

Competition for time: evidence for an overlooked, diversity-maintaining competitive mechanism

Jacob Levine¹, Stephen Pacala¹, and Jonathan Levine²

¹Princeton University

²Princeton Environmental Institute

April 16, 2024

Abstract

Understanding how diversity is maintained in plant communities requires that we first understand the mechanisms of competition for limiting resources. In ecology, there is an underappreciated, but fundamental distinction between systems in which the depletion of limiting resources reduces the growth rates of competitors versus systems in which resource depletion reduces the time available for competitors to grow, a mechanism we call “competition for time.” Importantly, modern community ecology, and our framing of the coexistence problem are built on the implicit assumption that competition reduces the growth rate. However, recent theoretical work suggests competition for time may be the predominant competitive mechanism in a broad array of natural communities, a significant advance given coexistence follows naturally when species compete for time. In this study we first introduce competition for time conceptually using a simple model of interacting species. Then, we perform an experiment in a Mediterranean annual grassland to determine whether competition for time is an important competitive mechanism in a field system. Indeed, we find that species respond to increased competition through reductions in their lifespan rather than their rate of growth. In total, our study suggests competition for time may be overlooked as a mechanism of biodiversity maintenance.

Competition for time: evidence for an overlooked, diversity-maintaining competitive mechanism

By Jacob I. Levine^{1,2}, Stephen W. Pacala^{1,3}, and Jonathan M. Levine^{1,4}

¹Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ

²Corresponding author, 310.754.6059, jacoblevine@princeton.edu, Department of Ecology and Evolutionary Biology, Princeton University, 106A Guyot Ln, Princeton, NJ 08544

³pacala@princeton.edu

⁴levinej@princeton.edu

Statement of authorship: JIL, SWP, and JML conceived of the study, JIL and JML designed the experiment, JIL implemented the experiment, conducted all mathematical and statistical analyses, and wrote the first draft of the manuscript, all authors contributed substantially to revisions.

Data availability statement: The data that support the findings of this study are openly available in Dryad at DOI: <https://doi.org/10.5061/dryad.wh70rxwtr>.

Running title: Competition for time

Keywords: species coexistence, resource competition, phenology, biodiversity, competition for water, competition for light, succession, temporal niche, annual plants, mechanistic competition models

Article type: Perspective; **Abstract word count:** 200; **Main text word count:** 7499; **Number of references:** 94; **Number of figures:** 7

Abstract

Understanding how diversity is maintained in plant communities requires that we first understand the mechanisms of competition for limiting resources. In ecology, there is an underappreciated, but fundamental distinction between systems in which the depletion of limiting resources reduces the growth rates of competitors versus systems in which resource depletion reduces the time available for competitors to grow, a mechanism we call “competition for time.” Importantly, modern community ecology, and our framing of the coexistence problem are built on the implicit assumption that competition reduces the growth rate. However, recent theoretical work suggests competition for time may be the predominant competitive mechanism in a broad array of natural communities, a significant advance given coexistence follows naturally when species compete for time. In this study we first introduce competition for time conceptually using a simple model of interacting species. Then, we perform an experiment in a Mediterranean annual grassland to determine whether competition for time is an important competitive mechanism in a field system. Indeed, we find that species respond to increased competition through reductions in their lifespan rather than their rate of growth. In total, our study suggests competition for time may be overlooked as a mechanism of biodiversity maintenance.

1 **Introduction**

2 Understanding the forces structuring plant communities is central to predicting how these systems will
3 respond to anthropogenic disturbance, climate change, and species invasions (Vitousek *et al.* 1997; Shea
4 & Chesson 2002; Pearson & Dawson 2003; Sax *et al.* 2007; Gilman *et al.* 2010; Alexander *et al.* 2015;
5 Anderegg *et al.* 2022). Resources such as light, nitrogen and water are consistently shown to limit the
6 production of plant biomass, and competition for these resources is generally appreciated to be among
7 the dominant processes structuring plant communities (Cody & Diamond 1975; Connell 1983; Schoener
8 1985; Fowler 1986; Tilman 1987; Bazzaz 1991; Callaway & Walker 1997; Casper & Jackson 1997;
9 Ricklefs 2004). Unsurprisingly then, the most influential theories evaluating plant community structure
10 have focused on resource competition, generating important predictions for the controls over dominance,
11 coexistence, succession and invasion (Hutchinson 1961; MacArthur & Levins 1967; MacArthur &
12 Wilson 1967; Horn 1971; Levins & Culver 1971; Tilman 1980; Chesson 2000; Amarasekare 2003;
13 McGill *et al.* 2006; Cavender-Bares *et al.* 2009).

14
15 While the primacy of resource competition is rarely challenged, how we conceptualize this process may
16 have large implications for its inferred role in shaping community structure and ultimately global change
17 responses. In particular, there is a fundamental contrast between cases where competition for limiting
18 resources harms individuals' rates of biomass growth (e.g. MacArthur & Levins 1967; Chesson 1994;
19 Brown *et al.* 2004; Lyu & Alexander 2023), and where competition reduces the time available for
20 biomass growth, a mechanism we call "competition for time" (Fig. 1; (Odum 1969; Horn 1971, 1974;
21 Drury & Nisbet 1973; Schoener 1973; McIntosh 1981; Levine & Rees 2004; Detto *et al.* 2022; Levine *et*
22 *al.* 2022). Competition for time can have long term population dynamic consequences when organisms
23 reduce one another's duration of growth within repeated bouts of competition (Fig. 2). These

24 competitive bouts may, for example, represent periods of competition for light among shade-intolerant
25 forest trees after a disturbance event, or competition for water among annual plants after a winter rainy
26 season.

27

28 Due to the repeated nature of the competitive bouts in these and other systems, competition for time can
29 drive exclusion or coexistence on longer, population dynamic time scales. For example, if iterated over
30 multiple years, the competition for time dynamic over an annual plant's lifetime may result in the
31 eventual exclusion of that species from a community. Competition that reduces biomass growth rates
32 similarly affects multiyear population dynamics. Yet models that exclusively focus only on this
33 population-dynamic timescale (e.g. years in an annual plant system) necessarily miss the short-term
34 responses to competition and their implications for the dynamics of plants in nature. Indeed, classic
35 models of community dynamics, such as Lotka-Volterra, Beverton-Holt, and MacArthur Consumer
36 Resource models define competition as a factor that simply reduces population growth (MacArthur &
37 Levins 1967; Wangersky 1978; Chesson 1990; Tilman 1990; Berezansky & Braverman 2004). And as
38 we will show here, the choice of functional relationships between population growth and competitor
39 density in these models is consistent with competition harming biomass growth rates but not the time for
40 growth (MacArthur 1970; Wangersky 1978; Tilman 1990; Berezansky & Braverman 2004). The
41 assumption that competition harms biomass growth is similarly reflected in empirical work, where
42 individual biomass growth over an interval of time is used as a proxy for the performance of a
43 population (e.g. Wilson & Tilman 1991; Aguiar *et al.* 2001; Seabloom *et al.* 2003; Vilà & Weiner 2004;
44 Funk & Wolf 2016).

45

46 Assuming that competition harms biomass growth rates rather than the time for growth has important
47 implications for how we study and frame the problem of species coexistence. When competition is
48 mediated by reductions in biomass growth rates, the species that can grow at the lowest level of the
49 limiting resource dominates, and endogenous opportunities for coexistence are few (MacArthur & Levins
50 1967; Levin 1970). In such cases, coexistence is thought to rest on some external mechanism that
51 disrupts competitive exclusion, such as specialization on multiple limiting resources, density dependent
52 enemy attack, or the temporal storage effect (MacArthur 1970; Chesson 2000; Post 2019). Identifying
53 these mechanisms, where they occur in nature, and their implications for biodiversity under global
54 change has been a major focus of community ecology for the last half-century (MacArthur 1970; Levins
55 1979; Tilman 1980, 1994; Chesson 2000; Litchman & Klausmeier 2008; Angert *et al.* 2009; Levine &
56 HilleRisLambers 2009; Barabás *et al.* 2016; Levine *et al.* 2017; Usinowicz *et al.* 2017; Rudolf 2019;
57 Van Dyke *et al.* 2022).

58

59 In contrast, when competition reduces the time available for growth, diversity is naturally favored
60 (Odum 1969; Horn 1974; McIntosh 1981; Caspersen & Pacala 2001; Levine & Rees 2004; Detto *et al.*
61 2022; Levine *et al.* 2022). This is because species have the opportunity to divide time into periods over
62 which each species is the best competitor (Detto *et al.* 2022; Levine *et al.* 2022), a division that is
63 frequently the result of species' differences in their access to or tolerance of limited resources. Dividing
64 time particularly enhances intraspecific relative to interspecific competition when species follow a
65 tradeoff between competitive ability and longevity. Under such a tradeoff, which often emerges from
66 ecophysiological constraints on growth and resource use (Solbrig & Orians 1977; Detto *et al.* 2022;
67 Levine *et al.* 2022), time is divided into periods of decreasing diversity as shorter-lived, faster growing
68 species drop out, granting slower competitors a temporal refuge. If this procession is regularly reset, for

69 example by disturbance, then high diversity can be maintained in the long run (Detto *et al.* 2022; Levine
70 *et al.* 2022). Although competition for time has long been appreciated to operate in successional
71 systems, it has recently been suggested to work in a wider range of communities, including systems of
72 annual plants competing for water. The implication of this recent work is that competition for time may
73 be an overlooked mechanism of species coexistence in nature (Levine *et al.* 2022).

74

75 Though the notion that competition for time may help maintain biodiversity in a broad array of natural
76 systems is exciting, it has not been explicitly defined in the context of simple and general mathematical
77 models, nor empirically tested outside succession-driven plant communities. In this paper, we first
78 introduce competition for time conceptually and illustrate its special properties using a simple model.
79 Then, we determine whether competition for time may be a more broadly important mechanism of
80 competition and coexistence by experimentally testing its importance in a system without traditional
81 successional dynamics: water-limited, Mediterranean annual plants. Using a pairwise competition
82 experiment in Southern California, U.S.A., we test several key predictions about the nature of
83 competition in the system. Specifically, we evaluate two alternative hypotheses: that the effect of
84 competition for water on an individual's fecundity is driven by 1) reduced lifespan or 2) reduced
85 biomass growth rate. Next, we quantify species' biomass growth rates and determine their tolerance to
86 dry soil conditions, allowing us to test whether species follow a tradeoff between biomass growth rate
87 and longevity through the season. Last, we evaluate the consequences of this tradeoff for species
88 coexistence.

89

90 **A broadening array of systems in which species may compete for time**

91 Competition for time is classically exemplified by secondary succession in light-limited forests, wherein
92 resource-demanding pioneer species are gradually overtopped and replaced by taller, slow-growing
93 species following disturbance (Clements 1916; Horn 1974). In such systems, competition for time
94 emerges because greater densities of tall individuals cause short individuals to be overtopped earlier,
95 harming their total reproduction. Though the ability of growth-longevity tradeoffs to maintain high
96 degrees of diversity in successional forests has been well-known for over a century (Clements 1916;
97 Odum 1969; Horn 1971; Drury & Nisbet 1973; McIntosh 1981; Pacala & Rees 1998; Caspersen &
98 Pacala 2001), this mechanism is rarely invoked outside of secondary forest succession. However, recent
99 theoretical work suggests that competition for time may occur far more broadly, including in systems
100 without successional dynamics.

101

102 For example, recent advances in modeling the ecophysiology of plant growth under water limitation
103 (e.g. Wolf *et al.* 2016) suggest communities of water-limited plants may compete for time (Levine *et al.*
104 2022). Specifically, theory suggests these communities are characterized by a kind of within-growing-
105 season succession where, instead of dying as a result of being overtopped by taller individuals in a forest
106 system, plants stop growing when they close their stomates in response to drying soil conditions
107 between precipitation events (Solbrig & Orians 1977; Levine *et al.* 2022). Competition for time arises
108 because competitors consume the shared water resource, and thereby cause individuals to stop growing
109 earlier than they would in the absence of competition (Levine *et al.* 2022). In such systems, variation in
110 species' tolerance to dry soil conditions generates a pattern of sequential shutoffs wherein drought-
111 intolerant species, much like pioneer species in successional forests, grow only for a short time
112 following rain before closing their stomates and shutting down. Meanwhile, drought-tolerant species
113 continue to grow long into the dry period much as slow-growing, tall tree species eventually overtop

114 pioneer species. And as in light-limited forests, a tradeoff between competitive ability and longevity
115 emerges naturally from ecophysiological constraints, as drought-tolerance is achieved through
116 investment in specialized structures such as thick-walled xylem at the cost of investment in productive
117 leaf tissue (Solbrig & Orians 1977; Levine *et al.* 2022). This tradeoff can operate to maintain diversity in
118 annual communities with a seasonal pulse of rainfall or perennial systems with intermittent storms
119 (Levine *et al.* 2022).

120

121 Competition for time differs from other temporal coexistence mechanisms in several important ways.
122 Greatest among these is the source of temporal structuring. Other prominent temporal coexistence
123 mechanisms like the storage effect depend on species-specific responses to fluctuating temperature,
124 precipitation, nutrient availability, or other external factors, to generate the temporal offset between
125 species (Chesson 1994, 2000; Angert *et al.* 2009; Wolkovich & Cleland 2011; Usinowicz *et al.* 2017;
126 Post 2019). When species compete for time, however, variation in the environment is almost entirely
127 endogenous. In forests, for example, the fluctuations in light are determined by the changing density of
128 taller competitors (Odum 1969; Horn 1971; Detto *et al.* 2022); in water-limited plant communities, the
129 timing of stomatal closure (and the duration of plant growth) is driven by the rate of transpiration by
130 competitors (Levine *et al.* 2022). This endogenous temporal structure reduces the requirements for, and
131 is responsible for the stability of coexistence when species compete for time (Detto *et al.* 2022; Levine
132 *et al.* 2022).

133

134 **Coexistence in a simple model of competition for time**

135 Here we provide a simple mathematical treatment of competition for time to show why coexistence
136 emerges naturally from the structure of the competition. In particular, we emphasize the unique

137 functional forms relating population growth to competitor density that emerge at the population dynamic
138 time scale when species reduce one another's time for growth within repeated competitive bouts. These
139 functional forms illustrate the tendency of competition for time to maintain species diversity and arise
140 when the time within bouts is divided into periods of decreasing diversity, a result of variation in
141 species' longevity.

142

143 Competition for time has three essential requirements: 1) species transition from a state of active growth
144 to one of inactivity, 2) the timing of this transition is a function of competition, and 3) inactive species
145 do not exert a competitive effect on active species. In the models discussed in this paper, we also assume
146 the transition from growth to inactivity is abrupt. Provided the three criteria are met, competition for
147 time can still occur when the transition is gradual, but elements of growth-mediated competition are
148 introduced.

149

150 How these requirements generate a division of time among competitors is illustrated by the case of light-
151 limited secondary succession. Following disturbance, individuals of all species begin growth from seed
152 at roughly the same time (Clements 1916; Horn 1974). Then, as species are overtopped by taller
153 competitors they die, leaving behind only their dormant seeds or shade tolerant recruits, which have no
154 effect on the canopy trees. This process leaves an ever decreasing subset of species in the canopy until
155 only a few "climax species" remain (Whittaker 1953; Horn 1974; Caspersen & Pacala 2001; Detto *et al.*
156 2022). Thus, species vary in longevity because of their height relative to competitors, and because all
157 species are initially present, the lifetime of the stand is divided into periods of declining diversity. A
158 similar pattern arises when perennial plants compete for water, except that longevity is defined by the
159 duration of physiological activity between storms rather than total lifespan. There, variation in tolerance

160 to dry soil conditions causes species to close their stomates and cease growth at different times, meaning
161 the interval between storms is divided into periods with decreasing diversity of physiologically active
162 species (Levine *et al.* 2022). When combined with the fact that longevity itself is determined by
163 competition in such systems, this pattern of declining diversity generates the unique population-dynamic
164 functional forms which define competition for time and promote diversity.

165

166 The case studies above could be regarded as the dynamical consequence of an extreme step-functional
167 form relating growth and uptake to the availability of the limiting resource (light or water), rendering
168 competition for time a special form of resource competition. However, with strict competition for time –
169 where individuals grow at resource-unconstrained rates until low resource levels cause an abrupt shut
170 down – there is a monotonic relationship between cumulative resource use and the shortening of the
171 growing time for competitors. This means that the rates of resource and time consumption can be used
172 interchangeably, and species can potentially coexist by dividing the time axis. While individuals do not
173 actually consume time in a physical sense, the phrase “competition for time” is dynamically accurate,
174 more evocative, and much simpler than “competition for resources with step-functional dependence of
175 resource uptake and growth on resource levels”. Just as predator species differing in their functional
176 responses are argued to “consume” and subdivide the “variance” in their prey’s oscillations (Armstrong
177 & McGehee 1980; Chesson 2000) competition for time could have similar synthetic utility.

178

179 To illustrate the functional forms of density dependence favoring coexistence with this mechanism, we
180 consider the simplest possible model of competition for time: a community of plants with discrete
181 generations competing for a single limiting resource. Though this model describes only a subset of the
182 communities which might exhibit competition for time in nature, the insights apply broadly, and the

183 model can be adapted to more complex systems with slight modifications. We begin with the assumption
184 that an individual's lifetime reproductive output is equal to the product of three terms: 1) a biomass
185 growth rate, g , 2) the length of its lifespan within competitive bouts (longevity), t , and 3) the rate at
186 which it converts biomass to offspring, f . Absent intraspecific variation in these three terms, the per
187 capita population growth rate of a species i from one generation to the next can be expressed:

$$\frac{n_i(T + 1)}{n_i(T)} = f g_i t_i \quad (1)$$

188 where $n_i(T)$ is the population density of species i in generation T . For simplicity we assume the rate of
189 biomass conversion to offspring, f , is common to all species, though this assumption can be relaxed
190 with minimal consequence.

191

192 Strict competition for time occurs when t_i , the time for growth within a generation, is reduced by
193 increasing competitor density, and g_i , the biomass growth rate and f , the conversion of biomass to
194 offspring, are constants unaffected by competition. Thus, phenology in this model is a plastic species
195 trait. This contrasts with growth-mediated competition, where g_i is affected by competition and t_i is a
196 constant.

197

198 In nature, reductions to the time for growth, t_i , occur because competitors deplete a shared resource
199 necessary for growth, and when that depletion is sufficient to reach a species' critical resource level, that
200 species stops growing. For example, low soil water potential driven by competitor uptake of water may
201 cause a plant to close its stomates and cease growth, or light-preemption may cause a tree to senesce.

202 Therefore, for a wide range of models, we can express t_i as an initial resource pool divided by the rate at
203 which the resource is consumed, a function of competitor density. After numbering species according to

204 their longevity such that species 1 stops growing at a higher resource level than species 2, an expression
205 for how t_i declines with neighbor density is:

$$\begin{aligned} t_1(n_1, n_2) &= \frac{R_1}{\alpha_1 n_1 + \alpha_2 n_2} \\ t_2(n_1, n_2) &= \frac{R_1}{\alpha_1 n_1 + \alpha_2 n_2} + \frac{R_2}{\alpha_2 n_2} \end{aligned} \quad (2)$$

206 where R_1 is the fraction of the resource pool accessible to both species, and R_2 is the fraction of the
207 resource pool only accessible to species 2 because species 1 has stopped growing. This partitioning
208 naturally arises when species 1 has a higher requirement of the resource for growth than species 2. α_i is
209 the rate at which species i consumes the resource per unit density (i.e. the rate of crown expansion or
210 transpiration).

211

212 The difference between competition for time and growth-mediated competition is evident in the
213 expression for the longer-lived species 2. Because species 2 can continue to grow at lower resource
214 levels than species 1, there is a period after species 1 stops growing in which species 2 experiences
215 competition only from itself (Fig. 2A). Therefore, species 2's total lifespan is the sum of two time
216 periods, one in which both species 1 and 2 are actively growing $\left(\frac{R_1}{\alpha_1 n_1 + \alpha_2 n_2}\right)$, and one in which only
217 species 2 is active $\left(\frac{R_2}{\alpha_2 n_2}\right)$.

218

219 Equation 2 describes the outcome of a single bout of competition (Fig. 2A). These bouts are then
220 repeated many times, following equation 1, to generate the long-term population dynamics which
221 determine species coexistence (Fig. 2B). Specifically, when equation 2 is substituted into equation 1, we
222 obtain the following expression for the intergenerational dynamics:

$$\begin{aligned}\frac{n_1(T+1)}{n_1(T)} &= f g_1 \left(\frac{R_1}{\alpha_1 n_1 + \alpha_2 n_2} \right) \\ \frac{n_2(T+1)}{n_2(T)} &= f g_2 \left(\frac{R_1}{\alpha_1 n_1 + \alpha_2 n_2} + \frac{R_2}{\alpha_2 n_2} \right)\end{aligned}\tag{3}$$

223 Observe that this functional relationship between population and competitor density, and in particular
 224 the nested structure of the terms describing density dependence for species 2, is distinct from the forms
 225 that would ever emerge in common models of species competition such as Lotka-Volterra, Beverton-
 226 Holt or MacArthur Consumer Resource models (MacArthur 1970; Wangersky 1978; Berezansky &
 227 Braverman 2004, see Appendix 3.6 for these models' forms of density dependence). Therefore, even
 228 though these models do not explicitly specify that competition reduces individual biomass growth rates,
 229 the forms they employ cannot capture the essence of competition for time.

230

231 To illustrate how competition for time promotes coexistence, we solve for the invasion growth rates of
 232 the model in equation 3.

$$\begin{aligned}IGR_1 &= \frac{g_1 R_1}{g_2 (R_1 + R_2)} \\ IGR_2 &= \infty\end{aligned}\tag{4}$$

233 The invasion growth rate for species 1 shows that because it is shorter-lived than species 2 ($R_1 + R_2 >$
 234 R_1), it must have a higher biomass growth rate ($g_1 > g_2$) to invade species 2 at equilibrium (for IGR_1 in
 235 Equation 4 to exceed 1) (Fig. 3A). Meanwhile, the longer-lived species 2 automatically has a refuge
 236 from interspecific competition after species 1 stops growing, resulting in infinite growth as it drops to
 237 near zero density in the invader state (note that the second term in Equation 3, $\frac{R_2}{\alpha_2 n_2}$, goes to infinity as
 238 species 2's density goes to zero). As a result, species 2 can never be competitively excluded by species 1
 239 and will always invade. Notably, the mutual invasibility condition in equation 4 also implies the

240 existence of a globally stable equilibrium (Appendix 1.1.1). The take home message from these invasion
241 growth rates is that opportunities for coexistence abound when the shorter-lived species has a higher
242 biomass growth rate (Fig. 3A).

243

244 Importantly, Equation 3 can easily be extended to communities of arbitrary size (Appendix 1.1 and 1.2),
245 meaning that competition for time can explain the coexistence of any number of species with the
246 appropriate growth-longevity tradeoff. Moreover, even if the pool of species entering a community
247 exhibits no such tradeoff, the community assembly process will whittle the system down such that the
248 subset of species that do coexist will follow this tradeoff (Levine et al. 2022).

249

250 We acknowledge that equations 3 and 5 are just one way in which competition for time may be
251 expressed in a natural community, and in many systems the functional form will differ. Though these
252 new functional forms will alter the invasion condition from equation 4, the general requirement for
253 coexistence that species tradeoff growth and longevity remains valid. We describe three ways to adapt
254 this generalized model for specific systems: one in the next section, and two in Appendix 1.1.2.

255

256 **Competition for time in Mediterranean annual plant communities**

257 Thus far we have presented a simple model of competition for time to illustrate its inherent ability to
258 generate coexistence. In this section, we present a competition for time model motivated by an empirical
259 system and the ecophysiology of the species that make up that system, laying the context for
260 experimentally testing its predictions in nature. In (Levine *et al.* 2022) we developed such a model for
261 water competition among Mediterranean annual plants. This model represents a concrete example of
262 competition for time in a system not typically thought of as successional.

263

264 In Mediterranean annual plant communities, individuals germinate during a short rainy season and then
265 compete for water over the course of the subsequent dry season until the soil becomes too dry to
266 maintain growth; at which point individuals convert available biomass to seed and then die. The
267 ecophysiological model developed in (Levine *et al.* 2022) predicts that these plants' growth response to
268 water limitation is abrupt: plants grow all-out until soil water availability reaches a species-specific
269 threshold, after which they almost immediately stop growing. When competitors consume the shared
270 water resource, they cause this threshold to be reached sooner. Thus, the primary effect of increased
271 competition for water is decreased lifespan rather than decreased biomass growth rate. In other words,
272 the plants compete for time.

273

274 The basic outline of the model is as follows: a year begins with the onset of the rainy season at which
275 point all individuals of all species germinate synchronously. After germination, plants of species i grow
276 unfettered by neighbors at a rate γ_i until the soil water content drops below a species-specific critical
277 water content, w_i^* . We label the time at which this happens τ_i , which is equivalent to the length of
278 species i 's growing season and analogous to t_i from equation 1. At τ_i all individuals of species i
279 convert their biomass to germinable seeds. Here, we allow the rate of conversion from biomass to
280 germinable seeds to vary by species. These seeds then germinate at the start of the following rainy
281 season, restarting the cycle. Thus, the population dynamics are given by a modified version of equation
282 1:

$$\frac{n_i(T + 1)}{n_i(T)} = f_i \gamma_i \tau_i \quad (5)$$

283 Competition emerges because when individuals transpire water, they cause the soil water content to
284 reach their competitors' critical content sooner, shortening their competitors' lifespan τ_i and reducing

285 their final biomass, fecundity, and next year's population size following equation 5. The specific
 286 functional form of τ_i in a two-species system is given by the following expressions, where species 1 has
 287 a higher critical water content than species 2, and is therefore shorter-lived:

$$\tau_1 = \frac{w_0 - w_1^*}{\alpha_1 n_1 + \alpha_2 n_2}$$

$$\tau_2 = \frac{w_0 - w_1^*}{\alpha_1 n_1 + \alpha_2 n_2} + \frac{w_1^* - w_2^*}{\alpha_2 n_2} \quad (6)$$

288 Here w_0 is the volumetric soil water content at the start of the dry season, and α_i describes the effect of
 289 species i on soil water availability (Appendix 1). Each term on the right-hand side of equation 6 is the
 290 length of time required for the actively growing species to consume the amount of water available
 291 during a given period (the numerator of each term).

292

293 For each species there exists a value of τ_i which we call the species' "break even time," τ_i^* , at which it
 294 makes just enough seeds that its population density is stable from one year to the next. This can be
 295 calculated by setting the annual population growth rate from equation 5 to 1, and solving for τ_i^* :

$$\tau_i^* = \frac{1}{f_i \gamma_i} \quad (7)$$

296 The resulting expression shows that a species' break-even time is determined by its biomass growth rate,
 297 γ_i , and conversion of biomass to fecundity, f_i , such that if either increases, it needs less time to break-
 298 even in terms of population growth.

299

300 Species coexist in this model when they follow a tradeoff between break-even time and critical water
 301 content that is decreasing and concave-up, a relationship which guarantees shorter-lived species have
 302 higher biomass growth rates or higher biomass to fecundity conversion rates than longer-lived species
 303 (Fig 3). In the model the rate at which an individual consumes soil water, α_i , is a function of its leaf area

304 (Appendix 1). And so, a further consequence of higher growth rates in this model is a greater per capita
305 effect on soil water availability.

306

307 In (Levine *et al.* 2022) we show that this growth-longevity tradeoff emerges naturally from
308 ecophysiology if species maintain growth at lower water content by investing carbon which could
309 otherwise be used for productive leaves in more expensive structures such as thick-walled xylem or deep
310 roots. We note that because this tradeoff is a requirement for coexistence, any coexisting community of
311 species will appear to follow it regardless of whether it is prescribed by physiology. We also note that
312 competition for time dynamics do not hinge on whether the species follow a growth-longevity tradeoff.
313 However, because the tradeoff is a consequence of the underlying ecophysiology and consistent with the
314 requirements for high diversity, empirically evaluating it is one goal of this study.

315

316 **Experimental evidence that species compete for time**

317 Empirically testing competition for time in a non-successional system is essential to demonstrating its
318 broader generality. To this end, we conducted a field experiment to assess whether Mediterranean annual
319 plants, whose coexistence is not typically associated with succession, compete for time. Specifically, we
320 asked two questions: 1) When species compete for water, does water limit individuals' biomass growth
321 rates or the duration of their biomass growth? 2) Do species follow a growth-longevity tradeoff of the
322 form required for coexistence?

323

324 To answer these questions, we planted focal individuals of five species of California annual plants in
325 plots with either a) a monoculture of a given competitor species or b) no competitors (control). Over the
326 course of a single growing season we quantified the growth of each focal individual, the time at which

327 its growth ceased, and its final seed production. Then, we analyzed these growth patterns to determine
328 whether the effect of competition on seed production was mediated primarily by reductions in growing
329 season length, or growth rate (i.e. does the response to competition follow Fig. 1A or B?). To answer
330 question 2, we used estimates of the growth, fecundity and critical water contents of the focal
331 individuals to test whether they followed a decreasing and concave-up growth-longevity tradeoff (Fig.
332 3B). To specifically implicate competition for water as the mechanism driving reductions in biomass
333 growth rate or growing season length, we tested each of the hypothesized relationships diagrammed in
334 Figure 4.

335

336 *Study site*

337 The experiment was performed at the University of California Natural Reserve System's Sedgwick
338 Reserve in northern Santa Barbara County, CA, USA. The study site is located at an elevation of 730m
339 on a southern facing slope in the foothills of the San Rafael mountains and is characterized by serpentine
340 soils. The reserve receives 380 mm of rainfall on average. However, rainfall is highly variable across
341 years and in the year of this study (2020-2021), the site received only 180 mm of rain.

342

343 *Experimental Design*

344 We established fifty-two 1.33 m^2 plots, each of which was randomly assigned to receive 8 g of seed
345 m^{-2} of one of six study species designated as a background competitor (Pacific fescue, *Festuca*
346 *microstachys*; chia, *Salvia columbariae*; Chile lotus, *Acmispon wrangelianus*; dwarf plantain, *Plantago*
347 *erecta*; goldfields, *Lasthenia californica*; silverpuffs, *Uropappus lindelyi*). Even though all 8-10 plots
348 per competitor species were sown with the same seed mass, variable germination generated significant
349 variation in competitor density that we used to test our hypotheses. Moreover, an additional ten plots

350 were randomly assigned to receive no background competitor. We sowed a small number of focal
351 individual seeds of each of the study species into all these plots, allowing us to measure how each
352 species responds to competition from each background competitor species. By quantifying, in all plots,
353 1) soil water content, 2) background competitor density (through germination counts in four 0.08 m^2
354 subplots per plot), 3) the biomass gain of focal individuals (nondestructively), and 4) seed production of
355 focal individuals, we were able to estimate all of the hypothesized dependencies between competitor
356 density, soil moisture, season length, and growth rate visualized in Fig. 4.

357

358 *Do species compete for time?*

359 To evaluate the two alternative hypotheses, competition for time vs. growth-mediated competition, we
360 employed two analyses. The first is a comparison of the relationships between competitor density and
361 season-length, and competitor density and biomass growth rate. We quantified season length (or life
362 span) as the date each focal reached its peak biomass, determined by interpolating measurements of the
363 biomass of each focal taken at regular intervals through the growing season (Appendix 3). Due to the
364 dry nature of the experimental year, early-phenology species senesced earlier than expected. As a result,
365 our first intensive allometric samples sometimes occurred after an individual reached peak biomass. This
366 resulted in truncated estimates of growing season length for early-phenology species. We account for
367 this by using censored data models where appropriate (Appendix 3.4).

368

369 Average biomass growth rate was calculated from a focal individual's peak biomass, initial biomass at
370 first measurement, and season length (Appendix 3.4.4). We compared the statistical support for
371 relationships between competitor density and (1) growing season length and (2) biomass growth rate by
372 fitting two linear mixed effects models, one for each relationship, using Hamiltonian Monte Carlo as

373 implemented in the package brms in R (Bürkner 2017) and comparing effect sizes and posterior
374 uncertainties. These two relationships are agnostic to the limiting resource, and thus evaluate our
375 alternative hypotheses in their most basic form.

376

377 The goal of the second analysis was to more rigorously evaluate the specific predictions of the
378 theoretical model as they relate to water competition, depicted by the directed acyclic graph in Fig. 4. To
379 do so we performed a Bayesian path analysis to quantify the relationships between competitor density
380 and seed production as mediated by soil water content, lifespan, and biomass growth rate (Fig. 4). This
381 model was also fit using Hamiltonian Monte Carlo. Specifically, this second model quantified
382 relationships between competitor density and four response variables: 1) soil water availability, 2)
383 lifespan, τ_i (as explained in the prior paragraph), 3) average biomass growth rate (as explained in the
384 prior paragraph), and 4) focal plant fecundity. Soil water availability was quantified as the average
385 difference between the water content of plots kept free of vegetation and the plot in which the focal
386 individual was growing. We let the model arbitrate the length of the period over which this average was
387 taken, always ending at the last measurement before a focal individual's end-of-season date. Fecundity
388 was expressed as the deviation of the focal plant's seed production from its species' average
389 reproduction. All continuous variables were normalized to standard units to aid both model convergence
390 and the comparison and interpretation of effect sizes. Please see Appendix 3 for a more complete
391 description of the statistical methodology.

392

393 *Do species follow a growth-longevity tradeoff?*

394 To determine whether the species in this study adhered to a growth-longevity tradeoff of the form
395 required for coexistence, we quantified the biomass growth rate and fecundity conversion rate, which

396 together determine the break-even time and critical water content of each species (Fig. 3B). We
397 estimated critical water content by lining up each focal individual's date of maximum biomass and the
398 soil moisture in that focal's plot, interpolated from regular measurements of volumetric soil water
399 content.

400

401 To quantify a possible growth-longevity tradeoff, we used nonlinear least squares to fit a negative
402 exponential curve to species' critical water contents and their break-even time – the inverse of the
403 product of their fecundity and biomass growth rates. We chose a negative exponential simply because it
404 is a flexible form that meets the criteria for the growth-longevity tradeoff required to maintain high
405 diversity.

406

407 *Results*

408 We found strong evidence that competition was primarily expressed through reductions in growing
409 season length, but not growth rate (Fig. 5, 6). For four of the five focal species, the estimated effect of
410 competitor density on lifespan was negative (Fig. 5). In contrast, only one of the five focal species
411 experienced reductions in biomass growth rate because of competition (Fig. 5).

412

413 The results of our more detailed analysis of competition for water per se provided even stronger support
414 for the competition for time hypothesis (Fig. 6). We found that the effect of competition for water on
415 focal fecundity was mediated by a reduction in species' growing season lengths (Fig 6. A-C), but not in
416 their growth rates (Fig. 6 D-F). In fact, the estimated effect of competition on a focal individual's
417 reproduction as mediated by season length was almost 25 times larger than the effect of competition as
418 mediated by growth rate (-0.54 [-0.86, -0.29] vs. -0.022 [-0.11, 0.07]; Appendix 3.4.1). For *A*.

419 *wrangelianus*, a species with intermediate seed production, the competition for time effect corresponded
420 to a decrease in fecundity from 319 seeds to 21 seeds in response to a one s.d. increase in competitor
421 density.

422

423 Breaking these effects down to their component parts, we found clear statistical evidence that increased
424 competitor density was associated with dryer soil conditions, that dryer soil conditions were associated
425 with shorter season lengths, and that shorter season lengths were associated with reduced fecundity (Fig.
426 6). Please see tables S8, S9, and S10 in Appendix 3 for a full list of estimated parameters and posterior
427 uncertainties. Though we found that the effect of growth rate on fecundity was greater in magnitude than
428 the effect of season length on fecundity (0.56 [0.37, 0.75] vs. 0.27 [0.12, 0.43]; Fig. 6F), we did not
429 observe compelling evidence that growth rate was influenced by competitors' effect on soil moisture or
430 otherwise (Fig. 6 C,D). We infer that variation in growth rate among individuals of the same species,
431 though clearly important in determining fecundity, is driven primarily by noncompetitive factors (Fig.
432 6). The estimated effect of soil water availability on growth rate was negative, but it was both small and
433 uncertain relative to the effect on season-end date (-0.1 [-0.35, 0.15]), and positive effects of water
434 availability on growth rate were assigned substantial probability.

435

436 The negative exponential fit passed within the 95% credible intervals for each species' combination of
437 break-even time and critical water content, indicating that the species may follow a tradeoff of the form
438 required for the maintenance of diversity (Fig. 7; *L. californica* is not represented in this plot due to its
439 very low germination as a focal species). This tradeoff is also reflected in the differential consumption of
440 soil water by each species (Appendix 3.1). Though the tradeoff form appears plausible, we note that the
441 small total number of species makes rigorously evaluating the correct tradeoff form impossible. The

442 species' apparent adherence to the tradeoff corresponded to relatively high estimated probabilities of
443 coexistence – roughly 60% across all species pairs.

444

445 **Discussion**

446 In this study we introduced competition for time as a formal mechanism of competition and coexistence
447 in plant-communities. In addition, we demonstrated the importance of competition for time in
448 structuring plant growth, reproduction, and phenology in the field, indicating it may play a broader role
449 in maintaining diversity than previously thought (Fig. 5-6; Appendix 3.4-3.9). For all species in the
450 empirical study, the consumption of soil water by competitors caused focal individuals to stop growing
451 earlier, and therefore accumulate less biomass and produce fewer seeds than individuals grown without
452 competitors. While we observed some decline in biomass growth rate due to competition, as assumed by
453 more traditional growth-mediated competition models, the magnitude of this effect was both small and
454 uncertain relative to the effect of competition on the time for growth (Fig. 5 and 6, Appendix 3.3-3.4).

455

456 Our simple model, and one tailored to the biology of Mediterranean annual communities both show that
457 when species compete for time, coexistence is favored if they follow a tradeoff between biomass growth
458 rate and longevity. This tradeoff ensures slower growing competitors are compensated by a longer
459 lifespan. Our experiment suggested species could plausibly follow such a tradeoff (though the number of
460 species and high degree of uncertainty limits our ability to make a stronger claim). Species with shorter
461 growing seasons (higher critical water contents) tended to have higher growth rates (shorter break-even
462 times; Fig. 7). This pattern was associated with a high probability of predicted coexistence for most
463 species pairs in this study, though its likely other coexistence mechanisms also play a role in maintaining
464 diversity in this system.

465

466 *Implications of competition for time for plant species coexistence and community structure*

467 The appearance of competition for time in a community of plants not undergoing secondary succession
468 indicates that competition for time may be currently overlooked as a mechanism of species coexistence.
469 Our experiment suggests Mediterranean annual plant diversity is in part maintained by emergent
470 phenological variation, which allows species to divide the growing season into periods of decreasing
471 diversity as the soil dries (Fig. 5-7; Appendix 3.6, 3.7, 3.8). Though this exact structure may be
472 particular to Mediterranean annual plants, the revelation that competition for time dynamics can play out
473 on short time scales, and without regular disturbance, suggests analogous mechanisms may be present in
474 a wider variety of natural systems than typically appreciated.

475

476 The contributions of competition for time to coexistence may be underappreciated in part because most
477 models of competition are defined solely at the population dynamic timescale; they miss the distinction
478 between competition for time and growth-mediated competition that operate within competitive bouts
479 (Macarthur & Levins 1967; Wangersky 1978; Berezansky & Braverman 2004; Detto *et al.* 2022; Levine
480 *et al.* 2022). The lack of attention paid to competition for time in community ecology may also follow
481 from a focus on modeling populations rather than individuals. For both Mediterranean annual plants and
482 forest trees, competition for time acts on the individual, the entity whose lifetime is shortened by
483 increased resource limitation (Detto *et al.* 2022; Levine *et al.* 2022). As we demonstrated in this paper,
484 processes operating on these shorter timescales, and on individuals, generate functional forms of density
485 dependence at the population dynamic scale atypical of most competition models (Wangersky 1978;
486 Chesson 1990; Berezansky & Braverman 2004). Yet these are forms that promote coexistence.

487

488 In this paper we have primarily discussed “strict” competition for time, wherein competition is
489 experienced solely through reductions in the time available for growth while biomass growth rate is
490 constant. This assumption appears reasonable for the Mediterranean annual plant system in which we
491 performed our experiment. In nature however, strict competition for time is likely rare relative to cases
492 in which both the time available for growth and the rate of biomass accumulation are harmed by
493 competition. Many studies have demonstrated substantial competitive effects on individual biomass
494 growth rates (e.g. Goldberg 1987; Wilson & Tilman 1991; Coomes & Allen 2007; Anderegg &
495 HilleRisLambers 2019), including in successional forests known to experience competition for time
496 (Canham *et al.* 2006; Rollinson *et al.* 2016). As of now, the implications of interactions between these
497 forms of competition are understudied, making this an important topic for future research. Initial
498 theoretical work done on the annual plant model suggests high diversity is still feasible when both
499 mechanisms are present (Levine *et al.* 2022).

500

501 *Relationship to other coexistence mechanisms*

502 Of course, ecologists have long recognized the importance of temporal variation as a means for species
503 to coexist on an apparently singular resource (Levins 1979; Chesson 1985; Post 2019), and this has also
504 been posed many times for communities of Mediterranean annual plants (Hooper & Dukes 2010;
505 Wolkovich & Cleland 2011; Chesson *et al.* 2013; Mathias & Chesson 2013; Godoy & Levine 2014;
506 Alexander *et al.* 2015; Kraft *et al.* 2015). What sets competition for time apart from these mechanisms is
507 the way temporal variability is generated, and the resulting ease of coexistence. Typically, temporal
508 variation is treated as a fixed characteristic of the environment, generated by pulsed resource inputs
509 (Chesson *et al.* 2004; Letten *et al.* 2018), seasonal weather patterns (Usinowicz *et al.* 2017), inter-annual
510 variation in climate (Adler *et al.* 2006; Angert *et al.* 2009), or otherwise. Under competition for time,

511 though a pulsed resource supply is prerequisite, subsequent variation in the environment is
512 endogenously generated by resource uptake by the competitors themselves. Species affect the shared
513 resource in sequence, exerting the most impact in the period in which they are also the greatest
514 beneficiary, leading to diversity-maintaining self-limitation (Detto *et al.* 2022; Levine *et al.* 2022).

515

516 Past studies of foraging behavior in animal communities have identified a similar competitive
517 mechanism to the one described in this paper. For example, Schoener 1973 presents a model where
518 species reduce the feeding time of competitors through interference interactions. The frequency of these
519 interactions increases with competitor density, leading to reduced feeding time and reproductive output
520 (Schoener 1973, 1974). Thus, the net effect of competition in this system is similar to the one identified
521 here. However, there is a key difference: because species are not differentiated by their tolerance to
522 resource limitation, these models lack the endogenous variability in longevity that fosters coexistence
523 under competition for time. Some have posited that interference competition may drive the evolution of
524 temporal niches as a means of avoidance (e.g. Carothers & Jaksic 1984), but the importance of
525 endogenous niche differentiation and growth-longevity tradeoffs when species compete for time has not
526 been identified.

527

528 The competition for time framework can also help us understand puzzling elements of other previously
529 published competition models. For example, competition-colonization tradeoff models (Hastings 1980;
530 Tilman 1994), are often viewed as idiosyncratic given they support unlimited diversity, exhibit
531 extinction cascades, and require a strict competitive asymmetry for coexistence (Yu & Wilson 2001). If
532 one recasts the competition colonization model in terms of the fate of individuals rather than populations
533 competing for patches (as it is normally written), it reveals how this mechanism is simply competition

534 for time. More specifically, superior competitors shorten an individual's expected lifespan by either
535 displacing it or preventing its establishment in the first place (Appendix 1.6). Thereby, competition for
536 limited patches effectively results in competition for time, just as competition for water drives
537 competition for time in our Mediterranean annual model. In fact, the competition-colonization model
538 bears close resemblance to a successional competition for time model recently published by Detto *et al.*
539 (2022). Both models include asymmetric competition, and both result in extinction cascades.
540 This connection demonstrates how building analogies between competition for time and other models
541 may lead to a more unified theory of coexistence.

542

543 *The role of stochasticity in competition for time models*

544 The theory described in this paper is completely deterministic, and therefore an abstraction of natural
545 systems where environmental stochasticity can be prominent (Chesson & Warner 1981; Gravel *et al.*
546 2011). Prior theoretical studies of environmental variation's impact on coexistence show how it can
547 either harm coexistence by reducing species' population growth rates, or foster coexistence through
548 mechanisms like the storage effect (Levins 1979; Gravel *et al.* 2011; Hallett *et al.* 2019). Interestingly,
549 when species compete for time the effect of environmental stochasticity doesn't fit neatly into these
550 expectations. As we show through simulation analysis in Appendix 1.3, increasing variation in initial
551 resource supply (e.g. rainfall in Mediterranean annual plant systems) can erode diversity. However,
552 rather than harming each species' ability to coexist, this variation disproportionately impacts short-lived
553 species, meaning long-lived species are resilient to stochastic resource supply. This discrepancy occurs
554 because the growing time of short-lived species is closely tied to initial resource supply, whereas long-
555 lived species are dependent on the resource left by short-lived species after they cease growth (Levine *et*
556 *al.* 2022). There are of course many potential sources of stochasticity apart from initial resource supply.

557 For example, prior theoretical work has also shown that intraspecific variability in species' traits is likely
558 to erode diversity (Detto et al. 2022).

559

560 *Future directions*

561 This study establishes that competition for time dynamics are indeed present and important in a non-
562 successional field system. However, it remains unclear how widespread competition for time is, and if
563 so, whether it promotes coexistence as predicted in Levine *et al.* (2022) and this study. In addition to
564 further work in water-limited plant communities (particularly those dominated by perennials), systems
565 governed by light competition, but lacking secondary-successional dynamics as typically conceived,
566 could be a good candidate for future experiments (Detto *et al.* 2022). For example, non-forest plants
567 whose phenology is driven primarily by sequential overtopping (e.g. old-field perennial grasses) likely
568 experience competition for time. In general, further theory and empirical studies linking the identity of
569 the limiting resource to the relative degree of competition for time versus growth-mediated competition
570 could help generate a more predictive understanding of species coexistence.

571

572 *Conclusion*

573 In this paper we have articulated a simple model of competition for time and shown that this process is
574 an important mechanism of competition in a system without successional dynamics, acting within a
575 single growing season in a water-limited plant community. This finding suggests the potentially broader
576 importance of competition for time as a mechanism of diversity maintenance, and future work should
577 seek to determine exactly how prevalent it is. If the mechanism proves widespread, species coexistence
578 may prove less of an ecological paradox.

579

580 **Acknowledgements**

581 This work was performed (in part) at the University of California Natural Reserve System Sedgwick
582 Reserve DOI: 10.21973/N3C08R. We are grateful to Ryan Fass for his tireless work in the field and
583 input on experimental design and logistics. We also thank Angela Giordani, Kate McCurdy, Lyza
584 Johnsen, Nikki Evans, Heather Constable, and the rest of the Sedgwick Natural Reserve staff and faculty
585 for their continued, generous support of our research. This work was supported by the Mary and Randall
586 Hack Graduate Award for Water and the Environment, by National Science Foundation award DEB-
587 2022213 to JML, and by the National Science Foundation Graduate Research Fellowship DGE-2039656
588 to JIL.

References

- 589 Adler, P.B., HilleRisLambers, J., Kyriakidis, P.C., Guan, Q. & Levine, J.M. (2006). Climate variability has a
590 stabilizing effect on the coexistence of prairie grasses. *Proceedings of the National Academy of*
591 *Sciences*, 103, 12793–12798.
- 592 Aguiar, M.R., Lauenroth, W.K. & Peters, D.P. (2001). Intensity of intra- and interspecific competition in
593 coexisting shortgrass species. *Journal of Ecology*, 89, 40–47.
- 594 Alexander, J.M., Diez, J.M. & Levine, J.M. (2015). Novel competitors shape species' responses to climate
595 change. *Nature*, 525, 515–518.
- 596 Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: a synthesis.
597 *Ecology Letters*, 6, 1109–1122.
- 598 Anderegg, L.D.L. & HilleRisLambers, J. (2019). Local range boundaries vs. large-scale trade-offs: climatic
599 and competitive constraints on tree growth. *Ecology Letters*, 22, 787–796.
- 600 Anderegg, W.R.L., Wu, C., Acil, N., Carvalhais, N., Pugh, T.A.M., Sadler, J.P., *et al.* (2022). A climate risk
601 analysis of Earth's forests in the 21st century. *Science*, 377, 1099–1103.
- 602 Angert, A.L., Huxman, T.E., Chesson, P. & Venable, D.L. (2009). Functional tradeoffs determine species
603 coexistence via the storage effect. *Proceedings of the National Academy of Sciences*, 106,
604 11641–11645.
- 605 Armstrong, R.A. & McGehee, R. (1980). Competitive Exclusion. *The American Naturalist*, 115, 151–170.
- 606 Barabás, G., J. Michalska-Smith, M. & Allesina, S. (2016). The Effect of Intra- and Interspecific
607 Competition on Coexistence in Multispecies Communities. *The American Naturalist*, 188, E1–
608 E12.

609 Bazzaz, F.A. (1991). Habitat Selection in Plants. *The American Naturalist*, 137, S116–S130.

610 Berezansky †, L. & Braverman, E. (2004). On Impulsive Beverton-Holt Difference Equations and their
611 Applications. *Journal of Difference Equations and Applications*, 10, 851–868.

612 Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a metabolic theory of
613 ecology. *Ecology*, 85, 1771–1789.

614 Bürkner, P.-C. (2017). **brms** : An R Package for Bayesian Multilevel Models Using Stan. *J. Stat. Soft.*, 80.

615 Callaway, R.M. & Walker, L.R. (1997). Competition and facilitation: a synthetic approach to interactions
616 in plant communities. *Ecology*, 78, 1958–1965.

617 Canham, C.D., Papaik, M.J., Uriarte, M., McWilliams, W.H., Jenkins, J.C. & Twery, M.J. (2006).
618 Neighborhood Analyses Of Canopy Tree Competition Along Environmental Gradients In New
619 England Forests. *Ecological Applications*, 16, 540–554.

620 Carothers, J.H. & Jaksic, F.M. (1984). Time as a Niche Difference: The Role of Interference Competition.
621 *Oikos*, 42, 403–406.

622 Casper, B.B. & Jackson, R.B. (1997). Plant competition underground. *Annual review of ecology and
623 systematics*, 28, 545–570.

624 Caspersen, J.P. & Pacala, S.W. (2001). Successional diversity and forest ecosystem function. *Ecol Res*, 16,
625 895–903.

626 Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009). The merging of community ecology
627 and phylogenetic biology. *Ecology Letters*, 12, 693–715.

628 Chesson, P. (1990). MacArthur’s consumer-resource model. *Theoretical Population Biology*, 37, 26–38.

629 Chesson, P. (1994). Multispecies Competition in Variable Environments. *Theoretical Population Biology*,
630 45, 227–276.

631 Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and
632 Systematics*, 31, 343–66.

633 Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., *et al.* (2004).
634 Resource pulses, species interactions, and diversity maintenance in arid and semi-arid
635 environments. *Oecologia*, 141, 236–253.

636 Chesson, P., Pacala, S. & Neuhauser, C. (2013). 10. Environmental Niches and Ecosystem Functioning. In:
637 *10. Environmental Niches and Ecosystem Functioning*. Princeton University Press, pp. 213–245.

638 Chesson, P.L. (1985). Coexistence of competitors in spatially and temporally varying environments: A
639 look at the combined effects of different sorts of variability. *Theoretical Population Biology*, 28,
640 263–287.

641 Chesson, P.L. & Warner, R.R. (1981). Environmental Variability Promotes Coexistence in Lottery
642 Competitive Systems. *The American Naturalist*, 117, 923–943.

643 Clements, F.E. (1916). *Plant Succession: An Analysis of the Development of Vegetation*. Carnegie
644 Institution of Washington.

645 Cody, M.L. & Diamond, J.M. (1975). *Ecology and evolution of communities*. Harvard University Press.

646 Connell, J.H. (1983). On the Prevalence and Relative Importance of Interspecific Competition: Evidence
647 from Field Experiments. *The American Naturalist*, 122, 661–696.

648 Coomes, D.A. & Allen, R.B. (2007). Effects of size, competition and altitude on tree growth. *Journal of
649 Ecology*, 95, 1084–1097.

650 Detto, M., Levine, J.M. & Pacala, S.W. (2022). Maintenance of high diversity in mechanistic forest
651 dynamics models of competition for light. *Ecological Monographs*, 92, e1500.

652 Drury, W.H. & Nisbet, I.C.T. (1973). Succession. *Journal of the Arnold Arboretum*, 54, 331–368.

653 Elzinga, J.A., Atlan, A., Biere, A., Gigord, L., Weis, A.E. & Bernasconi, G. (2007). Time after time:
654 flowering phenology and biotic interactions. *Trends in Ecology and Evolution*, 22, 432–439.

655 Fargione, J. & Tilman, D. (2005). Niche differences in phenology and rooting depth promote coexistence
656 with a dominant C4 bunchgrass. *Oecologia*, 143, 598–606.

657 Forrest, J. & Miller-Rushing, A.J. (2010). Toward a synthetic understanding of the role of phenology in
658 ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*,
659 365, 3101–3112.

660 Fowler, N. (1986). The role of competition in studies of spatial pattern. *Annual Review of Ecology and*
661 *Systematics*, 17, 89–110.

662 Fridley, J.D. (2012). Extended leaf phenology and the autumn niche in deciduous forest invasions.
663 *Nature*, 485, 359–362.

664 Funk, J.L. & Wolf, A.A. (2016). Testing the trait-based community framework: Do functional traits
665 predict competitive outcomes? *Ecology*, 97, 2206–2211.

666 Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010). A framework for community
667 interactions under climate change. *Trends in Ecology & Evolution*, 25, 325–331.

668 Godoy, O. & Levine, J.M. (2014). Phenology effects on invasion success: Insights from coupling field
669 experiments to coexistence theory. *Ecology*, 95, 726–736.

670 Goldberg, D.E. (1987). Neighborhood Competition in an Old-Field Plant Community. *Ecology*, 68, 1211–
671 1223.

672 Gravel, D., Guichard, F. & Hochberg, M.E. (2011). Species coexistence in a variable world. *Ecology*
673 *Letters*, 14, 828–839.

674 Hallett, L.M., Shoemaker, L.G., White, C.T. & Suding, K.N. (2019). Rainfall variability maintains grass-forb
675 species coexistence. *Ecology Letters*, 22, 1658–1667.

676 Hastings, A. (1980). Disturbance, coexistence, history, and competition for space. *Theoretical*
677 *Population Biology*, 18, 363–373.

678 Hooper, D.U. & Dukes, J.S. (2010). Functional composition controls invasion success in a California
679 serpentine grassland. *Journal of Ecology*, 98, 764–777.

680 Horn, H.S. (1971). *The Adaptive Geometry of Trees*. Princeton University Press.

681 Horn, H.S. (1974). The Ecology of Secondary Succession. *Annual Review of Ecology and Systematics*, 5,
682 25–37.

683 Hutchinson, G.E. (1961). The paradox of the plankton. *The American Naturalist*, 95, 137–145.

684 Kraft, N.J.B., Godoy, O. & Levine, J.M. (2015). Plant functional traits and the multidimensional nature of
685 species coexistence. *Proceedings of the National Academy of Sciences of the United States of*
686 *America*, 112, 797–802.

687 Letten, A.D., Dhami, M.K., Ke, P.-J. & Fukami, T. (2018). Species coexistence through simultaneous
688 fluctuation-dependent mechanisms. *Proceedings of the National Academy of Sciences*, 115,
689 6745–6750.

690 Levin, S.A. (1970). Community Equilibria and Stability, and an Extension of the Competitive Exclusion
691 Principle. *The American Naturalist*, 104, 413–423.

692 Levine, J.I., Levine, J.M., Gibbs, T. & Pacala, S.W. (2022). Competition for water and species coexistence
693 in phenologically structured annual plant communities. *Ecology Letters*, 25, 1110–1125.

694 Levine, J.M., Bascompte, J., Adler, P.B. & Allesina, S. (2017). Beyond pairwise mechanisms of species
695 coexistence in complex communities. *Nature*, 546, 56–64.

696 Levine, J.M. & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species
697 diversity. *Nature*, 461, 254–257.

698 Levine, J.M. & Rees, M. (2004). Effects of Temporal Variability on Rare Plant Persistence in Annual
699 Systems. *Am. Nat.*, 164, 350–363.

700 Levins, R. (1979). Coexistence in a Variable Environment. *The American Naturalist*, 114, 765–783.

701 Levins, R. & Culver, D. (1971). Regional coexistence of species and competition between rare species.
702 *Proceedings of the National Academy of Sciences*, 68, 1246–1248.

703 Litchman, E. & Klausmeier, C.A. (2008). Trait-Based Community Ecology of Phytoplankton. *Annual
704 Review of Ecology, Evolution, and Systematics*, 39, 615–639.

705 Lyu, S. & Alexander, J.M. (2023). Compensatory responses of vital rates attenuate impacts of
706 competition on population growth and promote coexistence. *Ecology Letters*, 26, 437–447.

707 MacArthur, R. (1970). Species packing and competitive equilibrium for many species. *Theoretical
708 Population Biology*, 1, 1–11.

709 MacArthur, R. & Levins, R. (1967). The Limiting Similarity, Convergence, and Divergence of Coexisting
710 Species. *The American Naturalist*, 101, 377–385.

711 MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press.

712 Mathias, A. & Chesson, P. (2013). Coexistence and evolutionary dynamics mediated by seasonal
713 environmental variation in annual plant communities. *Theoretical Population Biology*, 84, 56–
714 71.

715 McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from
716 functional traits. *Trends in Ecology & Evolution*, 21, 178–185.

717 McIntosh, R.P. (1981). Succession and Ecological Theory. In: *Forest Succession: Concepts and
718 Application*, Springer Advanced Texts in Life Sciences (eds. West, D.C., Shugart, H.H. & Botkin,
719 D.B.). Springer, New York, NY, pp. 10–23.

720 Odum, E.P. (1969). The Strategy of Ecosystem Development. *Science*, 164, 262–270.

721 Pacala, S.W. & Rees, M. (1998). Models Suggesting Field Experiments to Test Two Hypotheses Explaining
722 Successional Diversity. *The American Naturalist*, 152, 729–737.

723 Pearson, R.G. & Dawson, T.P. (2003). Predicting the impacts of climate change on the distribution of
724 species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, 12, 361–
725 371.

726 Post, E. (2019). *Time in Ecology*. Princeton University Press.

727 Ricklefs, R.E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, 7,
728 1–15.

729 Rollinson, C.R., Kaye, M.W. & Canham, C.D. (2016). Interspecific variation in growth responses to
730 climate and competition of five eastern tree species. *Ecology*, 97, 1003–1011.

731 Rudolf, V.H.W. (2019). The role of seasonal timing and phenological shifts for species coexistence.
732 *Ecology Letters*, 22, 1324–1338.

733 Sax, D.F., Stachowicz, J.J., Brown, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D., *et al.* (2007). Ecological
734 and evolutionary insights from species invasions. *Trends in Ecology & Evolution*, 22, 465–471.

735 Schoener, T.W. (1973). Population growth regulated by intraspecific competition for energy or time:
736 Some simple representations. *Theoretical Population Biology*, 4, 56–84.

737 Schoener, T.W. (1974). Competition and the form of habitat shift. *Theoretical Population Biology*, 6,
738 265–307.

739 Schoener, T.W. (1985). Some comments on Connell's and my reviews of field experiments on
740 interspecific competition. *The American Naturalist*, 125, 730–740.

741 Seabloom, E.W., Harpole, W.S., Reichman, O.J. & Tilman, D. (2003). Invasion, competitive dominance,
742 and resource use by exotic and native California grassland species. *Proceedings of the National*
743 *Academy of Sciences of the United States of America*, 100, 13384–13389.

744 Shea, K. & Chesson, P. (2002). Community ecology theory as a framework for biological invasions.
745 *Trends in Ecology & Evolution*, 17, 170–176.

746 Solbrig, O.T. & Orians, G.H. (1977). The Adaptive Characteristics of Desert Plants: A cost/benefit analysis
747 of photosynthesis leads to predictions about the types and distributions of desert plants.
748 *American Scientist*, 65, 412–421.

749 Tilman, D. (1980). Resources: A Graphical-Mechanistic Approach to Competition and Predation. *The*
750 *American Naturalist*, 116, 362–393.

751 Tilman, D. (1987). The Importance of the Mechanisms of Interspecific Competition. *The American*
752 *Naturalist*, 129, 769–774.

753 Tilman, D. (1990). Constraints and Tradeoffs : Toward a Predictive Theory of Competition and
754 Succession Author (s): David Tilman Published by : Wiley on behalf of Nordic Society Oikos
755 Stable URL : <http://www.jstor.org/stable/3565355> REFERENCES Linked. *Oikos*, 58, 3–15.

756 Tilman, D. (1994). Competition and Biodiversity in Spatially Structured Habitats Author (s): David
757 Tilman Stable URL : <http://www.jstor.org/stable/1939377> REFERENCES Linked references are
758 available on JSTOR for this article : You may need to log in to JSTOR to access the, 75, 2–16.

759 Usinowicz, J., Chang-Yang, C.-H., Chen, Y.-Y., Clark, J.S., Fletcher, C., Garwood, N.C., *et al.* (2017).
760 Temporal coexistence mechanisms contribute to the latitudinal gradient in forest diversity.
761 *Nature*, 550, 105–108.

762 Van Dyke, M.N., Levine, J.M. & Kraft, N.J.B. (2022). Small rainfall changes drive substantial changes in
763 plant coexistence. *Nature*, 611, 507–511.

764 Vilà, M. & Weiner, J. (2004). Are invasive plant species better competitors than native plant species? –
765 evidence from pair-wise experiments. *Oikos*, 105, 229–238.

766 Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmánek, M. & Westbrooks, R. (1997). Introduced Species:
767 A Significant Component of Human-Caused Global Change. *New Zealand Journal of Ecology*, 21,
768 1–16.

769 Wangersky, P.J. (1978). Lotka-Volterra Population Models. *Annual Review of Ecology and Systematics*, 9,
770 189–218.

771 Whittaker, R.H. (1953). A Consideration of Climax Theory: The Climax as a Population and Pattern.
772 *Ecological Monographs*, 23, 41–78.

773 Wilson, S.D. & Tilman, D. (1991). Component of Plant Competition Along an Experimental Gradient of
774 Nitrogen Availability. *Ecology*, 72, 1050–1065.

775 Wolf, A., Anderegg, W.R.L. & Pacala, S.W. (2016). Optimal stomatal behavior with competition for water
776 and risk of hydraulic impairment. *Proceedings of the National Academy of Sciences of the United*
777 *States of America*, 113, E7222–E7230.

778 Wolkovich, E.M. & Cleland, E.E. (2011). The phenology of plant invasions: A community ecology
779 perspective. *Frontiers in Ecology and the Environment*, 9, 287–294.

780 Wright, S.J. & Van Schaikt, C.P. (1994). Light and the phenology of tropical trees. *Am. Nat*, 143, 192–
781 199.

Figures

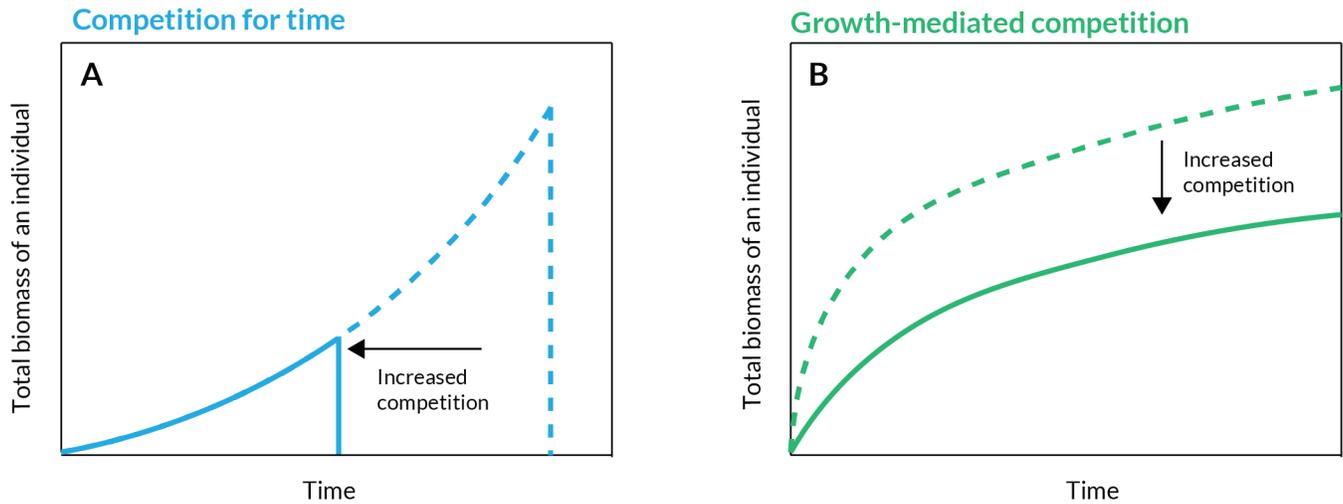


Figure 1 - Comparison of individual growth trajectories under competition for time and growth-mediated competition. Both panels show the effect of increased competition on the cumulative biomass accumulation of an individual. Panel A illustrates how under competition for time, increased densities of competitors cause individuals to finish growth earlier, leading to reduced total biomass accumulation without affecting the rate of biomass growth. Panel B illustrates how when competition is expressed through reductions in the growth rate, individuals grow slower at all points in time, and total biomass is thus reduced without changes to the individual's longevity.

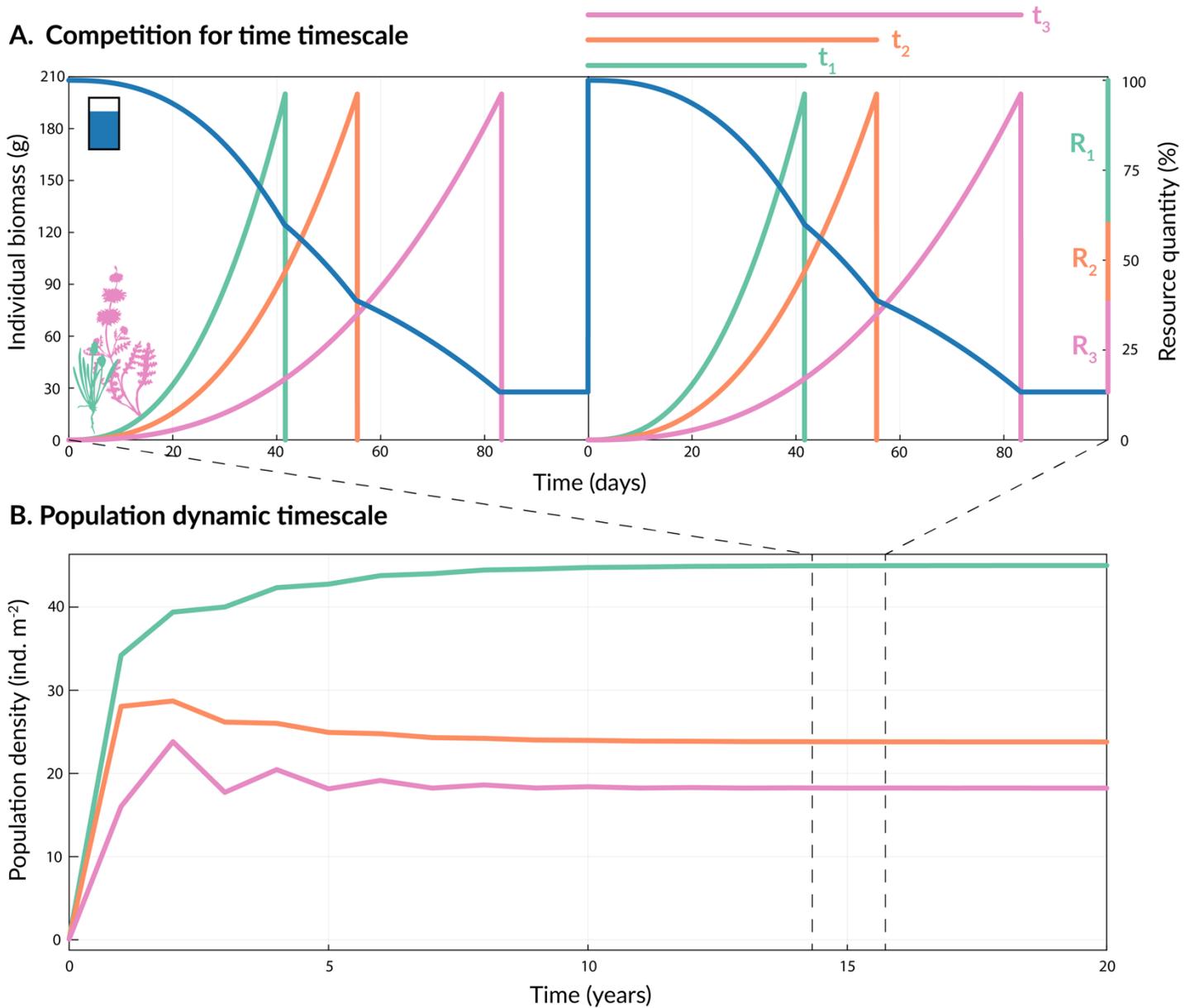
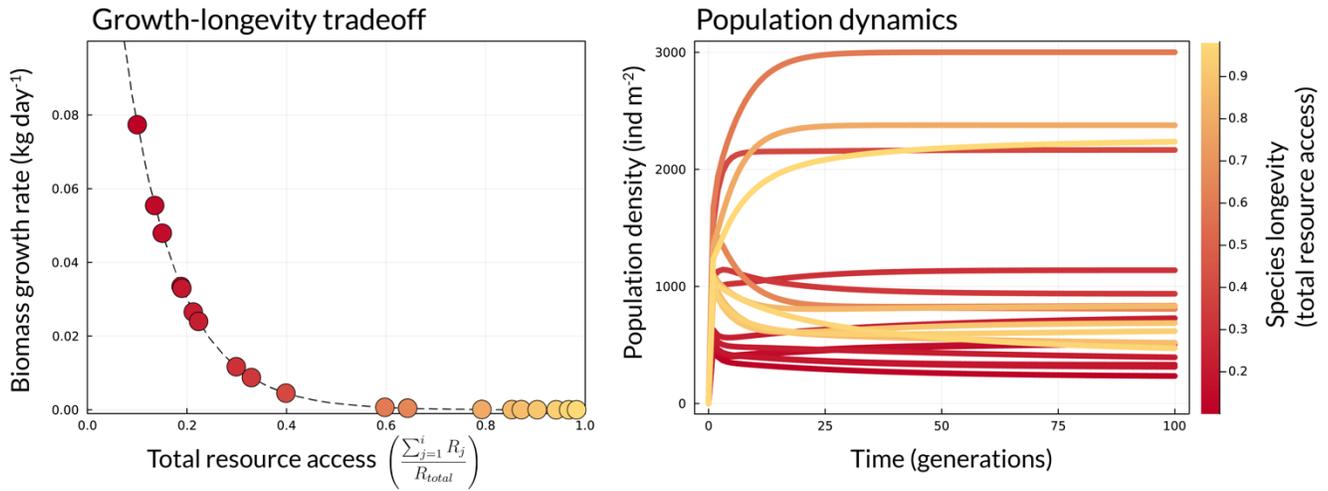


Figure 2 – Competition for time operates within competitive bouts (Panel A) but due to the repetition of the bouts, it ultimately affects population dynamics on a longer time scale (Panel B). In Panel A, three species deplete one another's time for growth within a bout of competition. The blue line shows the dynamics of the resource for which the species are competing, which is reset periodically (for example through winter rains in a Mediterranean annual plant community, or disturbance in a light-limited plant community). The green, orange, and pink lines show the accumulation of biomass of the three

competing species which vary in their longevity. Note that the shorter-lived species accumulate biomass faster than the longest-lived species, reflecting a growth-longevity tradeoff. The dynamics are shown over two iterations while the species are at population dynamic equilibrium. Panel B shows the population dynamics of these same three species as they increase from a low initial density.

A. Simple competition for time model



B. Competition for time among Mediterranean annual plants

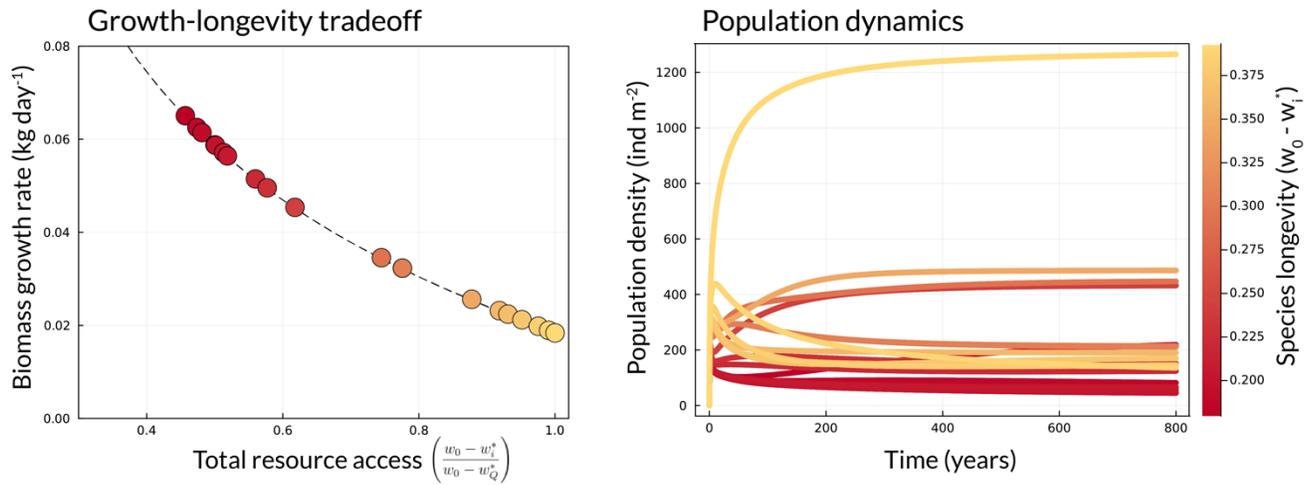


Figure 3 - Panel A illustrates how a growth-longevity tradeoff maintains high diversity in the simple model of competition for time first presented in the manuscript. The left plot shows the tradeoff itself, as quantified by species total resource access ($\sum_1^i R_j$) and biomass growth rate. Points denote the characteristics of individual species positioned along this tradeoff, with darker colors indicating longer-lived species. On the right the population dynamics of each of the species whose characteristics are plotted on the left are shown across years. Note that they all coexist. Any additional species which falls along this tradeoff will be able to invade successfully and coexist with the others. Species which fall above the tradeoff curve, however, would be competitively excluded. Panel B shows the exact same

dynamics except that they are for the model of Mediterranean annual plants. For these species, the growth longevity tradeoff is quantified by total volume of water access ($w_0 - w_i^*$) divided by total water available ($w_0 - w_Q^*$) and biomass growth rate, where species Q is the species with the lowest critical water content.

Alternative Hypotheses

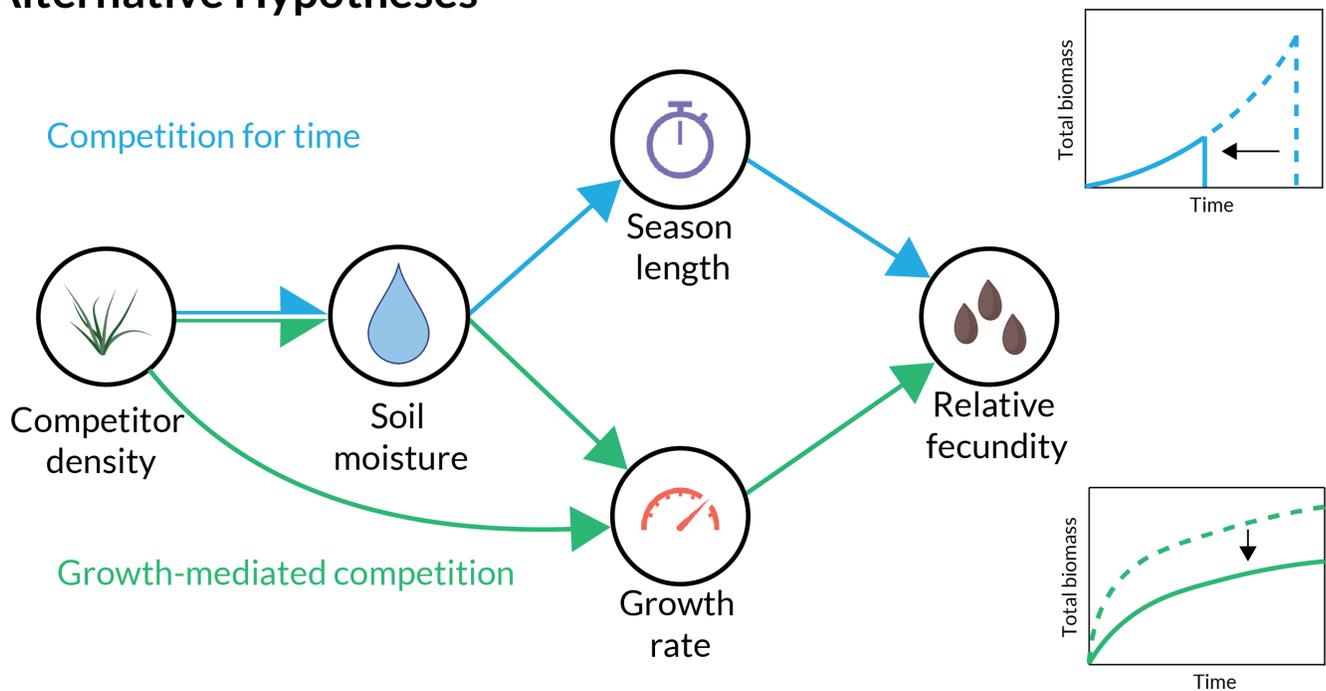
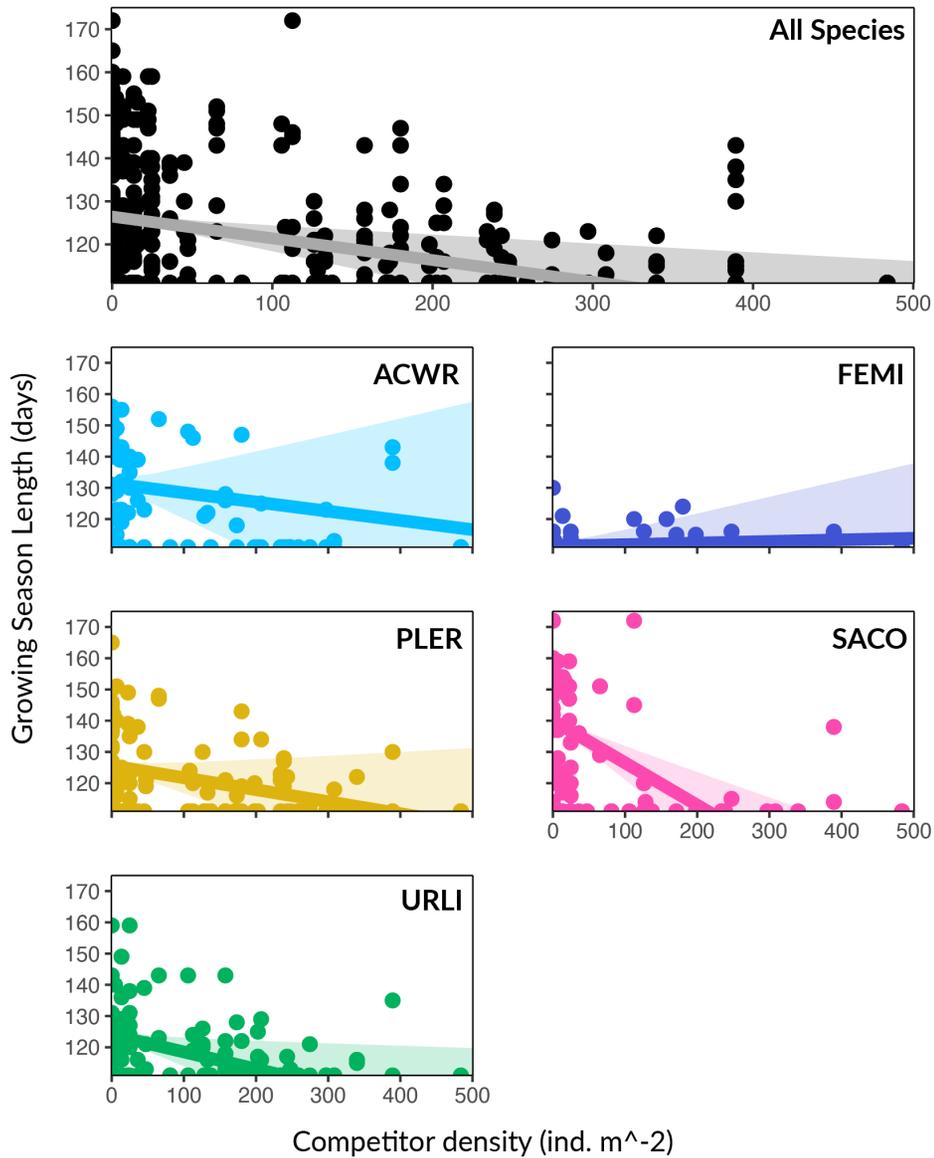


Figure 4 – A directed acyclic graph showing the alternative hypotheses tested in the competition for time experiment. The blue path (top) describes the causal pathway expected when Mediterranean annual plants compete for time: Increased competitor density results in lower soil water availability, which in turn causes individuals to senesce earlier in the growing season, which finally depresses their fecundity. The green path (bottom) describes the causal pathway expected when these species compete solely through reductions in biomass growth rate: increased competitor density, through reduced soil moisture or otherwise, causes individuals to accumulate biomass more slowly, which harms their total reproduction.

Effect of competition on time



Effect of competition on growth rate

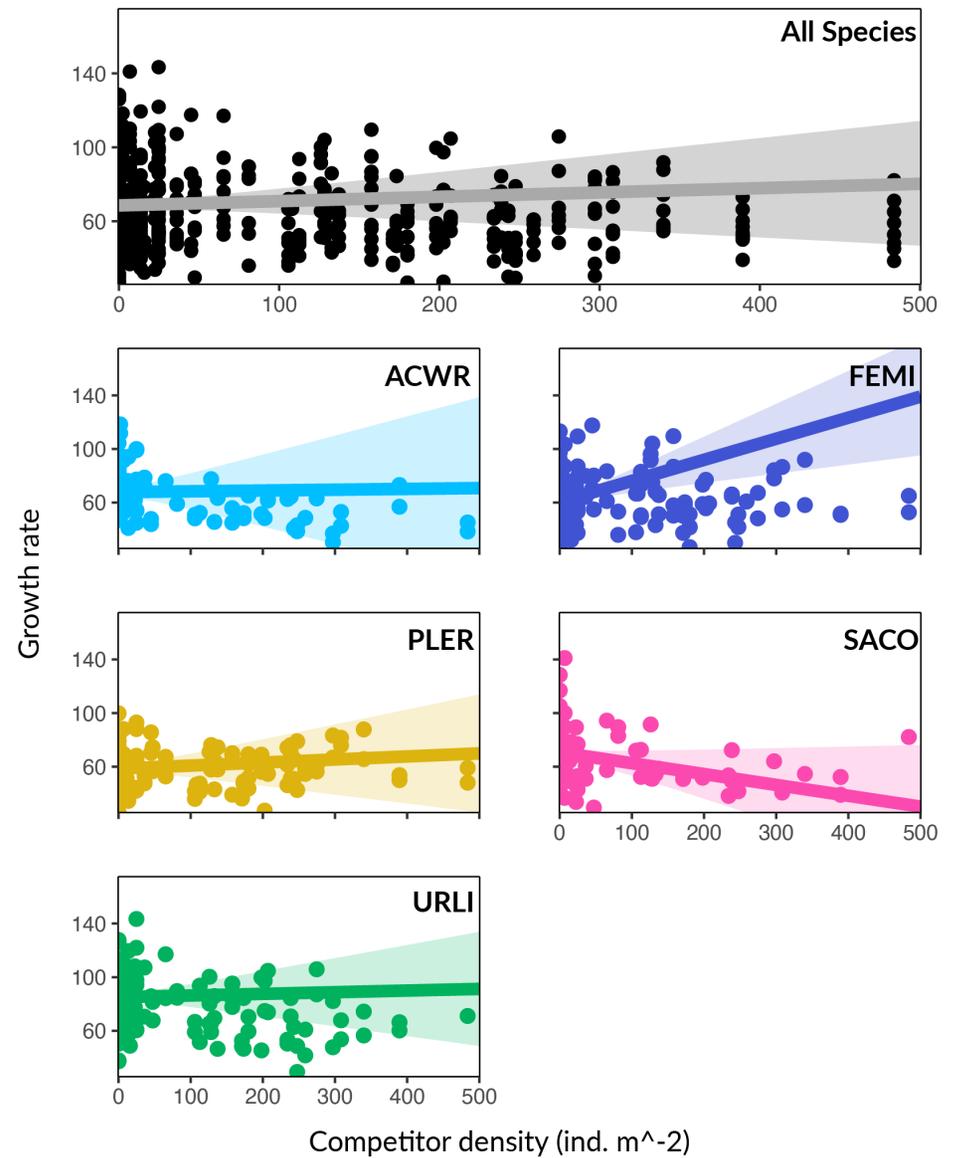
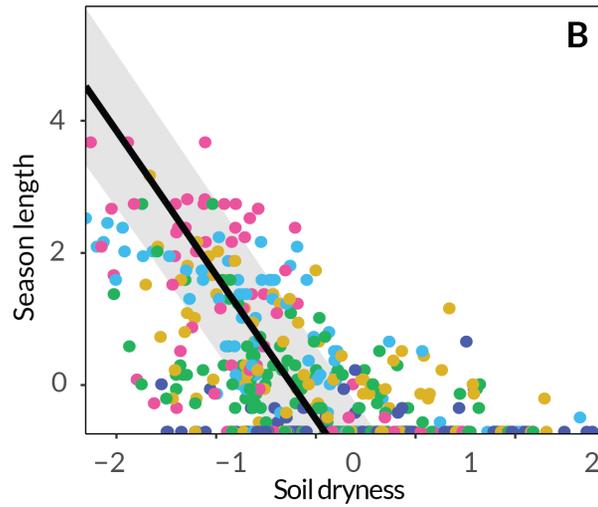
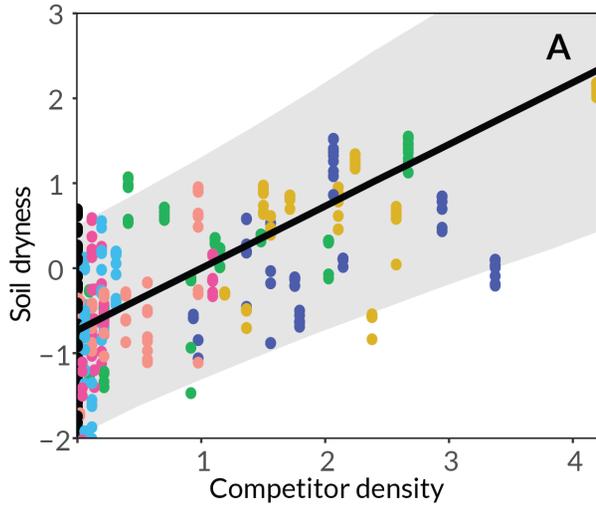


Figure 5 – Results of an analysis comparing the effect of competitor density on growing season length (competition for time, left panel) and the effect of competitor density on biomass growth rate (growth-mediated competition, right panel). The uppermost plot in each panel shows the overall

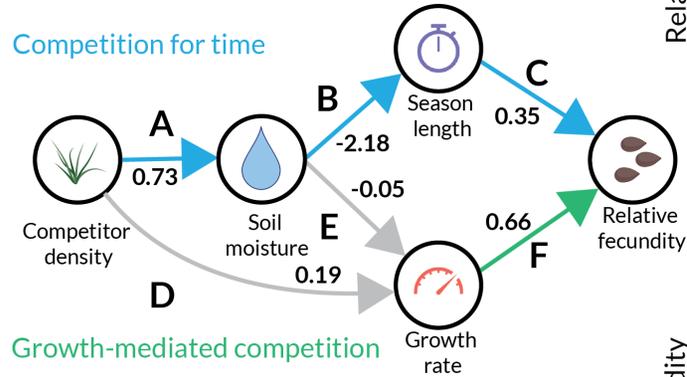
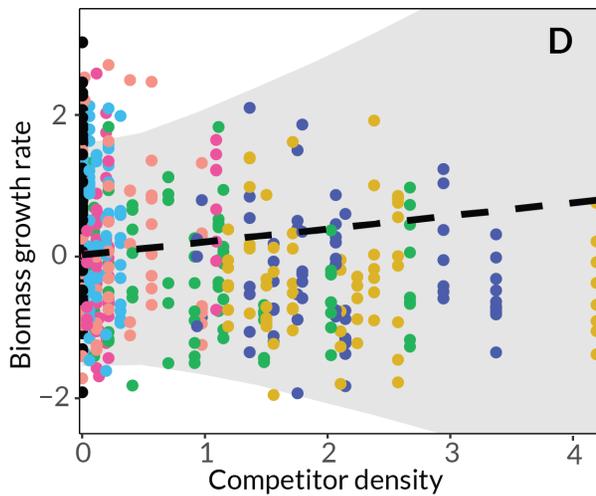
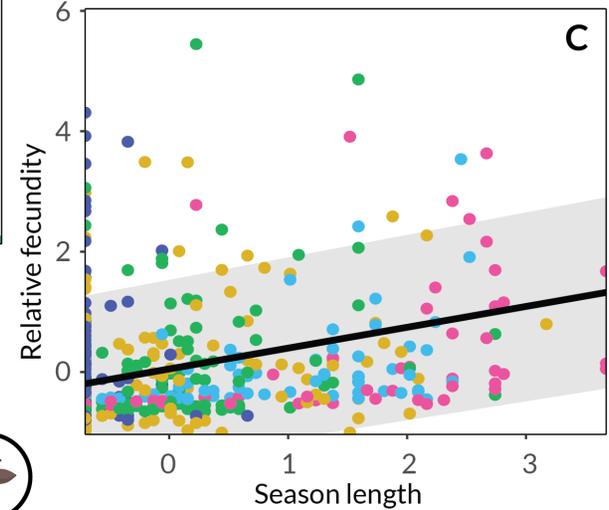
relationship across all competitor and focal species. The plots below show the relationship for each focal species, including data for all competitor species. Lines represent expected values as taken from the posterior distribution of the model, while shaded areas represent 95% credible intervals for the relationship.

The mechanisms of competition: season-length vs. growth rate

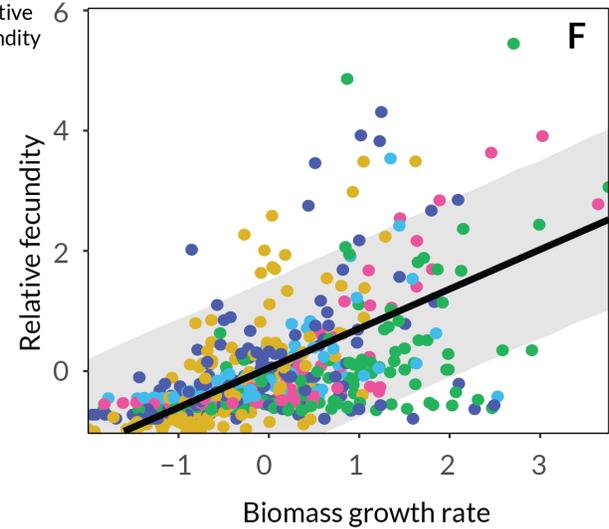
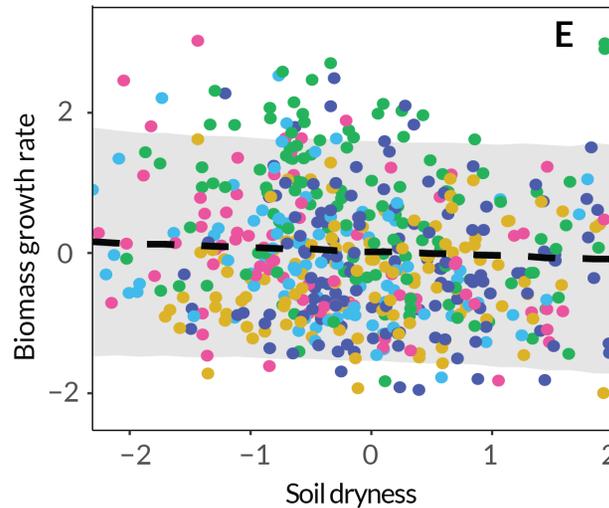


Full path effects (competition for time):

$A+B+C$
-0.54



Growth-mediated competition



Full path effects (growth-mediated competition):

$A+E+F$
-0.02

$D+F$
0.12

Focal species

- FEMI
- URLI
- PLER
- ACWR
- SACO
- LACA
- CONTROL

Figure 6 - Summary of results from the Bayesian multilevel model analysis used to test the water competition hypotheses in Figure 4. Each panel shows the observed (points) and modeled (lines) relationship corresponding to an arrow in the central model schematic in Figure 4. Solid lines indicate that the relationship was clearly supported by the data, while dotted lines indicate a lack of statistical support. All variables were transformed to standard units to facilitate comparison of effect sizes. The means and standard deviations for each variable are as follows: competitor density ($\mu = 88.3$, $\sigma = 115.4$), soil dryness ($\mu = 0.08$, $\sigma = 0.05$), biomass growth rate ($\mu = 6.7e^{-3}$, $\sigma = 2.0e^{-3}$), season length ($\mu = 121.0$, $\sigma = 14.0$). Relative fecundity is expressed as standard deviations from each species' mean fecundity. In panels B, C, E, and F, points are colored according to the focal species. In panels A and D, points are colored according to treatment background species. Black points indicate data from control plots. Though models were fit with interactions by species, these were of small and uncertain magnitude. Thus, only the aggregated relationships are shown here.

A. Growth-longevity tradeoff

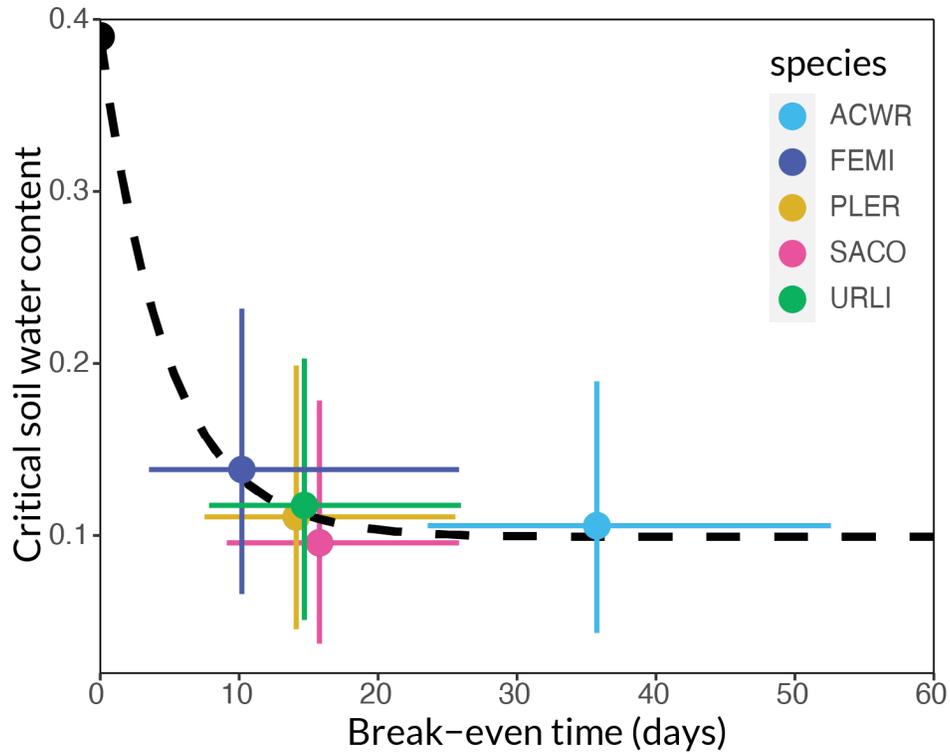


Figure 7 - The observed tradeoff between break-even time and critical soil water content. The points show the mean of the posterior predictions for each species' break-even time and critical soil water content, while lines show 95% credible intervals. The dashed line is a negative exponential fit by nonlinear least-squares to the species' characteristics, passing through the initial water content (black point on y-axis).