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Optimal resource allocation and prolonged dormancy strategies in herbaceous plants

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10 **Title:** Optimal resource allocation and prolonged dormancy strategies in herbaceous plants

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21 **Summary**

22

- 23 1. Understanding the fitness consequences of different life histories is critical for explaining
24 their diversity and for predicting effects of changing environmental conditions. However,
25 current theory on plant life histories relies on phenomenological, rather than mechanistic,
26 models of resource production.
- 27 2. We combined a well-supported mechanistic model of ontogenetic growth that
28 incorporates differences in the size-dependent scaling of gross resource production and
29 maintenance costs with a dynamic optimization model to predict schedules of

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30 reproduction and prolonged dormancy (plants staying below ground for ≥ 1 growing
31 season) that maximize lifetime offspring production.

32 3. Our model makes three novel predictions: First, maintenance costs strongly influence the
33 conditions under which a monocarpic or polycarpic life history evolves and how
34 resources should be allocated to reproduction by polycarpic plants. Second, in contrast to
35 previous theory, our model allows plants to compensate for low survival conditions by
36 allocating a larger proportion of resources to storage and thereby improving overwinter
37 survival. Incorporating this ecological mechanism in the model is critically important
38 because without it our model never predicts significant investment into storage, which is
39 inconsistent with empirical observations. Third, our model predicts that prolonged
40 dormancy may evolve solely in response to resource allocation tradeoffs.

41 4. *Significance*: Our findings reveal that maintenance costs and the effects of resource
42 allocation on survival are primary determinants of the fitness consequences of different
43 life history strategies, yet previous theory on plant life history evolution has largely
44 ignored these factors. Our findings also validate recent arguments that prolonged
45 dormancy may be an optimal response to costs of sprouting. These findings have broad
46 implications for understanding patterns of plant life history variation and predicting plant
47 responses to changing environments.

48
49 **Keywords:** life history, resource allocation, maintenance, dormancy, monocarpic, polycarpic

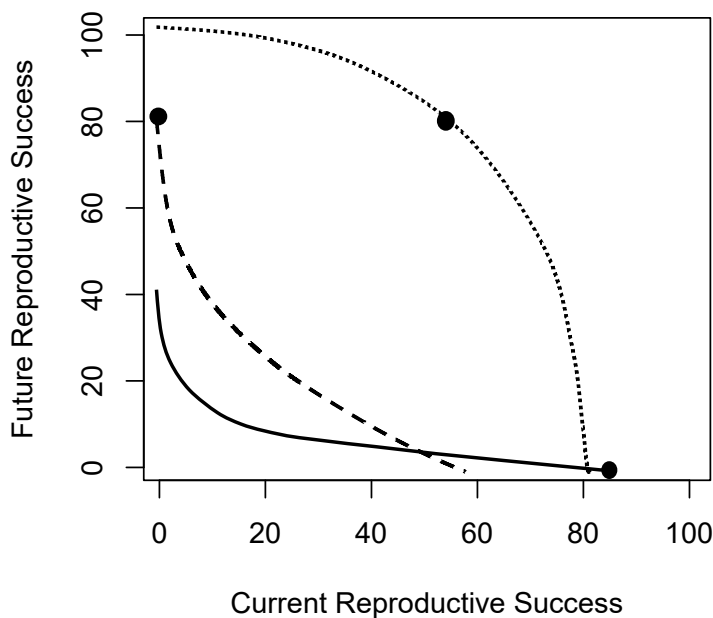
50
51 **Introduction**

52
53 A long-standing issue for plant ecologists is understanding the conditions under which
54 different life histories evolve. Herbaceous plants (plants with aboveground structures that die
55 back between growing seasons) show a wide variety of life histories; some use all resources for
56 reproduction in a single growing season and die (i.e., semelparous or monocarpic plants), while
57 others reproduce in several growing seasons (i.e., iteroparous or polycarpic plants). Among those
58 that use all resources for a single, suicidal reproductive event, some reproduce and die in their
59 first growing season (i.e., annuals) while some forego reproduction for several seasons before
60 reproducing (i.e., monocarpic perennials). Polycarpic herbaceous plants also vary in the extent

61 and duration of periods of prolonged dormancy in which no aboveground parts are produced, and
62 therefore no reproduction or photosynthesis can occur (e.g., Lesica & Steele, 1994; Lesica &
63 Crone, 2007; Shefferson *et al.*, 2018). Classic life history theory provides some insight into the
64 general demographic tradeoffs that might favor the evolution of such life histories [e.g.,
65 (Charnov & Schaffer, 1973; Stearns, 1976; Hart, 1977)] but does not elucidate how these
66 conditions arise from the resource allocation tradeoffs individuals face. A mechanistic
67 understanding of the role of natural selection in generating these diverse life histories requires
68 understanding the factors that shape the relationship between individuals' resource allocation and
69 their expected lifetime reproductive success.

70 If resources are limited, plants face a tradeoff between allocating resources to
71 reproduction in the current growing season and to storage for the next growing season.
72 Allocating more resources to reproduction increases current reproductive output, but if all
73 resources are used for reproduction the plant must die. Allocating resources to storage, on the
74 other hand, may increase future resource accumulation by increasing survival (Boyce & Volenec,
75 1992) and facilitating growth in subsequent growing seasons (Zimmerman & Whigham, 1992;
76 Wyka, 1999). This creates a tradeoff between current and future reproductive success. The
77 consequences of this tradeoff for a plant's expected lifetime reproductive success can be
78 illustrated by a curve relating current reproduction and expected future reproduction over the
79 range of available allocation options, ranging from completely foregoing current reproduction to
80 using all resources to reproduce and dying (Fig. 1) (Gadgil & Bossert, 1970; Schaffer, 1974;
81 Pianka & Parker, 1975; Pianka, 1976). If plants have evolved resource allocation strategies that
82 maximize lifetime reproduction, then a plant's resource allocation should optimally balance this
83 tradeoff by maximizing the sum of current and future expected reproduction (Fig. 1) (Gadgil &
84 Bossert, 1970; Schaffer, 1974; Pianka & Parker, 1975; Pianka, 1976).

85



86
 87 Figure 1. Examples of potential tradeoffs between current and future reproductive success. Points
 88 represent the allocation of resources to current reproduction that maximizes the sum of current
 89 and future reproductive success. If small allocations to current reproduction strongly decreases
 90 future reproductive success (solid line and dashed line), then individuals should allocate either all
 91 (solid line) or none (dashed line) of their resources to reproduction. If small allocations to current
 92 reproduction only weakly decrease future reproductive success, individuals should allocate an
 93 intermediate proportion of available resources to current reproduction (dotted line).

94
 95 The way in which the tradeoff between current and future reproduction changes over a
 96 plant's lifetime determines the schedule of allocation decisions that should evolve by natural
 97 selection (Pianka & Parker, 1975; Pianka, 1976). Determining the factors that underlie changes
 98 in the tradeoff between current and future reproduction over a plant's lifetime is therefore critical
 99 for determining the conditions under which different life history strategies should evolve. In
 100 general, current reproductive success depends on the resources available for reproduction and the
 101 efficiency with which resources allocated to reproduction can be converted into offspring. Future
 102 reproductive success, on the other hand, depends on the relationship between the resources

103 retained as storage and the resources available in the next growing season, as well as the
104 probability of survival.

105 Previous models of plant life history strategies have primarily focused on the effect of
106 storage on future resources (Iwasa & Cohen, 1989; Klinkhamer *et al.*, 1997; but see Pugliese,
107 1988). These models assume that net photosynthate production increases monotonically with the
108 size of the plant's photosynthetic structures and that plants with greater storage at the beginning
109 of the growing season are capable of producing a larger initial photosynthetic biomass. This
110 results in a positive relationship between storage and future resource availability. However, this
111 implicitly assumes that the allometric scaling of gross resource production and maintenance is
112 similar. More recent theory suggests that resource production may generally increase less
113 quickly with biomass than the costs of maintaining existing tissues (West *et al.*, 2001). Thus, net
114 resource production initially increases with biomass due to the increase in gross resource
115 production, but decreases to zero as the costs of maintaining existing tissues approach the total
116 quantity of resources produced (West *et al.*, 2001). Net resource production may therefore be
117 greatest at an intermediate biomass [i.e., a unimodal function of biomass, (West *et al.*, 2001)]. As
118 a result, the benefit of increasing storage to begin the growing season with greater biomass may
119 be fundamentally limited by the costs of maintaining existing tissues. This would contrast
120 previous models in which the benefit of beginning the season with greater biomass depends only
121 on the net photosynthetic rate and the length of the growing season (Iwasa & Cohen, 1989). How
122 this difference in the relationship between storage and future resource availability affects the
123 optimal life history strategy of herbaceous plants is currently unexplored.

124 Instead of sprouting in a given growing season, herbaceous plants may stay below ground
125 in what has been referred to as "prolonged dormancy" or "vegetative dormancy" (Lesica &
126 Steele, 1994; Shefferson *et al.*, 2018). Prolonged dormancy has been widely proposed to
127 represent a bet-hedging strategy that reduces variation in fitness caused by temporal variation in
128 environmental conditions (Shefferson, 2009; Jäkäläniemi *et al.*, 2011; Hawryzki *et al.*, 2011;
129 Gremer *et al.*, 2012; Gremer & Sala, 2013). However, the evolution of prolonged dormancy may
130 also be favored by costs associated with the seasonal re-growth of aboveground structures *per se*
131 (e.g., reduced potential for future growth and reproduction due to expenditure of resources stored
132 in perennating organs, or greater mortality due to increased herbivory or water stress) (Lesica &
133 Crone, 2007; Shefferson, 2009; Shefferson *et al.*, 2014, 2018). Entering prolonged dormancy

134 may allow plants to circumvent these costs while also potentially accumulating resources that
135 increase survival or reproduction in subsequent growing seasons. Shefferson et al. (2014) found
136 that observed frequencies of prolonged dormancy in yellow lady's slipper orchid (*Cypripedium*
137 *parviflorum*) and common hepatica (*Anemone americana*) were better predicted by demographic
138 models that incorporated relationships between prolonged dormancy and survival in subsequent
139 growing seasons than those that accounted for stochastic environmental variation. Similarly, in
140 Spalding's silene (*Silene spaldingii*), prolonged dormancy was associated with increased
141 flowering probabilities in subsequent growing seasons (Lesica & Crone, 2007). In bitterroot
142 milkvetch (*Astragalus scaphoides*), plants that prolonged dormancy had lower concentrations of
143 stored non-structural carbohydrates (NSC) at the beginning of the growing season but
144 accumulated as much NSC by the end of the growing season as plants that sprouted (Gremer *et*
145 *al.*, 2010). More generally, prolonged dormancy appears to be more common among herbaceous
146 plants that accumulate resources through mycorrhizal associations and may therefore be less
147 dependent upon photosynthesis for resource production (Shefferson *et al.*, 2018). While these
148 empirical data suggest a role of prolonged dormancy in balancing life history tradeoffs caused by
149 costs of sprouting, to our knowledge no theoretical study has assessed the plausibility of costs of
150 sprouting as a general explanation for the evolution of prolonged dormancy in herbaceous plants.

151 In this study, we use a stochastic dynamic programming model that explicitly links
152 individuals' allocation decisions with their current and future reproductive success to predict the
153 schedules of reproduction and prolonged dormancy that maximize lifetime reproductive success.
154 The tradeoff between current and future reproduction in the model emerges from mechanistic
155 descriptions of the consequences of a plant's resource allocation, including allocating resources
156 to sprouting. Similar models have been used previously to predict optimal life history strategies
157 in plants (e.g., (Pugliese, 1988; Iwasa & Cohen, 1989; Klinkhamer *et al.*, 1997), and we expand
158 on this foundation in four key directions. First, we derive the relationship between a plant's
159 storage and its future resource production using a mechanistic model of resource production that
160 accounts for differences in the scaling of resource production and maintenance costs with mass
161 (West *et al.*, 2001). Second, the relationship between storage and future resource production in
162 our model accounts for the effect of mass on survival during the growing season (Cook, 1980;
163 Solbrig, 1981; Schmitt *et al.*, 1987; Cain, 1990; Roach & Gampe, 2004; Shefferson, 2006;
164 Tenhumberg *et al.*, 2015). Third, we account for the effect of a plant's storage on the probability

165 that it survives to the next growing season (Boyce & Volenec, 1992). Fourth, we incorporate the
166 potential for plants to enter prolonged dormancy to explore the conditions under which periods
167 of prolonged dormancy represent an adaptive solution to resource allocation tradeoffs associated
168 with sprouting.

169

170 *Methods*

171

172 *Model Overview*

173

174 The model considers exclusively sexually reproducing, herbaceous plants that are either
175 hermaphroditic or female, are not pollen limited, and which grow in seasonal environments and
176 must therefore spend the non-growing season below ground. We are concerned with predicting
177 the between-season resource allocation strategies that maximize plant fitness; thus, we divide a
178 plant's life into discrete growing seasons $y = (1, 2, 3, \dots, Y)$, beginning with the first growing
179 season in which a seed germinates. We used stochastic dynamic programming (SDP) to
180 determine the life history decisions at the end of each growing season that maximize a plant's
181 lifetime reproductive success. An SDP model has three components: the state variables and their
182 dynamics, the set of decisions, and the pay-off function (Bellman, 1957; Clark & Mangel, 2000).
183 The optimal set of decisions for a given state maximizes the total fitness (i.e., the sum of current
184 and future fitness) from the current time point to the end of the individual's lifetime (Bellman,
185 1957; Clark & Mangel, 2000). Current fitness depends on the consequences of a given set of
186 decisions for immediate reproductive output, whereas future fitness depends on how the
187 consequences of those decisions for an individual's state affect the total fitness gained from the
188 next season onward. To avoid searching all possible sequences of future decisions forward in
189 time to calculate the future fitness associated with the state in the next season, we work
190 backward in time from the end of an individual's life (Y), taking advantage of the fact that the
191 optimal decision for each state maximizes fitness from that season onward. Thus, the future
192 fitness payoffs for the different states that an individual could possess in the next season as a
193 result of their decisions are already known—they are the total fitness payoffs already calculated
194 for the next season. The optimal state-dependent decisions predicted by the model can then be

195 used to predict the optimal life history (i.e., the among-season schedule of reproduction and
196 dormancy) given an individual's initial state.

197 Our model considers three states V , D , and y . V specifies the amount of resources at the
198 beginning of the growing season (hereafter “spring storage” for brevity, although the model also
199 applies to plants growing in non-temperate seasonal environments), D specifies whether a plant
200 sprouted ($D = 0$) or entered prolonged dormancy ($D = 1$), and y indicates plant age in growing
201 seasons. Thus, for a plant of a given spring storage V and dormancy status D having experienced
202 y previous growing seasons, the expected fitness accrued between season y and the end of the
203 plant's lifetime Y is $F[V, D, y]$. For an exclusively sexually reproducing plant, the expected
204 fitness can be approximated by the sum of seed production in the current season and the expected
205 seed production in all future seasons of life, assuming the plant expresses the optimal life history
206 strategy in future seasons. We do not attempt to model the optimal allocation of resources used
207 in reproduction among offspring (i.e., the model does not consider tradeoffs between quantity
208 versus quality of offspring) and, for simplicity, we assume that any reproduction takes place in a
209 single reproductive bout at the end of the growing season. We set the terminal fitness function
210 (i.e., the future fitness expectation for a plant in the final season Y of its life, $F[V, D, Y + 1]$) to 0
211 because no fitness can be accrued after death. A plant's expected lifespan depends on how
212 resources are allocated (described below). Thus, to ensure that our model predictions are not
213 affected by the assumption of a fixed lifespan (Houston & McNamara, 1985; Real, 1990) we set
214 Y to 1000 growing seasons, which is much larger than the maximum possible lifespan given our
215 model parameters (Table 1). We consider values of $V = (0, 1, 2, 3, \dots, 150)$, as this well exceeds
216 the amount of spring storage that plants accumulate over their lifetime for the parameter values
217 we explore. Thus, the state space for our model consisted of $V = (0, 1, 2, 3, \dots, 150)$, $D = (1, 2)$,
218 and $y = (1, 2, 3, \dots, 1000)$, for a total of 300,000 combinations of state variables.

219 The life history decisions we focus on are (1) the dormancy status in the next growing
220 season [sprouting ($D = 0$) or prolonged dormancy ($D = 1$)] and (2) the proportion r of resources
221 allocated to reproduction in the current growing season versus storage kept over the non-growing
222 season (hereafter “overwinter storage”). Note that we do not model seed dormancy, but rather
223 prolonged dormancy *sensu* Lesica & Steele (1994), in which plants remain underground during
224 one or more growing seasons following germination. The initiation and maintenance of
225 prolonged dormancy is poorly understood; however, at least some of the physiological changes

226 that determine the conditions under which plants resume growth appear to occur at the onset of
 227 seasonal dormancy (Tylewicz *et al.*, 2018). We therefore assume that both decisions occur at the
 228 end of each growing season. Because the optimal allocation to reproduction r may depend on
 229 whether the plant decides to enter dormancy or sprout in the next season, we assume that these
 230 decisions are made simultaneously. In other words, fitness is maximized over the possible
 231 combinations of r and D ; a plant's reproductive allocation is not constrained by a prior choice of
 232 dormancy status in the next season, nor vice versa.

233 Importantly, the options available to the plant at the end of a growing season depend on
 234 its current dormancy state. For sprouted plants (current dormancy $D = 0$), the plant may allocate
 235 a proportion r of the resources expected to be available at the end of the season, $S(y)$, to
 236 reproduction, with the remainder $(1 - r) * S(y)$ retained as overwinter storage, and decide
 237 whether to sprout again in the next season (D stays 0) or enter prolonged dormancy (D changes
 238 to 1). Because resources are typically lost between growing seasons (Wyka, 1999), the spring
 239 storage in the next growing season $V(1 - r, y + 1) = \gamma * (1 - r) * S(y)$, where γ represents the
 240 proportion of storage remaining after overwintering (e.g., due to losses from respiration,
 241 herbivory, or disease). Thus, for sprouted plants ($D = 0$), the fitness payoff associated with the
 242 optimal life history decisions is

$$F[V,0,y] = \max_{D,r} \{R(r) + \xi(1 - r) * F[V(1 - r, y + 1), D, y + 1]\} \quad (1)$$

243 where *max* indicates that the optimal plant life history decisions are the options that maximize
 244 the expected fitness, and the letters below the *max* indicates the decisions over which fitness is
 245 maximized. Thus, plants use the combination of dormancy decision D and allocation to
 246 reproduction r that maximizes the expected fitness. The $R(r)$ term specifies the number of
 247 offspring produced in the current growing season given r , which is either a linear or increasing
 248 exponential function of the quantity of resources allocated to reproduction, $R(r) = \beta[r * S(y)]$
 249 (Schaffer, 1974; Klinkhamer *et al.*, 1997). An increasing exponential relationship between
 250 offspring number and resources allocated to reproduction might arise if successful reproduction
 251 requires a large quantity of reserves to produce a large bolting structure [i.e., the "reproductive
 252 effort model" (Schaffer, 1974)] or to saturate seed predators (Janzen, 1976; Klinkhamer *et al.*,
 253 1997). The term $\xi(1 - r)$ represents the probability of surviving between growing seasons
 254 (hereafter "overwinter survival"), which depends on overwinter storage (Boyce & Volenec,
 255 1992), $(1 - r) * S(y)$, and is given by

$$\xi(1 - r) = 1 / \{1 + \exp[-\xi_0 - \xi_1 * (1 - r) * S(y)]\}. \quad (2)$$

256 This implies that any increase in r which determines seed production (current fitness) is traded
 257 off with a reduction in overwinter survival (future fitness). The term $F[V(1 - r, y + 1), D, y + 1]$
 258 represents the expected fitness from the next season onward, which depends on both the
 259 dormancy decision D and the allocation to reproduction r .

260 Dormant plants (current dormancy $D = 1$) cannot allocate any resources to reproduction
 261 in the current season ($r = 0$) because sexual reproduction cannot occur in the absence of
 262 aboveground structures. Thus, dormant plants only need to decide whether to remain dormant in
 263 the next growing season (D stays 1) or sprout (D changes to 0). The fitness payoff associated
 264 with the optimal life history decision for dormant plants ($D = 1$) is therefore

$$F[V, 1, y] = \max_D (\xi(1) * F[V(1, y + 1), D, y + 1]), \quad (3)$$

265 where fitness is maximized over the decision to sprout in season $y + 1$ ($D = 0$) or remain in
 266 prolonged dormancy instead ($D = 1$). Plants face the same overwintering conditions regardless of
 267 their decision to sprout or remain dormant in the next growing season, so overwinter survival ξ is
 268 independent of this decision and the spring storage in the following year is $V(1, y + 1)$
 269 $= 1 * \gamma * S(y)$. We assume that dormant plants have the potential to accumulate reserves during
 270 the growing season (i.e., $S(y) > 0$); these dynamics are described below (see *Within-season*
 271 *Resource Dynamics for Dormant Plants*).

272

273 *Within-season Resource Dynamics for Sprouting Plants:*

274

275 The resources available to a plant at the end of the season, $S(y)$, depends on the dormancy
 276 status of the plant. At the beginning of the first growing season and each subsequent season in
 277 which the plant sprouts (as opposed to entering or remaining in prolonged dormancy), the plant
 278 generates an aboveground photosynthetic structure of initial size $m_0(y)$ by converting stored
 279 resources (e.g., carbon, nitrogen) contained in the seed [$V(y = 1)$] or kept as overwinter storage
 280 from the previous growing season [$V(y > 1)$] with a conversion efficiency $0 \leq \alpha \leq 1$ (Chapin *et*
 281 *al.*, 1990) such that $m_0(y) = \alpha * V(y)$. Greater quantities of spring storage $V(y)$ thus support the
 282 generation of larger m_0 , consistent with empirical data (Zimmerman & Whigham, 1992; Wyka,
 283 1999) and theory predicting that plants should use stored resources to produce m_0 at the
 284 maximum possible rate before switching to rely on newly acquired resources for biomass

285 production (Iwasa & Cohen, 1989). It is possible that plants possess stored resources too large to
 286 exhaust by constructing m_0 at the maximum rate (Iwasa & Cohen, 1989) and consequently retain
 287 a portion of $V(y)$ as storage during the growing season. Including this possibility in our model
 288 did not affect the qualitative predictions of our model (because it is rarely optimal for plants to
 289 keep such a large amount of resources), so we present results for the simpler scenario in which
 290 plants exhaust their storage to produce the initial aboveground structure. After constructing m_0 ,
 291 plants acquire new resources over time in the growing season $0 \leq t \leq T$, where t is time within
 292 the season and T the length of the growing season. These resources are used to maintain existing
 293 tissues, to grow the size of the aboveground photosynthetic structure $m(t)$, and to increase the
 294 pool of stored reserve resources $s(t)$. The expected stored reserves available for reproduction and
 295 overwinter storage at the end of the season, $S(y)$, equal the total reserves accumulated by the end
 296 of the season $s(T)$ weighted by the probability μ of surviving to T .

297 To determine $s(T)$, we modified the general ontogenetic growth model of West et al.
 298 (West *et al.*, 2001) to consider the seasonal regrowth of photosynthetic structures and
 299 accumulation of stored reserves by an herbaceous plant. Gross photosynthate production at time t
 300 in the growing season increases with aboveground biomass $m(t)$ as $am(t)^{3/4}$ (Enquist *et al.*, 1998),
 301 where a is a taxon-specific constant and $m(t = 0) = m_0(y)$. The rate at which photosynthate is
 302 used to maintain existing tissues increases in direct proportion to biomass $bm(t)$ (West *et al.*,
 303 2001). Because reserves $s(t)$ are in part stored within vacuoles and plastids within existing
 304 cellular structures (Matile, 1987; Chapin *et al.*, 1990; Lewis & McCourt, 2004), we assume that
 305 the maintenance cost per unit of reserve resources (denoted c) is less than that of aboveground
 306 structures (denoted b). Thus, the net photosynthate $p(t)$ available to the plant at time t within the
 307 growing season is

$$p(t) = am(t)^{3/4} - bm(t) - cs(t), \quad 0 \leq t \leq T. \quad (4)$$

308 The amount of resources available to a plant at the end of the growing season $s(T)$ depends on a
 309 plant's investment into growing photosynthetic biomass, $m(t)$. Up to a point, greater investment
 310 in growing $m(t)$ increases $s(T)$ through compounding returns in terms of new resources gained
 311 (Chapin *et al.*, 1990). However, plants investing everything into $m(t)$ have no reserves left at the
 312 end of the growing season. Thus, $s(T)$ should tend to be highest for intermediate investments in
 313 photosynthetic biomass. Let g be the proportion of net photosynthate allocated to $m(t)$, and the
 314 remainder $(1 - g)$ is allocated to reserves $s(t)$. Assuming g does not change over the growing

315 season, the aboveground biomass $m(T)$ and reserve biomass $s(T)$ accumulated by the end of the
 316 season of length T are

$$m(T) = m_0 + g \int_0^T p(t) dt = m_0 + g \int_0^T [am(t)^{3/4} - bm(t) - cs(t)] dt, \quad 0 \leq t \leq T, \quad (5)$$

$$s(T) = (1 - g) \int_0^T p(t) dt = (1 - g) \int_0^T [am(t)^{3/4} - bm(t) - cs(t)] dt, \quad 0 \leq t \leq T. \quad (6)$$

317 In general, the change in m and s over t follows a logistic trajectory identical to that of the
 318 phenomenological von Bertalanffy growth model (Von Bertalanffy, 1957), in which growth
 319 slows as maintenance costs of existing tissues approaches the rate at which new resources are
 320 produced (West *et al.*, 2001).

321 The increase in initial photosynthetic biomass m_0 with spring storage $V(y)$ causes the
 322 relationship between $s(T)$ and g to differ among plants with different $V(y)$. Plants with greater
 323 spring storage $V(y)$ can, up to a point, accumulate greater $s(T)$ (Fig. S1), provided they allocate a
 324 smaller proportion g of net photosynthate to $m(t)$ to avoid excessive maintenance costs.
 325 However, if $V(y)$ is too large the plant accumulates fewer reserves than plants with smaller $V(y)$
 326 (Fig. S1), even if no net photosynthate is allocated to increasing m (i.e., $g = 0$). Thus, the
 327 difference in the scaling exponents for gross photosynthesis $am(t)^{3/4}$ and maintenance $bm(t) + cs(t)$
 328 causes the maximum quantity of reserves a plant can accumulate by T to be greatest for
 329 intermediate spring storage $V(y)$ (Fig. S1) because net photosynthate production is maximized at
 330 intermediate values of total biomass (West *et al.*, 2001).

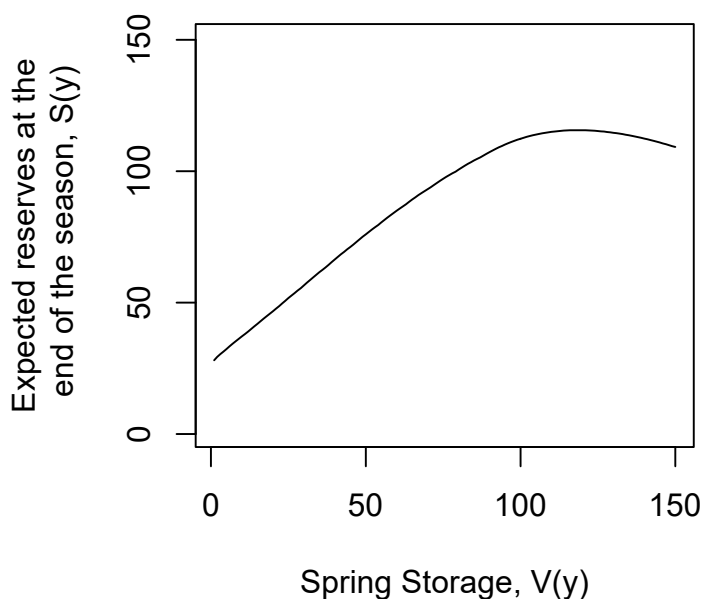
331 The probability of plants surviving the growing season increases with the size of the
 332 plant's aboveground structures (Cook, 1980; Solbrig, 1981; Schmitt *et al.*, 1987; Cain, 1990;
 333 Roach & Gampe, 2004; Shefferson, 2006; Tenhumberg *et al.*, 2015; but see Goldstein *et al.*,
 334 1985; Zhang *et al.*, 2009). We model the survival probability of a sprouted plant μ as an
 335 increasing logistic function of initial aboveground biomass m_0 and the allocation to growth g
 336 because larger values of either result in greater biomass during the growing season (Fig. S2). The
 337 effect of g depends on the length of the growing season, T . As T increases, μ increases more
 338 strongly with g because plants that allocate few resources to aboveground structures must
 339 survive a longer period of time at greater mortality risk. Thus

$$\mu = 1 / \{1 + \exp[-(\mu_0 - \mu_1 * m_0 - \mu_2 * g - \mu_3 * T - \mu_4 * g * T)]\}, \quad (7)$$

340 where $\mu_0 - 4$ represent the regression coefficients associated with the intercept (on the log odds
 341 scale), initial aboveground biomass m_0 , allocation to growth g , season length T , and the
 342 interaction between g and T , respectively.

343 In summary, the proportion g of net photosynthate allocated to photosynthetic structures
 344 versus storage during the growing season affects both the total reserves accumulated by the end
 345 of the season $s(T)$ and the probability μ of surviving to the end of the season. In our model, we
 346 used values of g that produce the greatest possible expected reserves at the end of the season,
 347 $S(y)$, for a given $V(y)$ (i.e., the greatest product of $s(T)$ and μ) (Fig. 2, Fig. S3).

348



349
 350 Figure 2. Relationship between spring storage $V(y)$ and the expected reserves available for
 351 reproduction and overwinter storage at the end of the growing season, $S(y)$. The expected
 352 reserves are equal to the total reserves accumulated, $s(T)$, weighted by the probability of survival
 353 μ . The reduction in $S(y)$ at high values of $V(y)$ is due to the costs of maintaining existing tissues.

354

355 *Within-season Resource Dynamics for Dormant Plants*

356

357 How stored resources change during the growing season for plants that undergo
 358 prolonged dormancy is relatively poorly understood. While stored resources are known to
 359 decline during seasonal dormancy (Boyce & Volenec, 1992; Wyka, 1999), some empirical
 360 evidence suggests that resource dynamics during prolonged dormancy may differ fundamentally
 361 from those during seasonal dormancy; indeed, plants undergoing prolonged dormancy may
 362 acquire similar quantities of resources as sprouted plants (Gremer *et al.*, 2010). The underlying
 363 processes may include the remobilization of structural carbohydrates (Gremer *et al.*, 2010) or the
 364 acquisition of new resources from mycorrhizal fungi (Shefferson, 2009; Shefferson *et al.*, 2018).
 365 The net outcome of such processes is likely an increasing function of the spring storage $V(y)$, as
 366 plants with larger storage may have greater quantities of structural carbohydrate and more
 367 extensive fungal connections but also pay greater maintenance costs. Thus, the reserve biomass
 368 accumulated by the end of the growing season, given the spring storage $V(y)$, is

$$s(T) = [i * V(y)] / [1 + i * \lambda * V(y)], \quad (8)$$

369 where i represents the maximum per-unit-storage rate of storage accumulation during prolonged
 370 dormancy and λ is the reciprocal of the theoretical maximum storage size. This parameterization
 371 allows us to consider scenarios in which $s(T)$ is relatively independent of $V(y)$ (i.e., high i),
 372 approximately a linear function of $V(y)$ (i.e., low i), or a saturating function of $V(y)$ (i.e.,
 373 intermediate i). A plant in prolonged dormancy survives to the end of the growing season with
 374 probability ν . We assume that survival increases with spring storage $V(y)$, as plants with greater
 375 spring storage are more likely to meet metabolic demands during the growing season. Thus, the
 376 probability of survival for a dormant plant ν is

$$\nu = 1 / \{1 + \exp[-\nu_0 - \nu_1 * V(y)]\}. \quad (9)$$

377 The expected stored reserves available at the end of the season, $S(y)$, then equal the total reserves
 378 accumulated by the end of the season $s(T)$ weighted by the probability ν of surviving to T .

379

380 **Results**

381

382 The SDP uses expected values for all life history parameters (Table 1), which do not vary
 383 between growing seasons y to predict the optimal resource allocation to reproduction, r^* , and
 384 whether a plant should enter dormancy, D . Further, our model does not assume a deterministic
 385 lifespan Y . Hence, changes in a plant's allocation patterns over its lifetime are determined by

386 changes in its storage $V(y)$, but are independent of y . To explore the conditions favoring the
 387 evolution of different life history strategies, we varied model parameters that influence 1) the
 388 relationship between overwinter storage and overwinter survival ξ , 2) the relationship between
 389 overwinter storage and expected future reserve availability $S(y + 1)$, 3) the relationship between
 390 the reserves allocated to reproduction $r * S(y)$ and the number of offspring produced, and 4) the
 391 benefits of entering prolonged dormancy. Default parameter values are provided in Table 1. We
 392 first describe the conditions under which the model predicts that a monocarpic life history should
 393 evolve. Monocarpic plants use all expected reserves $S(y)$ for a single reproductive event and die.
 394 If the flowering event happens after the first growing season, such plants are also annuals ($r^* = 1$
 395 at $y = 1$), otherwise they are monocarpic perennial plants. We then describe the factors
 396 underlying quantitative differences in resource allocation for polycarpic plants [i.e., plants that
 397 flower in more than one growing season over their lifetime and thus keep overwinter storage (r^*
 398 < 1)]. Finally, we explore the conditions under which prolonged dormancy can evolve in
 399 response to resource allocation tradeoffs associated with sprouting.

400

401

Symbol	Definition	Value
Y	Number of growing seasons	1000
α	Efficiency of converting storage to initial aboveground biomass	0.5
a	Maximum rate of photosynthate production per unit aboveground biomass	0.35
b	Metabolic costs of maintenance per unit aboveground biomass	0.10
c	Increase in metabolic maintenance cost per unit storage	0.01
T	Growing season length	150
μ_0	Minimum log odds of surviving the season	-1.35
μ_1	Effect of m_0 on the odds of surviving the season	0.09

μ_2	Effect of growth g on the odds of surviving the season	2.17
μ_3	Effect of T on the odds of surviving the season	-0.005
μ_4	Interaction between growth g and T on the odds of surviving the season	0.007
ξ_0	Minimum log odds of surviving over winter	-3.75
ξ_1	Effect of overwinter storage $(1 - r) * S(y)$ on the odds of overwinter survival	0.20
γ	Proportion of storage remaining after overwintering period	0
i	Maximum rate of storage increase per unit storage during prolonged dormancy	1
ν_0	Minimum log odds of survival during prolonged dormancy	0.5
ν_1	Effect of V on the odds of surviving the season	0.012

402 Table 1. Default parameter values used for the stochastic dynamic programming (SDP) model.

403

404 *Monocarpic Life Histories*

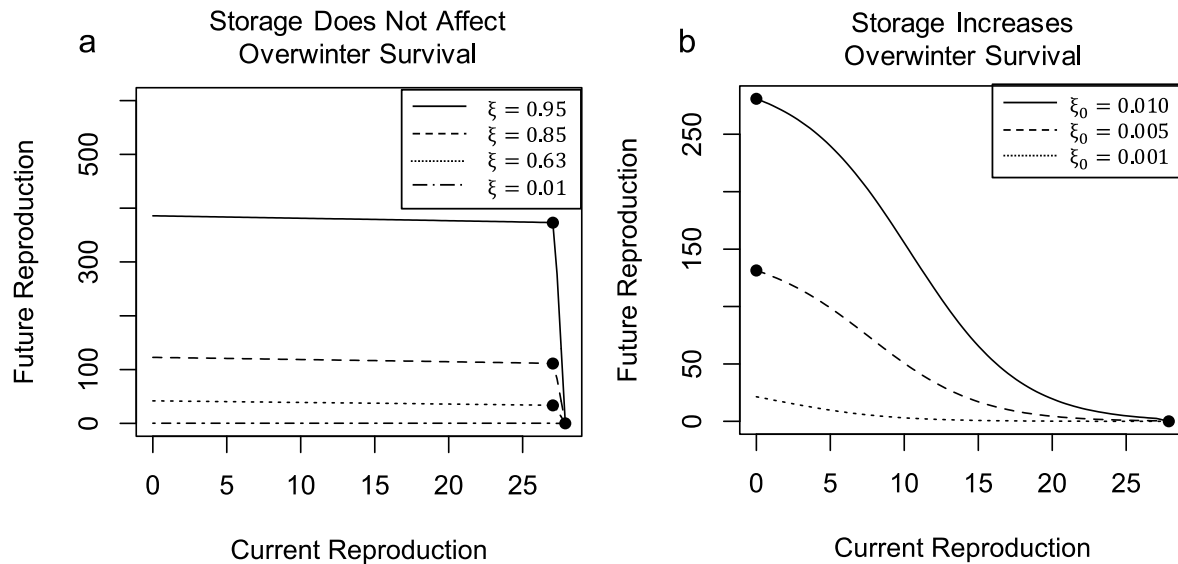
405

406 Our model predicts two situations in which plants should express a monocarpic life
 407 history in which all reserves $S(y)$ are used in a single, suicidal reproductive event [i.e., $r^* = 1$ for
 408 at least some $V(y)$]. In the first case, $r^* = 1$ for all $V(y)$; this implies that plants are obligate
 409 annuals, as $r = 1$ maximizes lifetime offspring production for any possible storage available in
 410 the seed $V(y = 1)$. This occurs if (1) the probability of surviving the winter ξ is low, (2) the
 411 expected reserves $S(y)$ that can be acquired during the growing season are low, or (3) a large
 412 proportion γ of storage is lost during the winter period.

413 In our model, the range of overwinter survival conditions for which an obligately annual
 414 strategy [i.e., $r^* = 1$ for all $V(y)$] is optimal depends strongly on the assumption that overwinter
 415 storage affects survival to the next growing season. This can be illustrated by comparing the
 416 tradeoff between current reproduction [i.e., $R(r)$] and future reproduction {i.e., $\xi(1 - r) * F$
 417 $[V(1 - r, y + 1), D, y + 1]$ } for different minimum probabilities of surviving the winter (defined

418 on the log-odds scale by ξ_0) to a scenario in which overwinter survival is independent of storage
 419 (i.e., ξ is fixed). While the precise shape of this tradeoff varies with spring storage $V(y)$, the
 420 range of overwinter survival conditions for which $r^* = 1$ is the same for all $V(y)$; thus, we can
 421 infer changes in the range of survival conditions for which an obligately annual strategy is
 422 optimal by visualizing the tradeoff between current and future reproduction for a single $V(y)$
 423 (Fig. 3).

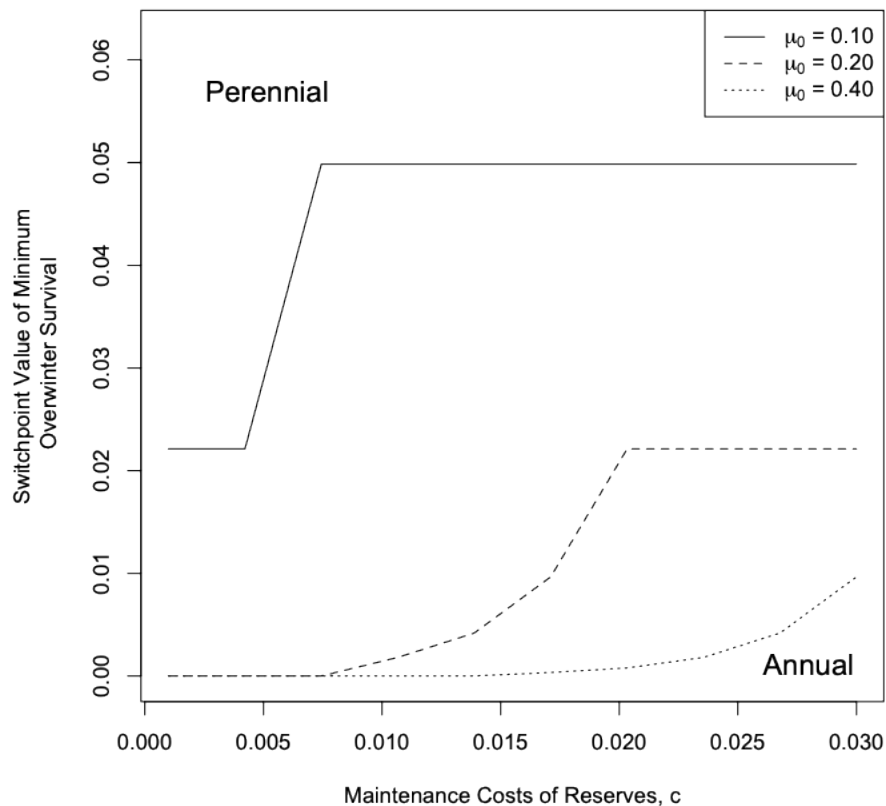
424 If overwinter survival is independent of overwinter storage, then the tradeoff between
 425 current and future reproduction is exceptionally weak (i.e., increasing current reproduction has
 426 little effect on future reproduction, Fig. 3a). This is because the benefit of large $V(y)$, and thus
 427 m_0 , is small due to the costs of maintenance (Fig. 2). Hence, for most survival scenarios, the sum
 428 of current and future reproduction is maximized when individuals keep a small quantity of
 429 reserves as storage and invest any remaining reserves in current reproduction (filled circles on
 430 solid, dashed, and dotted lines in Fig. 3a). This implies that a perennial polycarpic strategy is
 431 optimal and, because the quantity of storage kept is small, even plants with low $V(y)$ (e.g., early
 432 in life) can generate enough reserves to reproduce. An annual life history (i.e., using all reserves
 433 for current reproduction, filled circle on dash-dotted line in Fig. 3a) is predicted to evolve only if
 434 overwinter survival is exceptionally low (e.g., $\xi = 0.01$). In contrast, if plants can use storage to
 435 increase overwinter survival, then allocating resources to current reproduction drastically reduces
 436 future reproductive success (Fig. 3b) and, for most survival scenarios, plants should keep large
 437 quantities of storage to capitalize on future reproductive potential. This once again implies a
 438 perennial polycarpic strategy is optimal. However, because the quantity of storage kept is very
 439 large, plants with lower $V(y)$ may forego reproduction in the current growing season entirely
 440 (filled circles on solid and dashed lines in Fig. 3b). An obligately annual strategy becomes
 441 optimal if the minimum survival probability is low (filled circle on dotted line in Fig. 3b), but
 442 this occurs at values of minimum overwinter survival (ξ_0) for which a plant foregoing
 443 reproduction would still achieve a relatively high probability of survival (e.g., $\xi = 0.63$). In fact,
 444 a plant foregoing reproduction would experience the same probability of survival ($\xi = 0.63$) for
 445 which a perennial strategy is optimal if overwinter survival is independent of storage (cf. Fig.
 446 3a,b). Thus, when accounting for maintenance costs, the effect of storage on overwinter survival
 447 causes our model to predict an obligately annual strategy even if overwinter survival is relatively
 448 large.



449
 450 Figure 3. The effect of overwinter survival on the tradeoff between current and future
 451 reproductive success for scenarios in which the probability ξ of surviving over the winter a) is
 452 independent of overwinter storage or b) increases with overwinter storage. Note that in b) line
 453 types correspond to different minimum probabilities of survival ξ_0 . Points represent the
 454 allocation of resources to current reproduction that maximizes the sum of current and future
 455 reproductive success. Note that the precise shape of the curves, and thus the optimal allocation of
 456 resources, depends on spring storage $V(y)$; results are shown for $V(y) = 20$.

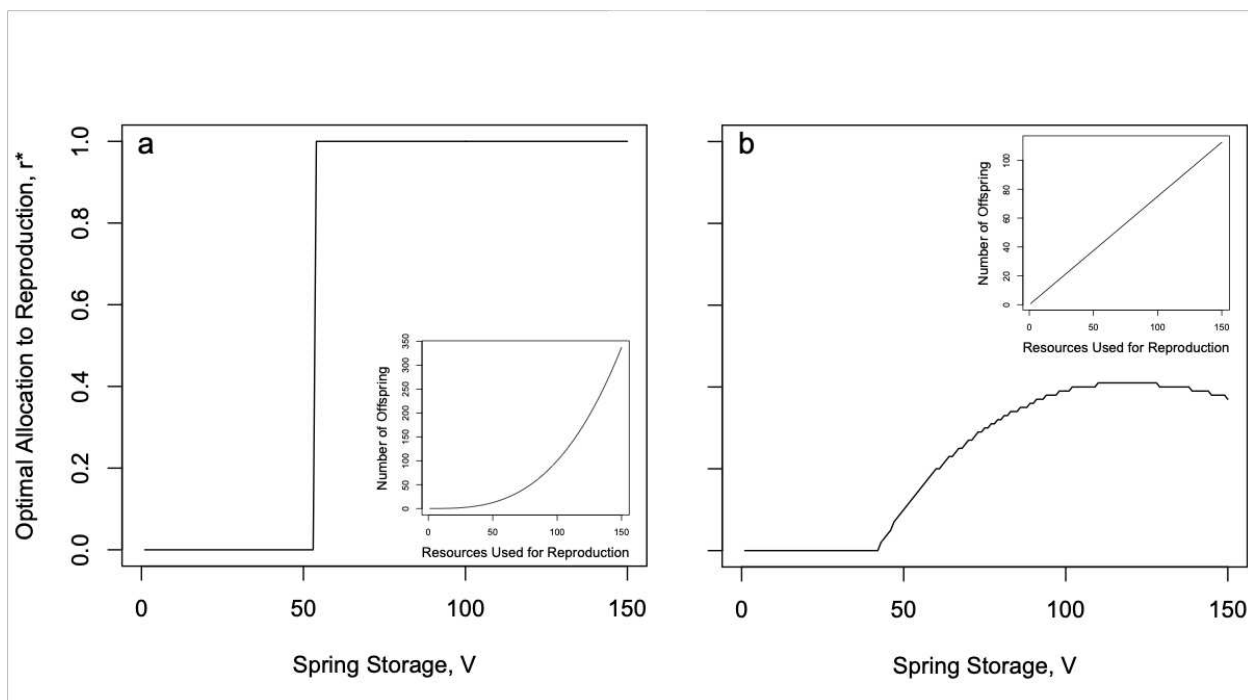
457
 458 Conditions leading to low expected reserves at the end of the season $S(y)$ generally
 459 decrease the benefit of allocating reserves to overwinter storage because $S(y)$ determines the
 460 maximum quantity of storage as well as the expected reserve acquired in the next growing
 461 season (*Notes S1*). In contrast to previous models that ignore maintenance costs, we find that the
 462 per-unit-biomass costs of maintaining reserves c is a key parameter influencing $S(y)$ and, thus,
 463 the conditions under which an obligately annual life history evolves. As maintaining storage
 464 becomes more expensive (i.e., c increases), $S(y)$ decreases, particularly for plants with high
 465 spring storage $V(y)$ (Fig. S4a). Consequently, the minimum overwinter survival probability ξ_0 at
 466 which an annual strategy becomes optimal (i.e., the switchpoint value) increases with c (Fig. 4).
 467 For a given c , the range of overwinter survival conditions for which an annual strategy is optimal
 468 increases further if the probability of surviving growing season is lower (illustrated by different

469 μ_0 values, in Fig. 4), as this further decreases $S(y)$ (Fig. S4b). Previous theory suggests that short
 470 growing seasons can also decrease $S(y)$, thereby favoring an annual life history (Iwasa & Cohen,
 471 1989); our model corroborates this result to a point (Fig. S5), but also suggests that $S(y)$ may
 472 decrease if growing seasons are very long due to a lower probability of surviving to the end of
 473 the season (not shown). Our model also reinforces previous theory (Iwasa & Cohen, 1989)
 474 predicting that high losses of storage over winter γ may also favor an annual strategy ($r^* = 1$ for
 475 $(1 - \gamma) > 0.7$, Fig. S6) by increasing the quantity of overwinter storage necessary to begin the next
 476 season with a given quantity of spring storage $V(y)$.
 477



478
 479 Figure 4. The minimum overwinter survival probability $\{1/[1+\exp(-\xi_0)]\}$ below which an annual
 480 strategy becomes optimal (the “switchpoint value”) plotted against the maintenance costs of
 481 reserves, c for different values of minimum within-season survival probabilities μ_0 . Note that for
 482 intermediate and high μ_0 the switchpoint value approaches but is not exactly equal to 0 at low c .
 483

484 The second case in which our model predicts plants should express a monocarpic life
485 history occurs if the number of offspring produced is an increasing exponential function of the
486 resources allocated to reproduction, consistent with previous theory (Schaffer, 1974; Janzen,
487 1976; Klinkhamer *et al.*, 1997). In this case, $r^* = 1$ for all $V(y)$ above a threshold value of $V(y)$
488 and $r^* = 0$ for all $V(y)$ below this threshold (Fig. 5a). Whether the predicted monocarpic life
489 history is annual or perennial depends on the storage within the seed $V(y = 1)$. If the storage
490 within the seed $V(y = 1)$ exceeds the threshold above which reproduction is optimal, then plants
491 will use all resources for reproduction at the end of the first season and die. This implies that
492 plants are facultatively annual. If $V(y = 1)$ is lower than the threshold, then individuals are
493 monocarpic perennials. The number of growing seasons needed to reach the threshold value of
494 $V(y)$, reproduce, and die depends on the seed storage $V(y = 1)$ and the relationship between $V(y)$
495 and the reserves accumulated by the plant in each growing season $S(y)$. For our default parameter
496 values (Table 1) and $V(y = 1) = 1$, for example, a plant would accumulate $S(y = 1) \approx 30$ units of
497 reserves in the first growing season (Fig. 2), all of which would be saved as storage for the
498 second season (Fig. 5a). In the second season, the plant would possess spring storage $V(y = 2)$
499 ≈ 30 and accumulate $S(y = 2) \approx 55$ (Fig. 2), again saving all as storage (Fig. 5a). In the third
500 season, $V(y = 3)$ would exceed the threshold for reproduction (Fig. 5a), and the plant would use
501 all reserves $S(y = 3)$ for reproduction and die. If we assume a linear relationship between seed
502 production and the resources allocated to reproduction, the model predicts either an obligately
503 annual strategy (see above) or a polycarpic perennial strategy (see below), but never a
504 monocarpic perennial strategy.



505

506 Figure 5. The optimal proportional allocation of reserves to reproduction r^* for different values
 507 of spring storage $V(y)$. Predictions are shown for a) an exponential relationship and b) a linear
 508 relationship between seed production and the quantity of reserves allocated to reproduction as
 509 shown in the inset figures.

510

511 *Polycarpic Life Histories*

512

513 If the optimal allocation of reserves to reproduction $r^* < 1$ for all $V(y)$, then reproduction
 514 is never suicidal, and plants are therefore polycarpic. For polycarpic plants, the optimal
 515 allocation of reserves to reproduction r^* changes with spring storage $V(y)$. This is because the
 516 model predicts that there is a target amount of storage that plants should keep overwinter (see
 517 below), yet the total quantity of reserves available to the plant $S(y)$ depends on $V(y)$ (Fig. 2). If
 518 $V(y)$ is small, plants cannot accumulate enough reserves by the end of the season to reach the
 519 target, so they forego reproduction and allocate all reserves to storage (e.g., for $V(y) < \sim 45$ in
 520 Fig. 5b). Plants with larger $V(y)$ accumulate enough reserves to reach this target and allocate any
 521 excess reserves to reproduction (i.e., $0 < r^* < 1$, Fig. 5b). The expected change in storage and
 522 reproduction over a polycarpic plant's life therefore depends on seed storage $V(y = 1)$. Plants
 523 with little seed storage $V(y = 1)$ may need to accumulate storage for one or more seasons before

524 the target storage is reached. Once the target storage is reached, individuals reinvest the same
 525 quantity of reserves into storage each season and use the excess for reproduction, resulting in a
 526 stable schedule of reserve production and reproductive output over the remainder of the plant's
 527 lifetime. In contrast, plants with large $V(y = 1)$ may generate enough reserves to begin
 528 reproducing in the first season. In this case, storage and reproductive output may be relatively
 529 constant over a plant's lifetime.

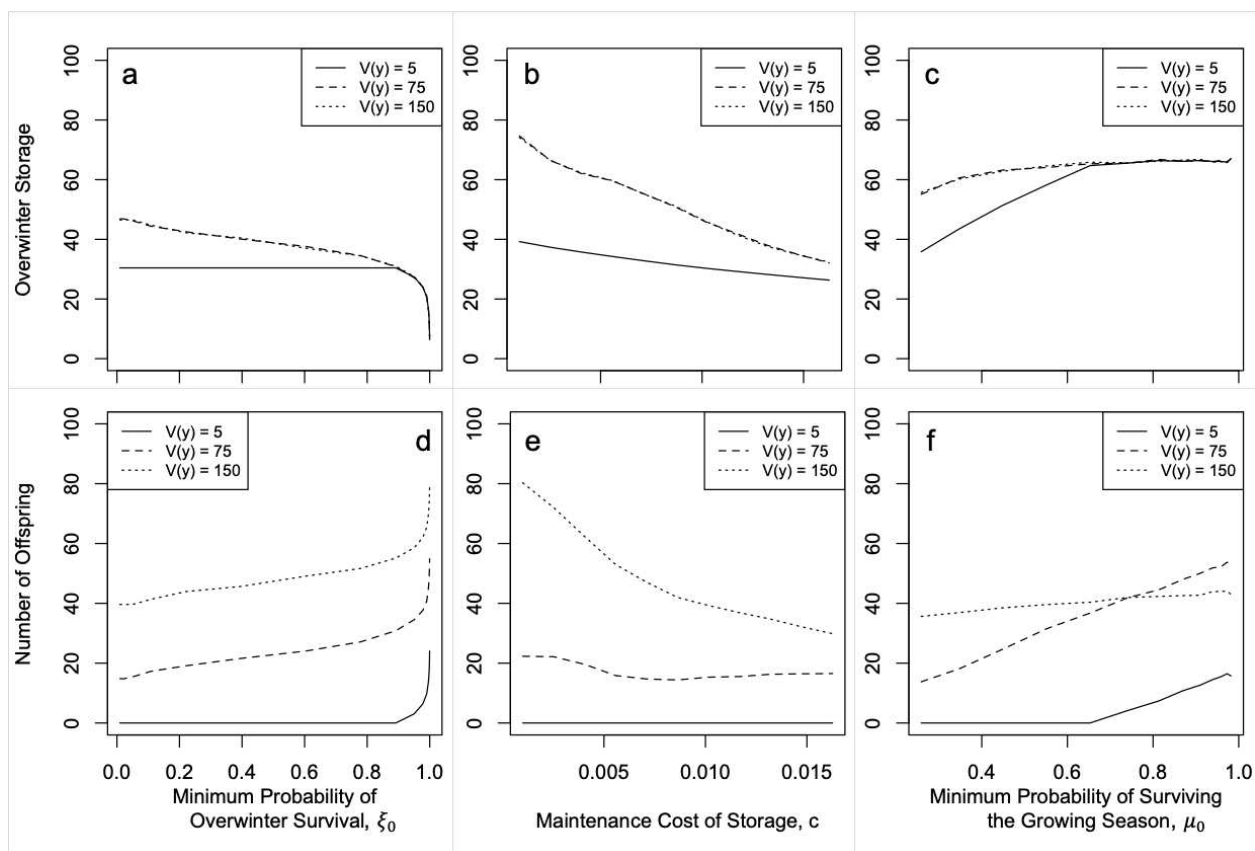
530 The optimal reproductive allocation of a polycarpic perennial can be understood in terms
 531 of the conditions that affect the target overwinter storage. In previous models, the target
 532 overwinter storage increases with overwinter survival and the reserves available to a plant at the
 533 end of the season (Iwasa & Cohen, 1989). These factors also affect the target overwinter storage
 534 in our model; however, the effect of overwinter survival is qualitatively different. In our model,
 535 plants can use overwinter storage to increase overwinter survival. As shown above (see *Results* –
 536 *Monocarpic Life Histories*), if maintaining tissues is costly, this effect of storage on overwinter
 537 survival can cause plants to forego reproduction entirely when they possess little spring storage
 538 (cf. Fig. 3a,b). With decreasing minimum probability of surviving the winter ξ_0 , polycarpic
 539 plants allocate a greater amount of resources to storage because it improves their chances of
 540 surviving the winter (Fig. 6a). The increase in overwinter storage necessarily decreases the
 541 excess reserves that can be used for reproduction; therefore, decreasing ξ_0 leads to a decrease in
 542 reproduction (Fig. 6d). The prediction that plants should evolve larger allocations to storage and
 543 decreased allocations to reproduction in environments characterized by lower overall survival is
 544 opposite the predictions of previous theory (Iwasa & Cohen, 1989).

545 Conditions leading to low $S(y)$ generally decrease the target overwinter storage, as
 546 predicted by previous theory (Iwasa & Cohen, 1989). This is because lower $S(y)$ decreases the
 547 amount of reserves the plant can accumulate in the next season and, in our model, also limits
 548 how much plants can store to improve overwinter survival. In contrast to previous theory,
 549 however, the magnitude of the decrease in overwinter storage and its consequences for
 550 reproduction depend on whether decreases in $S(y)$ are caused by an increase in the maintenance
 551 costs of storage c or a decrease in the minimum probability of surviving the growing season μ_0 .
 552 Decreases in $S(y)$ due to greater maintenance costs of reserves c are largest for those plants with
 553 high spring storage $V(y)$ and thus large m_0 (Fig. S4a). Thus, greater maintenance costs limit the
 554 increase in future reserve production a plant can achieve by increasing overwinter storage,

555 drastically decreasing the target overwinter storage (Fig. 6b). For those plants with high $V(y)$,
556 $S(y)$ decreases more quickly with increasing costs of maintaining reserves c than does the target
557 overwinter storage. Higher maintenance costs therefore lead to a decrease in both reproduction
558 (Fig. 6e, dotted line) and overwinter storage (Fig. 6b, dotted line) for plants with high $V(y)$. For
559 plants with intermediate $V(y)$, $S(y)$ and overwinter storage decrease at approximately the same
560 rate with increasing maintenance costs c , causing reproductive output to be relatively
561 independent of c (Fig. 6e, dashed line). Thus, decreases in $S(y)$ decrease the target overwinter
562 storage as in previous models (Iwasa & Cohen, 1989), but, if decreases in $S(y)$ are due to greater
563 maintenance costs, the consequences for reproductive output depend on a plant's spring storage
564 $V(y)$.

565 Decreases in $S(y)$ due to a lower minimum probability of surviving the growing season μ_0
566 , however, are greatest for plants with small $V(y)$ because they begin the season with smaller m_0
567 and therefore experience greater mortality risk (Fig. S4b). Because $S(y)$ for large plants is
568 relatively unaffected by μ_0 , the target overwinter storage changes little with μ_0 (Fig. 6c). Thus,
569 reproduction is largely independent of μ_0 for plants with large $V(y)$, but decreases at lower μ_0 for
570 plants with intermediate or low $V(y)$ because there are fewer reserves $S(y)$ (Fig. 6f) available to
571 meet the target overwinter storage. At sufficiently large μ_0 even plants with the smallest $V(y)$ can
572 reach the target overwinter storage and allocate excess reserves to reproduction (Fig. 6f, solid
573 line).

574



575
 576 Figure 6. Model parameters determining the optimal allocation of resources to overwinter
 577 storage (a-c) and reproduction (expressed as the number of offspring, d-f) for polycarpic plants.
 578 Shown are the effects of the minimum probability ξ_0 of surviving over winter (a, d), the
 579 maintenance cost of storage c (b, e), and the minimum probability μ_0 of surviving the growing
 580 season (c, f). Panels in the top row share an x-axis with the corresponding panel in the bottom
 581 row. Line types denote different values of spring storage $V(y)$ as indicated in the legend. Note
 582 that overwinter storage for individuals with $V(y) = 75$ (dashed lines) overlaps that of individuals
 583 with $V(y) = 150$ (dotted lines).

584

585

586 *Prolonged Dormancy*

587

588 Our model predicts that prolonged dormancy is part of an optimal life history strategy if
 589 dormant plants accumulate reserves and there is a high probability of surviving the season as a
 590 dormant plant v (Fig. 7). We explored the effect of varying the maximum increase in $s(T)$ with

591 $V(y)$ during dormancy, i , and the minimum probability of surviving prolonged dormancy ν_0 . The
 592 value of i required for dormancy to occur is lower at higher ν_0 ; however, high ν_0 alone does not
 593 result in dormancy. If dormancy occurs, then sprouted plants enter dormancy in the following
 594 growing season regardless of their spring storage $V(y)$ (Fig. 7a). However, dormant plants only
 595 remain dormant in the following season if they possess intermediate or low $V(y)$ (Fig. 7b). Thus,
 596 whether a plant remains dormant for only a single season or multiple consecutive seasons
 597 depends on the overwinter storage retained by sprouted plants and the change in storage during
 598 prolonged dormancy, as either can determine the storage available to the plant at the onset of
 599 prolonged dormancy.

600

601 ***FIGURE 7 UPLOADED SEPARATELY***

602

603 Figure 7. The minimum spring storage $V(y)$ for a) sprouted plants and b) dormant plants below
 604 which prolonged dormancy in the next season becomes optimal (the “switchpoint value”) plotted
 605 against the maximum change in storage during prolonged dormancy i for different values of
 606 minimum within-season survival probabilities ν_0 . For those cases in which the switchpoint
 607 equals the maximum $V(y)$, prolonged dormancy maximizes fitness for all possible spring storage
 608 values. Note that in b) there are two switchpoints (i.e., boundaries of the shaded regions) for each
 609 combination of i and ν_0 .

610

611 **Discussion**

612

613 Previous models of resource allocation by herbaceous plants assume that net
 614 photosynthate production increases monotonically with the size of the plant’s photosynthetic
 615 structures such that greater overwinter storage (and thus larger initial photosynthetic structures)
 616 always increases future resource availability (Iwasa & Cohen, 1989; Klinkhamer *et al.*, 1997).
 617 Moreover, previous models typically do not consider that the amount of stored resources may
 618 affect survival, or that plants may undergo periods of prolonged dormancy. Our model expands
 619 on this foundation by exploring the consequences of 1) net resource production being greatest at
 620 intermediate plant size due to differences in the scaling of gross photosynthate production and
 621 maintenance costs with size, 2) the effect of plant size on survival during the growing season, 3)

622 the effect of resource allocation decisions on overwinter survival, and 4) the benefits of periods
623 of prolonged dormancy in terms of increased survival and storage.

624 By incorporating theory on the allometric scaling of gross resource production and
625 maintenance costs (Enquist *et al.*, 1998; West *et al.*, 2001), we find that the benefit of storage for
626 future resource production is generally limited by the cost of maintaining existing tissues.
627 Consequently, maintenance costs are critical for determining the conditions under which
628 selection favors a monocarpic or polycarpic life history as well as the optimal allocation of
629 resources to reproduction by polycarpic plants. Moreover, by incorporating these limits to the
630 benefits of storage, we find that our model never predicts significant investment into storage
631 unless plants can increase subsequent survival by allocating a larger proportion of resources to
632 storage. Thus, in contrast to previous theory that does not consider maintenance costs (Iwasa &
633 Cohen, 1989; Klinkhamer *et al.*, 1997), our model suggests that the ability of plants to
634 compensate for low survival by increasing storage is a critically important ecological mechanism
635 for predicting large investments in storage consistent with empirical observations. The effect of
636 storage on overwinter survival can also result in seemingly counterintuitive relationships
637 between overwintering conditions and resource allocation, as plants inhabiting environments
638 with harsher winters (i.e., lower ξ_0) should allocate fewer reserves to current reproduction to
639 increase survival. Finally, we demonstrate that a life history in which plants undergo prolonged
640 dormancy [i.e., spend at least one growing season below ground, foregoing sexual reproduction
641 (Lesica & Steele, 1994)], can evolve in response to resource allocation tradeoffs alone if plants
642 can increase storage during dormancy (e.g., through reallocation of structural carbohydrates or
643 uptake from mycorrhizal fungi), particularly if dormancy also increases survival relative to
644 sprouting.

645

646 *Monocarpic Life Histories*

647

648 Our model corroborates previous theory predicting that herbaceous plants growing in
649 seasonal environments may evolve a monocarpic perennial life history if offspring production is
650 an accelerating (e.g., exponential) function of the resources allocated to reproduction (Schaffer,
651 1974; Janzen, 1976; Klinkhamer *et al.*, 1997). Several mechanisms have been proposed for how
652 such relationships arise, including saturation of seed predators and attraction of pollinators,

653 although empirical evidence for such mechanisms in monocarpic perennials remains equivocal
654 (Klinkhamer *et al.*, 1997). Moreover, because the reserves that can be accumulated during a
655 growing season depend on maintenance costs, these costs may be critical in determining the
656 number of growing seasons needed before a monocarpic perennial accumulates enough reserves
657 to reproduce and die.

658 The predictions of our model are also consistent with previous theory suggesting that an
659 annual life history should evolve if survival is low, growing seasons are unproductive, or
660 overwinter losses of storage are large (Iwasa & Cohen, 1989). This is largely unsurprising; for a
661 given relationship between storage and subsequent reserve production, a sufficiently large
662 average loss due to mortality or storage efficiency will prevent any possible allocation to storage
663 from producing a return of equivalent (or greater) reserves in the next season (Iwasa & Cohen,
664 1989). For herbaceous plants, these vital rates likely depend on abiotic environmental factors
665 such as temperature and precipitation [e.g. (Tenhumberg *et al.*, 2018), and citations therein] as
666 well as biotic factors such as competitor density (Tenhumberg *et al.*, 2015). For example, in the
667 common yellow monkeyflower (*Mimulus guttata*), annual ecotypes occurs more frequently in
668 environments with less late-summer precipitation (Hall & Willis, 2006) in which individuals
669 experience decreased survival (Hall & Willis, 2006) and are likely to be less productive. Similar
670 differences in water availability, and thus presumably survival and productivity, are associated
671 with variation in the frequency of annual ecotypes in wild rice (Morishima *et al.*, 1984). In the
672 forb *Streptanthus tortuosus*, variation within and among populations in the frequency of an
673 annual life history correlates with germination date, which in turns influences survival to
674 subsequent growing seasons (Gremer *et al.*, 2019).

675 While our model aligns with previous theory and empirical data on the general conditions
676 under which an annual life history should evolve, our model provides new perspectives on the
677 mechanisms underlying these predictions. Specifically, our model predicts that if maintaining
678 existing tissues is costly, an annual life history should evolve only if the chances of surviving to
679 future growing seasons are exceptionally low (Fig. 3a). This is because the benefit of large
680 quantities of storage in terms of future resource production is limited by the costs of maintaining
681 existing tissues; therefore, plants can virtually maximize future reproductive success by
682 allocating only a tiny fraction of resources to storage. The chances of surviving overwinter must
683 be very low for this strategy to become less profitable than an annual strategy. However, for

684 many plants, storage likely increases overwinter survival, for example by increasing cold
685 hardiness (Boyce & Volenec, 1992). Our model predicts that the effect of storage on overwinter
686 survival can restore strong tradeoffs between current and future reproductive success (Fig. 3b).
687 As a result, an annual life history may be optimal even when a plant has the capacity to achieve a
688 relatively high probability of surviving the winter because doing so comes at a large cost to
689 current reproduction. Of course, it is possible that in some cases the evolution of annual life
690 histories is associated with extremely low survival or low costs of maintenance (which should
691 result in stronger effects of storage on future resource production). Nevertheless, our model
692 predicts that, all other things equal, taxa in which storage more strongly affects overwinter
693 survival should generally show greater variation in the frequency of annual life histories among
694 environments differing in overall survival or productivity. Testing this prediction will ultimately
695 require the ability to disentangle the relative contributions of the effect of storage on future
696 resource production and on survival to the tradeoffs between current and future reproduction
697 (e.g., cf. Fig. 3a,b) in a variety of taxa. Such studies would undoubtedly be challenging, but may
698 ultimately resolve the physiological and ecological mechanisms underlying the evolution of
699 annual life histories predicted by our model.

700 Our model predicts that the overwinter survival conditions in which an annual strategy is
701 optimal depend strongly on the costs of maintaining existing tissues (Fig. 4), as these costs
702 determine the reserves the plant can acquire (Fig. S4a). This contrasts previous models in which
703 the reserves accumulated by the end of the season depend only on the spring storage, the size-
704 specific rate of net photosynthate production, and the length of the growing season (Iwasa &
705 Cohen, 1989; Klinkhamer *et al.*, 1997). Factors affecting the costs of maintaining tissues (e.g.,
706 temperature, plant architecture) may therefore represent a fundamental, yet underappreciated,
707 source of life history variation within and among plant taxa. In particular, empirical studies
708 exploring the effects of environmental conditions on maintenance costs may be critical for
709 understanding spatial and temporal patterns of life history variation and for predicting
710 consequences of environmental change at the individual and population levels. Future theoretical
711 work would benefit from exploring the extent to which the constraints imposed by maintenance
712 costs depend on other limiting resources that influence the plant's tradeoff between survival and
713 reproduction (e.g., water, micronutrients) (Cohen *et al.*, 2017).

714

715 *Polycarpic Life Histories*

716

717 Under conditions favorable for reserve accumulation, storage efficiency, and survival,
718 our model predicts that plants maximize their fitness by expressing a polycarpic strategy (i.e.,
719 reproducing in multiple growing seasons). However, our model suggests that the relationship
720 between the optimal allocation of resources to reproduction and the dynamics of survival and
721 reserve production is more complex than previously appreciated. Specifically, our model predicts
722 that overwinter survival and reserve production have contrasting influences on the optimal
723 allocation of reserves to reproduction. Increases in overwinter survival favor greater reproductive
724 allocation and less storage because a smaller amount of stored reserves in a favorable
725 environment (high ξ_0) achieves the same survival probability and, therefore, the same future
726 reproductive success, as a plant growing in less favorable environments (low ξ_0) that allocates
727 more resources to storage. This result is in direct contrast to previous theory on plant life history
728 evolution that predicts that greater overwinter survival should favor decreased investment in
729 current reproduction (Iwasa & Cohen, 1989). Thus, our model predicts greater overwinter
730 survival favors a polycarpic perennial strategy over an annual strategy (see above), but greater
731 overwinter survival also favors increased allocations to reproduction and less storage over the
732 range of conditions in which a polycarpic life history is optimal. In contrast, our model predicts
733 that increases in reserve production favor the evolution of greater allocation to storage due to
734 greater future fitness expectations, though the corresponding change in current reproduction
735 depends on the underlying cause of increased reserve production and on the plant's spring
736 storage. This leads to the seemingly counterintuitive prediction that in some cases the optimal
737 allocation of reserves between reproduction and storage for polycarpic plants might be relatively
738 independent of environmental conditions (e.g., temperature, precipitation) if those conditions
739 have similar effects on survival and reserve production. However, there are probably many
740 examples in which environmental conditions have somewhat different effects on survival versus
741 resource production. For example, environments differing in winter precipitation may differ
742 more strongly in overwinter survival than in productivity during the growing season. In these
743 cases, our model would predict the evolution of increased storage in environments where reserve
744 production is increased to a greater extent than survival or survival is decreased to a greater
745 extent than reserve production.

746 It is difficult to compare these model predictions to empirical patterns because current
747 studies on resource allocation among polycarpic plants occupying different environments
748 typically do not link ecological factors (e.g., temperature, precipitation) or large-scale
749 environmental gradients (e.g., latitudinal gradients) to resource production and survival. For
750 example, in purple loosestrife (*Lythrum salicaria*), individuals from higher latitude populations
751 produce larger storage organs (Olsson & Ågren, 2002). This pattern is consistent with our model
752 prediction if individuals can increase overwinter survival by increasing storage, and if high
753 latitude conditions result in a greater decrease in survival than reserve production. In the winter
754 rainfall region of South Africa, plants invest more heavily in overwinter storage organs if they
755 grow in habitats with lower precipitation during the winter (Procheş *et al.*, 2005). Low winter
756 precipitation likely decreases survival (low ξ_0 in our model). If plants can improve survival by
757 allocating resources to storage, larger storage organs in drier habitats would be consistent with
758 our model predictions. Low winter precipitation may also decrease reserve production in the
759 subsequent growing season; nevertheless, the observed patterns are consistent with our model,
760 provided that any decreases in reserve production are not large enough to outweigh the effect of
761 decreasing survival. It is of course possible that these storage organs store mostly water, which
762 our model does not consider explicitly. Additionally, few studies disentangle the relative
763 contribution of absolute resource availability and relative resource allocation. In one such study
764 of the perennial sunflower *Helianthus maximiliani*, higher latitude population produce a greater
765 number of flowers per unit biomass, suggesting reproductive allocation increases with latitude
766 (Kawakami *et al.*, 2011). This pattern is consistent with our model provided that high latitudes
767 are associated with greater decreases in reserve production than survival (e.g. because of lower
768 herbivore pressure). In summary, resolving the potentially differential effects of environmental
769 conditions on survival and reserve production will be essential in assessing the adaptive
770 significance of differences in resource allocation by polycarpic perennials.

771

772 *Prolonged Dormancy*

773

774 Our model demonstrates that resource allocation tradeoffs associated with sprouting are
775 sufficient for the evolution of prolonged dormancy, provided that individuals accumulate
776 resources during dormancy. These findings support recent verbal arguments suggesting that

777 resource allocation tradeoffs can contribute to the adaptive value of prolonged dormancy in the
778 absence of temporal variation in environmental conditions (Lesica & Crone, 2007; Shefferson *et al.*,
779 *et al.*, 2014, 2018), but also predict that increases in resource availability during dormancy should
780 be a general characteristic of plants in which such tradeoffs favor prolonged dormancy. There is
781 growing evidence that herbaceous plants may accumulate resources during prolonged dormancy
782 (Gremer *et al.*, 2010; Shefferson *et al.*, 2018), and thus it is possible that resource allocation
783 tradeoffs associated with sprouting may often contribute to the adaptive value of prolonged
784 dormancy. Additional studies providing direct evidence of changes in resource availability
785 during dormancy (e.g., Gremer *et al.*, 2010) will be instrumental in determining whether adaptive
786 responses to tradeoffs associated with sprouting *per se* provide a general explanation for patterns
787 of prolonged dormancy in herbaceous plants or operate only under relatively restrictive
788 taxonomic or ecological contexts.

789 Our model also predicts that the accumulation of resources by dormant plants should
790 more strongly favor the evolution of prolonged dormancy if plants experience high survival
791 during dormancy. While some observational studies suggest that dormancy may instead decrease
792 survival relative to sprouted plants (Hutchings, 1987; Shefferson *et al.*, 2003), these patterns may
793 reflect the tendency for plants at a survival disadvantage to enter prolonged dormancy. In at least
794 some cases, the apparent survival costs of prolonging dormancy appear to be due to correlations
795 between traits impacting survival (e.g., size) and the tendency to prolong dormancy rather than a
796 detrimental effect of dormancy on survival *per se* (Shefferson, 2006; Jäkäläniemi *et al.*, 2011).
797 Other observational and experimental studies have found no effects of prolonged dormancy on
798 survival (Shefferson *et al.*, 2005; Lesica & Crone, 2007). However, high survival during
799 prolonged dormancy is also a key prediction of the hypothesis that dormancy functions as a bet-
800 hedging strategy to circumvent temporal variation in environmental conditions (Shefferson,
801 2009; Jäkäläniemi *et al.*, 2011; Hawryzki *et al.*, 2011; Gremer *et al.*, 2012; Gremer & Sala,
802 2013). Empirical studies that compare the relative survival of sprouted versus dormant plants
803 during periods of favorable and stressful environmental conditions may help to disentangle the
804 relative contributions of tradeoffs associated with sprouting *per se* and bet hedging to patterns of
805 prolonged dormancy. If prolonged dormancy results in high survival relative to sprouted plants
806 only under periods of environmental stress, bet hedging may be a more likely explanation for the
807 prolonged dormancy. Studies explicitly testing the relative importance of tradeoffs associated

808 with sprouting and environmental variation in explaining observed demographic patterns (e.g.,
809 Shefferson *et al.*, 2014) will also be of critical importance in determining the relative importance
810 of these non-exclusive benefits of prolonged dormancy in natural populations.

811 The demographic patterns of dormancy predicted by our model, however, differ from
812 those often described for natural populations, suggesting that our model does not consider all
813 factors influencing dormancy. Our model predicts that for the parameter range where prolonged
814 dormancy is adaptive individuals should always enter prolonged dormancy following a growing
815 season in which they sprouted. Whether a plant remains dormant for more than one growing
816 season depends on the levels of storage when they first entered dormancy. However, in nature,
817 plants do not always enter prolonged dormancy following a growing season in which they
818 sprouted. The probability that sprouted plants enter dormancy in any given year is often affected
819 by short-term environmental stress such as shading, defoliation, and weather anomalies (e.g.,
820 precipitation, spring temperature) (Shefferson *et al.*, 2001, 2005; Knight, 2003; Ehrlén, 2003;
821 Lesica & Crone, 2007; Mceachern *et al.*, 2009; Reintal *et al.*, 2010). Our model did not consider
822 responses to such stressors but explored how expected average survival and productivity in
823 different environments influence the evolution of prolonged dormancy. Further, we have limited
824 understanding of the underlying dynamics of storage changes during dormancy, and therefore
825 how an individual's spring storage is related to the storage available following prolonged
826 dormancy. Future efforts to explicitly incorporate such stressors into our model and to resolve
827 the dynamics of storage changes during prolonged dormancy will be particularly helpful in
828 understanding the role of resource allocation tradeoffs in the evolution of prolonged dormancy.

829

830 *Conclusions*

831

832 In summary, our model demonstrates that relatively simple resource allocation tradeoffs
833 are sufficient to explain the evolution of different life history strategies observed in natural
834 populations of herbaceous plants, including strategies that incorporate bouts of prolonged
835 dormancy. We find that differences in how resource production and maintenance costs increase
836 with biomass introduce additional constraints on storage accumulation and reserve production,
837 fundamentally altering the nature of the tradeoff between current and future reproduction.
838 Consequently, we find that, in contrast to previous theory, the ability of plants to compensate for

839 low survival conditions by allocating a larger proportion of resources to storage is critically
840 important because without it our model never predicts significant investment into storage.
841 Finally, we demonstrate that resource allocation tradeoffs alone may be sufficient to favor the
842 evolution of prolonged dormancy.

843

844 **Data Archival Statement**

845

846 The results presented herein were generated using model code written in the *R* programming
847 language. Our model code is available from the Dryad Digital Repository:
848 <https://doi.org/10.5061/dryad.gmsbcc2k3> (Watts & Tenhumberg, 2020).

849

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854

855 **Author Contributions**

856

857 BT conceived the study; JCW and BT developed the model; JCW took the lead on model
858 programming, model analysis, and manuscript preparation; JCW and BT participated in
859 manuscript revisions.

860

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