences in phenology across latitude can buffer thermal exposure of
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46 237 different life stages across seasonal changes in the environments, effectively preserving the
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48 238 thermal niche across gradients in seasonality. For example, organisms frequently shorten
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50 239 growing seasons (with concomitant lengthening of dormancy) at high relative to low latitudes
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52 240 such that the reproductive stages of different populations experience relatively similar thermal
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55 241 environments for reproduction despite strong gradients in seasonality (Bradshaw and Lounibos
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57 242 1977; Ragland and Kingsolver 2008; Sheldon and Tewksbury 2014). Any modifications to life
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3 243 cycle timing therefore alter the selective environment experienced by a given life stage or critical
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5 244 life-history event (Donohue 2014; Donohue et al. 2010). Phenological shifts will have the
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8 245 maximum impact on fitness in the spring and fall when temperatures are crossing thresholds for
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10 246 activity, relative to mid-season when temperatures are uniformly hot (Levy et al. 2016).

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12 247 In the above examples, behavior and phenology serve to homogenize natural selection on some
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14 248 focal trait linked to fitness, e.g., the thermal optimum for performance traits such as sprint speed
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16 249 or flight duration, by allowing organisms to remain within their optimal or “pejus” temperatures
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19 250 (Pörtner 2010). However, changes in behavior and phenology can also increase heterogeneity of
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21 251 selective environments on other traits. For example, different thermoregulatory behaviors may
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23 252 lead to different exposure to predation (Huey and Slatkin 1976), and changes in phenology may
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25 253 change the availability of seasonally fluctuating food resources (Visser et al. 2006). Even
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27 254 considering only the thermal environment, changes in phenology cannot completely buffer
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29 255 against changing climates. For example, estimates of development rate based on the thermal
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31 256 sensitivity of insect development suggest that phenological shifts have partially, but incompletely
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33 257 buffered exposure to warmer temperatures associated with climate change (Buckley et al. this
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35 258 issue). The consequences of phenological shifts may also span generations, in cases where
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37 259 parental phenology determines the selective environment experienced by offspring (Crozier et al.
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39 260 2008; Edwards et al. this issue; Sheriff et al. 2015).

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41 261 In addition to altering phenology, spatial or behavioral adjustments can also determine an
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43 262 organism’s exposure to seasonal environmental stresses (Williams et al. 2016). Changes in
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45 263 thermoregulatory behavior across latitude or altitude can lead to similar body temperatures
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47 264 despite strong environmental clines (Adolph 1990; Huey et al. 2003). Differences in
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49 265 thermoregulatory ability across life stages can alter the strength of selection on physiological
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3 266 sensitivities, with less mobile life stages experiencing stronger selection on physiology, while
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5 267 mobile life stages can accommodate changing environmental conditions through shifts in
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8 268 thermoregulatory behavior (Kingsolver et al. 2011). Together with shifts in phenology, these
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10 269 forms of habitat selection will impact the selective environment and the degree of stress
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13 270 hardiness required by a given life stage.

14 15 16 271 **2.2 Gaps in knowledge**

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18 272 A first step towards understanding the impacts of phenological shifts on the physiological niche
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20 273 is to incorporate stage-specific physiological sensitivity into models predicting responses to
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22 274 environmental change. Any phenological shift that decouples a hardy life stage from a stressful
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25 275 period should increase mortality. There is increasing evidence that considering the physiological
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27 276 sensitivity of multiple life history stages may significantly improve forecasts of climate change
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29 277 impacts compared to predictions based on single life stages. Negative effects on a sensitive life
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32 278 stage can counter benefits in more robust life stages, and in some cases reverse predictions of
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34 279 relative susceptibility of species or populations to climate-induced declines (Levy et al. 2015;
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37 280 Radchuk et al. 2013). Moreover, different components of fitness differ in their thermal sensitivity
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39 281 (Bestion et al. 2015; Huey and Berrigan 2001), making it a challenge to determine which are the
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41 282 most appropriate fitness components to measure for any given system.

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43
44 283 Another gap in knowledge lies in predicting when phenology versus physiological sensitivity
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46 284 will respond to selection. Bradshaw and Holzapfel (2008) argue that the majority of known
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48 285 responses to contemporary climate change involve changes in phenology, not thermal
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50 286 physiology. This may partially reflect that phenology is more commonly measured. There are
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52 287 examples of rapid evolution of thermal physiology (Angilletta et al. 2007; Diamond et al. 2017;
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55 288 Higgins et al. 2014), suggesting that as more data become available we may see more instances

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3 289 of evolution of thermal physiology. Alternatively, precipitation changes may be more important
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5 290 than temperature in driving evolution in response to climate change (Siepielski et al. 2017). In
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8 291 some cases, phenological and physiological traits are genetically correlated, and will thus evolve
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10 292 jointly (Scheiner and Istock 1991; Wilczek et al. 2010). Finally, the degree to which
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12 293 phenological cuing predicts selective environments at different life stages and thereby alters
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14 294 adaptive outcomes is also important. Empirical studies could test how changes in phenology
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16 295 influence adaptive dynamics in other traits, such as physiological sensitivities. To our
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18 296 knowledge, there are currently no predictive models of the joint evolution of phenology and
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20 297 physiological sensitivity.
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24 25 298 **2.3 Significance and future prospects**

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27 299 A key next step is to identify sets of conditions under which phenology vs. physiological
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29 300 sensitivity should evolve so that empirical studies of the evolutionary potential of particular traits
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31 301 could be prioritized. Comparing evolution in systems with constrained phenology (due to day-
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33 302 length cues, snow melt constraints, etc.) to those where environmental conditions (e.g.,
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35 303 temperature, water availability) both determine phenology and exert selection is one potentially
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37 304 powerful approach. It is important to determine when evolution of phenology is sufficient to
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39 305 maintain fitness in the face of changing climates, versus when physiological adaptation is also
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41 306 required. One hypothesis is that phenological shifts will be the primary evolutionary response to
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43 307 changing environments when developmental transitions between stress-hardy and stress-
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45 308 susceptible life stages coincide with seasonal transitions (e.g. spring and fall). Conversely,
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47 309 phenological shifts are unlikely to affect stage-specific environmental exposure when
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49 310 developmental transitions occur mid-season. For example, for organisms with multiple
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51 311 generations during the growing season, all life-stages will experience summer temperatures, so
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3 312 phenological shifts are unlikely to buffer thermal exposure in mid-summer, suggesting that
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5 313 evolution of physiological sensitivity may be more important in these cases (Levins 1968).
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9 314 ***3) What are the critical physiological mechanisms governing seasonal***
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11 ***responses, and are they genetically constrained?***
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15 316 **3.1 Background**
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17 317 A core set of key phenotypes facilitate seasonal adaptation, including environmental sensing and
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19 318 downstream responses, thermal hardiness and thermoregulation, and dormancy. These complex
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21 319 seasonal phenotypes consist of coordinated modules of independent, but functionally related,
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23 320 traits. For example, during preparation for dormancy, mammals and insects must down-regulate
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25 321 reproduction, up-regulate fat accumulation and stress hardiness, then down-regulate metabolism
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27 322 (Košťál 2006; Staples 2016). These complex phenotypes are jointly regulated by single cues or
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29 323 the integration of multiple cues. Linking environmental changes to organismal responses requires
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31 324 elucidating the pathways through which environmental cues are sensed and transduced into
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33 325 physiological responses (Jennings et al. this issue) and how multiple traits may be coordinated by
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35 326 a single cue (Stager et al. 2015). One way that a single cue can control multiple traits is through
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37 327 pleiotropy, wherein one gene regulates multiple processes. Pleiotropy has been documented for
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39 328 the environmental regulation of multiple phenological transitions in plants, sometimes with the
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41 329 gene functioning in the same pathways and sometimes not (Auge et al. 2017; Chiang et al. 2009;
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43 330 Jiang et al. 2012). Pleiotropy may both promote and hinder multi-trait adaptation (Brakefield
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45 331 2006; Griswold and Whitlock 2003; Wagner et al. 2008). On one hand, placing the control of
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47 332 multiple traits under the influence of a single master regulator can help to better integrate whole-
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49 333 organism responses. If different traits are regulated by the same cue, changes in the seasonal
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3 334 coordination of cues may not disrupt the integration of functionally related phenotypes (Sinclair
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5 335 et al. 2013). On the other hand, negative or antagonistic pleiotropic effects can constrain the
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7 336 expression of optimal phenotypes of individual traits, compared to those that are more modular
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9 337 in their expression. For example, increases in stress resistance may trade-off against investment
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11 338 in other life history traits, such as fecundity (Schmidt et al. 2005). However, pleiotropic genes do
12
13 339 not always regulate multiple traits through concordant pathways or modes of gene regulation
14
15 340 (Auge et al. 2017). For example, genetic correlations between thermal hardiness of larval and
16
17 341 adult *Drosophila melanogaster* flies are weak or absent, with associated genes mainly affecting
18
19 342 hardiness in only one life stage (Freda et al. this issue). This may be important if different life
20
21 343 stages inhabit distinct thermal environments (Kingsolver et al. 2011; Woods et al. 2015). Traits
22
23 344 are also integrated at the physiological, morphological and behavioral levels, and these types of
24
25 345 constraints can also constrain evolutionary pathways (Ghalambor et al. 2003).
26
27 346 If traits are regulated by different cues – for example, if temperature affects one suite of traits
28
29 347 and day-length another - disruption of the seasonal coordination of these environmental cues
30
31 348 may also disrupt the integrated organismal response (Kristensen et al. 2015; Moyes et al. 2011).
32
33 349 Both genetic modularity and modular responses to different seasonal cues may allow for fine-
34
35 350 tuning of individual trait responses, but this potential may come at a cost of reduced robustness
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37 351 in the integrated response if environmental cues that were once synchronized become strongly
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39 352 asynchronous.
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51 354 **3.2 Knowledge gaps**

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53 355 We currently lack a detailed picture of the functional linkages between critical sensory systems,
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55 356 the physiological and developmental changes these sensory systems induce, and the underlying
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3 357 genetic architecture of integrated seasonal phenotypes for any species (Caro et al. 2013; Meuti
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5 358 and Denlinger 2013). Our understanding of the degree of evolutionary conservation of
6
7 359 mechanisms governing seasonal adaptation across species or populations is still at the anecdotal
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9 360 stage, lacking general principles. For example, some genes that regulate flowering time are
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11 361 conserved across flowering plants, but some are not (Simpson 2004). Similarly, while regulatory
12
13 362 network structure seems to be largely conserved across species of songbirds that diverged
14
15 363 roughly 45 million years ago, only a subset of the genes involved in those networks respond
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17 364 similarly to changing seasons across species (Cheviron and Swanson this issue). Another
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19 365 outstanding question relates to the degree and nature of genetic constraint for traits that underlie
20
21 366 seasonal adaptations. Potential genetic constraints stem from insufficient genetic variation either
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23 367 for single traits, or for multi-trait combinations (Arnold 1992). Similarly, constraints due to
24
25 368 pleiotropic effects on seasonally adaptive trait complexes are understudied, but are now
26
27 369 receiving increasing attention. Assessing magnitudes and causes of genetic correlations among
28
29 370 traits associated with adaptation to seasonality would provide important data on the evolutionary
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31 371 potential of responses to climate change (Shaw and Etterson 2012). An important next step is to
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33 372 incorporate genetic architectures of responses into models predicting responses to environmental
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35 373 change (Bay et al. 2017).

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375 **3.3 Significance and future prospects**

376 In taxa in which physiological determinates of phenology are well understood, it will be
377 important to determine the degree to which common genes and pathways regulate responses to
378 the environment, and then use a comparative approach to assess conservation of function in
379 related species. The inherent plasticity of phenological traits will complicate this effort;

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3 380 genotype-by-environment interactions can only be assessed by measuring genotypes, or the
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5 381 effects of specific alleles, across multiple environments. For example, Genome Wide Association
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7 382 Studies (GWAS) for phenology phenotypes may need to be applied across different thermal
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9 383 environments (Gienapp et al. submitted). Moreover, complex traits, such as those relevant to
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11 384 seasonal adaptation, are likely underlain by many genetic variants of small effect, which are
12
13 385 challenging to discover using traditional GWAS alone (Rockman 2012). Physiological traits are
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15 386 environmentally labile and often technically demanding to measure, requiring “low-throughput”
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17 387 acclimation experiments and extensive phenotyping efforts (Cobb et al. 2013). However, even
18
19 388 lacking specific knowledge of physiological mechanisms, quantitative genetic approaches can
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21 389 inform predictions of evolutionary responses to changing climates, and as a result, these studies
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23 390 represent important next steps (Reed et al. 2016).

24
25 391 A detailed understanding of the constraints on the evolution of the dynamic traits that underlie
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27 392 seasonal adaptation can enable predictions of evolutionary responses to changing climates
28
29 393 (Senner et al. in review). As a result, mechanistic studies of seasonal adaptations not only inform
30
31 394 basic questions on the evolution of complex traits, but also provide key insights into the
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33 395 robustness of species and populations in a changing world. Knowledge of the mechanisms and
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35 396 genes regulating phenological and behavioral adaptations, combined with knowledge of stage-
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37 397 specific physiological sensitivity, can be applied to predicting the geographic range of species
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39 398 (Morin et al. 2007).

399 ***4) How is changing seasonality impacting ecological interaction networks?***

400 **4.1 Background**

401 Every individual of every species comprising a biotic community pursues its own seasonal
402 schedules of maintenance and reproduction, manifested as annual routines – the scheduling of

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3 403 activities in a regular way over the year (McNamara and Houston 2008). The degree to which
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5 404 species vary in the environmental regulation of their phenology shapes seasonal patterns of
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8 405 presence, abundance, and trophic status, which in turn shapes the seasonality of food webs and
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10 406 other interactions (McMeans et al. 2015). As climate change decouples cues and drivers of
11
12 407 selection, organisms are shifting phenology to differing degrees (Edwards and Richardson 2004),
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15 408 because the underlying norms of reaction for responses to cues differ among organisms. This is
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17 409 leading to mismatches in ecological interactions, such as trophic and competitive interactions
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19 410 that affect fitness (Visser and Holleman 2001; Winder and Schindler 2004). As an example,
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21 411 breeding birds that rely on insects to feed nestlings have not altered their breeding time to match
22
23 412 the advanced date of insect emergence (Visser and Holleman 2001), resulting in avian population
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25 413 declines in temperate regions (Both et al. 2009). In some cases, natural selection may act to
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27 414 retain synchrony between partners (van Asch et al. 2013), but in other cases heritable variation in
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29 415 reaction norms will not be sufficient to keep pace with climate change (Visser 2008).
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34 416 **4.2 Gaps in knowledge**

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36 417 In order to predict how changing seasonality will impact ecological interaction networks, we
37
38 418 need to move beyond simple dyadic interactions (i.e. species vs. an abiotic condition, or one
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40 419 species vs. another species). To understand how network interactions are affected by shifts in
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42 420 phenology due to climate change, we need to assess how interaction strengths change
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44 421 systematically across gradients in seasonality (Humphries et al. this issue). One option for
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46 422 tackling these problems would be to use large-scale, coordinated sampling of interaction
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48 423 strengths in a relatively simple ecosystem replicated across a seasonal gradient with a known
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50 424 trajectory of environmental change. The interacting partners would need to be amenable to
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52 425 common garden experiments and to laboratory study in order to characterize their reaction norms
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3 426 in response to cues. Leveraging a system where long-term information on phenology exists (e.g.
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5 427 Long-Term Ecological Research sites [LTER], funded by US National Science Foundation)
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7
8 428 could be fruitful. Ideally, the system would also allow for a deeper understanding of the
9
10 429 conditions under which top-down versus bottom-up processes dominate responses to climate
11
12 430 change.

13
14 431 Evolutionary responses could allow species to maintain synchronization with the critical
15
16 432 resources they require. The timing of life history events are heritable traits that are subject to
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18 433 selection (Savolainen et al. 2007). However, the strength of selection will vary with the strength
19
20 434 of the temporal overlap of the ecological interaction. A major gap in our knowledge is how
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22 435 changes in temporal overlap among interacting species will alter selection and evolutionary
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24 436 responses to climate change, including the extent to which evolutionary responses may restore
25
26 437 mismatched interactions and thereby stabilize interaction networks.

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28 438 Phenological synchronization is believed to be especially critical for species in more seasonal
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30 439 environments where resources tend to be available during narrow windows of time and where
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32 440 species specialize on one phenological stage of their host (Varpe 2012). However, tropical
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34 441 species may also suffer from phenological mismatches, but we know little about recent shifts in
35
36 442 phenology in the tropics (Chambers et al. 2013). Thus, how changing seasonality impacts
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38 443 interaction networks is a question beyond the much studied seasonality of boreal and temperate
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40 444 environments.

41 445 **4.3 Significance and future prospects**

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43 446 Climate change will have direct physiological impacts on species that will alter their phenology
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45 447 and ecological interactions. Predicting which species are most vulnerable to climate change thus
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47 448 requires an integration across levels from the individual to the community. Given the strong
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3 449 linkages between cues, individual states, timing of life history events, and fitness (McNamara
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6 450 and Houston 2008), the biological impacts of seasonality may be a particularly fruitful arena for
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8 451 working towards the close integration of physiology, chronobiology, evolutionary ecology, and
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10 452 interaction networks. This work should merge proximate and ultimate perspectives and provide
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12 453 more mechanistic hypotheses about species potential to respond to climate change.
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17 Conclusions

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22 457 The questions raised here provide several important pathways forward for better understanding
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24 458 adaptation to seasonality. First, we suggest that understanding the relative contributions of
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26
27 459 genetic polymorphism, adaptive phenotypic plasticity, and bet-hedging in response to seasonality
28
29 460 is essential for understanding the capacity for and outcome of adaptive responses to climate
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31 461 change in seasonal environments. Identifying the cues that elicit plasticity, the environmental
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33 462 factors that exert selection on plastic phenotypes, and the probabilistic relationship between them
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35 463 is a major priority for predicting the adaptive value of plastic phenotypes. Next, in order to
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37 464 understand the evolutionary potential for adaptive change, we need to identify under which
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39 465 conditions phenology vs. direct physiological changes evolve. This would allow us to determine
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41 466 the amount of genetic constraint on the physiological mechanisms of seasonal responses,
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43 467 particularly by examining genetic architecture across multiple seasonally-linked traits. Finally,
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45 468 we need to link the individual and its annual routine to the community by examining the strength
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47 469 of interactions across gradients of seasonality. This will allow us to determine the relative
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49 470 importance of bottom-up vs. top down effects on ecological networks. Several ideal systems for
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3 471 addressing these goals exist—the key now is to concentrate our efforts on these questions. These
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6 472 issues are becoming increasingly pressing within the context of climate change.
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8 473 Given the scale of the task, efforts aimed at mechanistic dissection of seasonal phenotypes
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10 474 should perhaps be concentrated on a handful of strategically chosen model systems that are
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12 475 investigated from multiple perspectives by a collaborative research community. Ideally,
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15 476 information from these model systems may be leveraged in related species. At present, model
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17 477 systems including the great tit *Parus major*, the pitcher plant mosquito *Wyeomyia smithii*,
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19 478 Tephritid flies (*Rhagoletis* sp.), *Drosophila melanogaster*, and *Arabidopsis* sp. stand out as
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21 479 among the best-developed, owing to large research communities and a mature research
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23 480 infrastructure. It continues to be a challenge to combine demanding physiological experiments
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25 481 with genetic approaches, which require large sample sizes and research infrastructure beyond
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27 482 what is available for most species (e.g. genetic mapping of populations). In addition, the
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29 483 relationship between genotype and phenotype is complex and inferences differ depending on
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31 484 genetic background and whether studies are conducted in the field or laboratory (Sarup et al.
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33 485 2011), highlighting the importance of having a broad and ecologically relevant context for
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35 486 studies of seasonal adaptation (Rajpurohit et al. this issue).
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487

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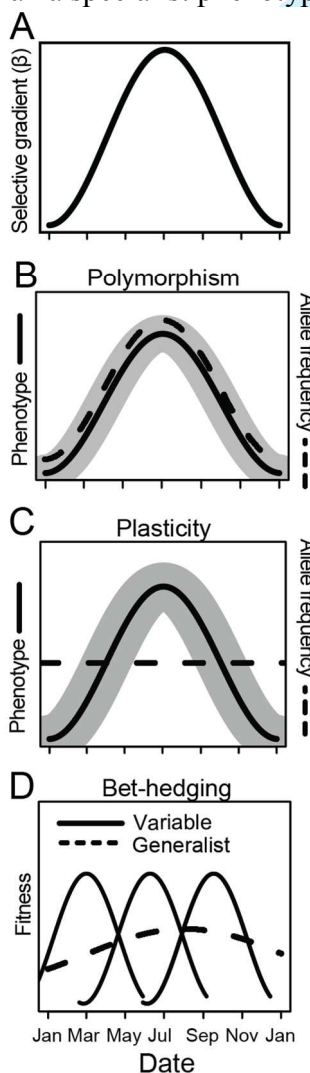
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For Peer Review

502 **Figures**

503 Fig. 1 – Outcomes of adaptation to seasonality. A) Selective gradients on life history traits
 504 fluctuate seasonally. B) For species with short generation times relative to season length, these
 505 fluctuating selective gradients can result in cyclic fluctuations in both phenotype (solid line) and
 506 allele frequency (broken line) at polymorphic loci, leading to maintenance of genetic
 507 polymorphisms within populations under certain conditions. C) Seasonal fluctuations can also
 508 be accommodated through phenotypic plasticity, whereby a single genotype produces multiple
 509 phenotypes in response to environmental variation. D) Unpredictable fluctuations will favor the
 510 evolution of bet-hedging, whereby a single genotype either produces multiple variable
 511 phenotypes whose fitness varies across the season (solid lines), or a single generalist phenotype
 512 whose fitness in summer is decreased but which has higher cumulative fitness across the year
 513 than a specialist phenotype.



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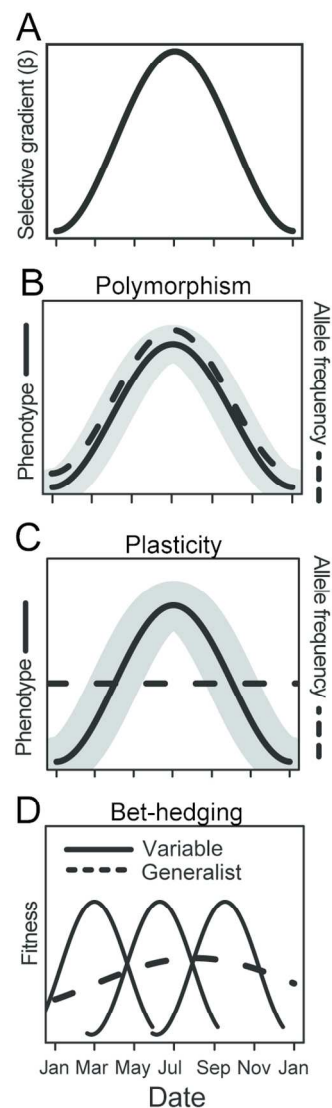


Fig. 1 – Outcomes of adaptation to seasonality. A) Selective gradients on life history traits fluctuate seasonally. B) For species with short generation times relative to season length, these fluctuating selective gradients can result in cyclic fluctuations in both phenotype (solid line) and allele frequency (broken line) at polymorphic loci, leading to maintenance of genetic polymorphisms within populations under certain conditions. C) Seasonal fluctuations can also be accommodated through phenotypic plasticity, whereby a single genotype produces multiple phenotypes in response to environmental variation. D) Unpredictable fluctuations will favor the evolution of bet-hedging, whereby a single genotype either produces multiple variable phenotypes whose fitness varies across the season (solid lines), or a single generalist phenotype whose fitness in summer is decreased but which has higher cumulative fitness across the year than a specialist phenotype.

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