

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

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## **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:

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

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.  $\alpha_i$  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:

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

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

230

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

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

The invasion growth rate for species 1 shows that because it is shorter-lived than species 2 ( $R_1 + R_2 > R_1$ ), it must have a higher biomass growth rate ( $g_1 > g_2$ ) to invade species 2 at equilibrium (for  $IGR_1$  in Equation 4 to exceed 1) (Fig. 3A). Meanwhile, the longer-lived species 2 automatically has a refuge from interspecific competition after species 1 stops growing, resulting in infinite growth as it drops to 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 species 2's density goes to zero). As a result, species 2 can never be competitively excluded by species 1 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  $\gamma_i$  until the soil water content drops below a species-specific critical  
277 water content,  $w_i^*$ . We label the time at which this happens  $\tau_i$ , which is equivalent to the length of  
278 species  $i$ 's growing season and analogous to  $t_i$  from equation 1. At  $\tau_i$  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  $\tau_i$  and reducing

285 their final biomass, fecundity, and next year's population size following equation 5. The specific  
 286 functional form of  $\tau_i$  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:

$$\begin{aligned}\tau_1 &= \frac{w_0 - w_1^*}{\alpha_1 n_1 + \alpha_2 n_2} \\ \tau_2 &= \frac{w_0 - w_1^*}{\alpha_1 n_1 + \alpha_2 n_2} + \frac{w_1^* - w_2^*}{\alpha_2 n_2}\end{aligned}\tag{6}$$

288 Here  $w_0$  is the volumetric soil water content at the start of the dry season, and  $\alpha_i$  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  $\tau_i$  which we call the species' "break even time,"  $\tau_i^*$ , 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  $\tau_i^*$ :

$$\tau_i^* = \frac{1}{f_i \gamma_i}\tag{7}$$

296 The resulting expression shows that a species' break-even time is determined by its biomass growth rate,  
 297  $\gamma_i$ , 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,  $\alpha_i$ , is a function of its leaf area



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

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

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

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

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

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

#### *Study site*

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

#### *Experimental Design*

We established fifty-two  $1.33\text{ m}^2$  plots, each of which was randomly assigned to receive 8 g of seed  $\text{m}^{-2}$  of one of six study species designated as a background competitor (Pacific fescue, *Festuca microstachys*; chia, *Salvia columbariae*; Chile lotus, *Acmispon wrangelianus*; dwarf plantain, *Plantago erecta*; goldfields, *Lasthenia californica*; silverpuffs, *Uropappus lindelyi*). Even though all 8-10 plots per competitor species were sown with the same seed mass, variable germination generated significant 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  $0.08\text{ m}^2$   
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,  $\tau_i$  (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

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

## Discussion

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

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

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## Figures

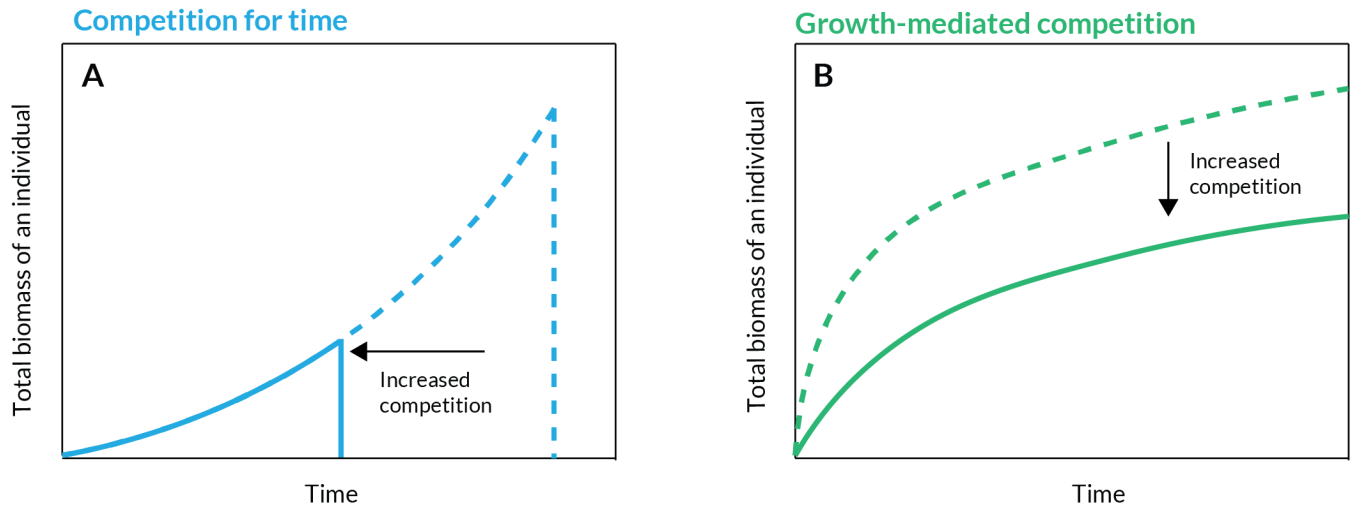


Figure 1 - Comparison of individual growth trajectories under competition for time and growth-mediated competition. Both panels show the effect of increased competition on the cumulative biomass accumulation of an individual. Panel A illustrates how under competition for time, increased densities of 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.

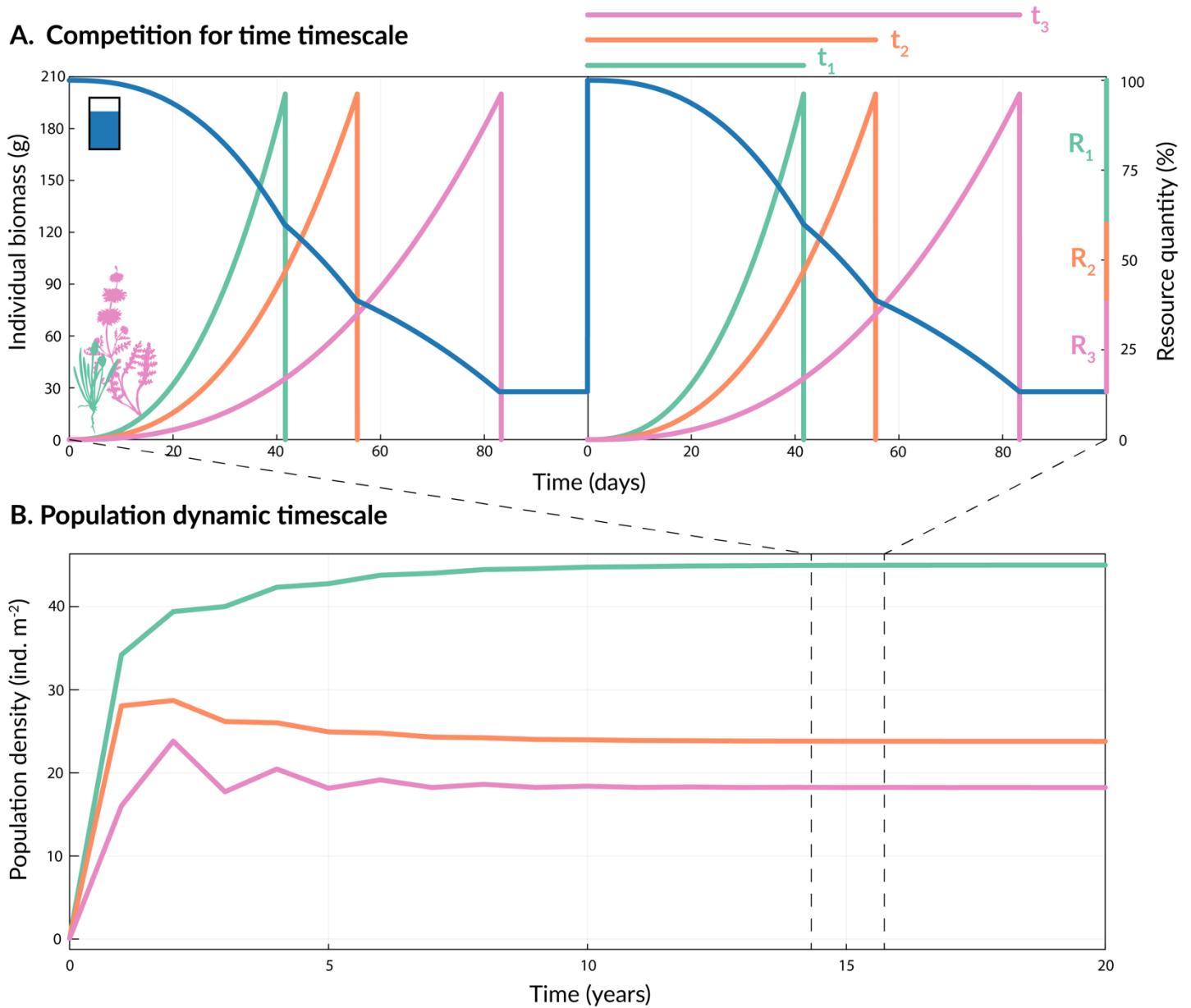
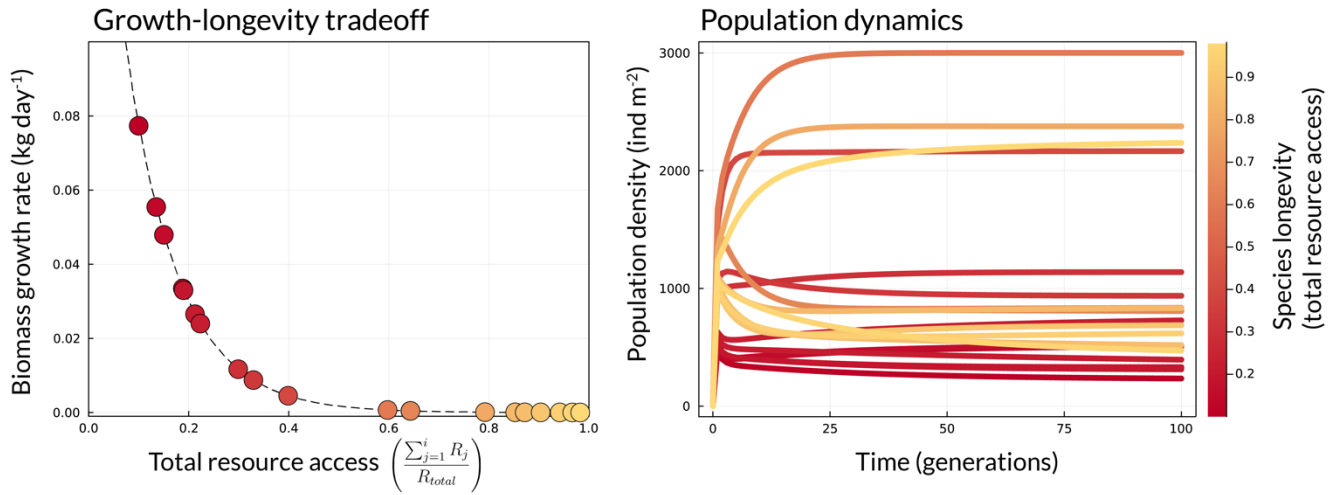


Figure 2 – Competition for time operates within competitive bouts (Panel A) but due to the repetition of the bouts, it ultimately affects population dynamics on a longer time scale (Panel B). In Panel A, three species deplete one another's time for growth within a bout of competition. The blue line shows 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

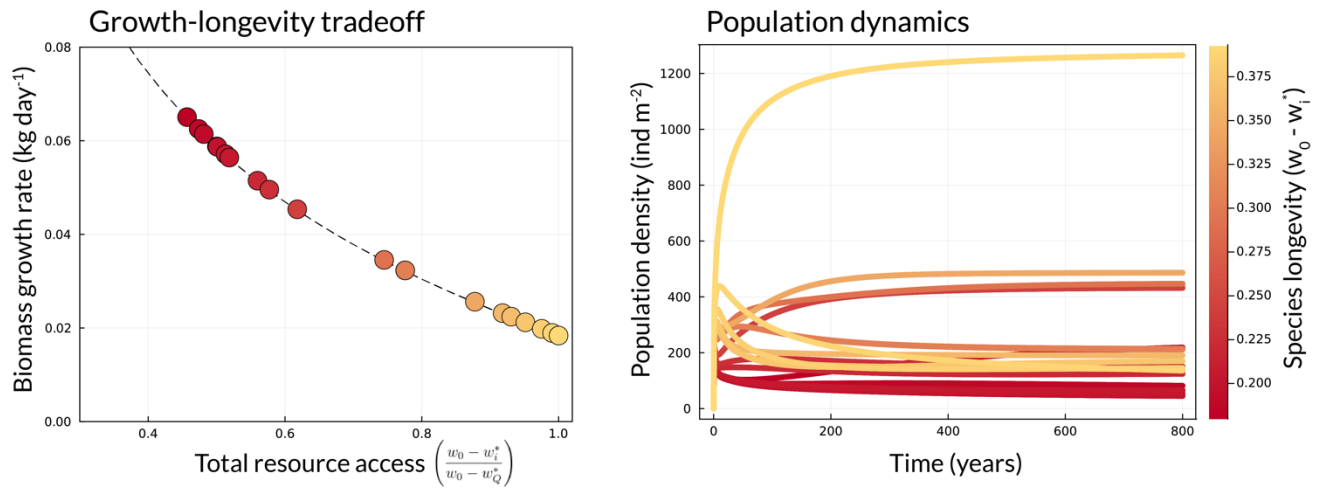


Figure 3 - Panel A illustrates how a growth-longevity tradeoff maintains high diversity in the simple model of competition for time first presented in the manuscript. The left plot shows the tradeoff itself, as quantified by species total resource access ( $\sum_1^i R_j$ ) and biomass growth rate. Points 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

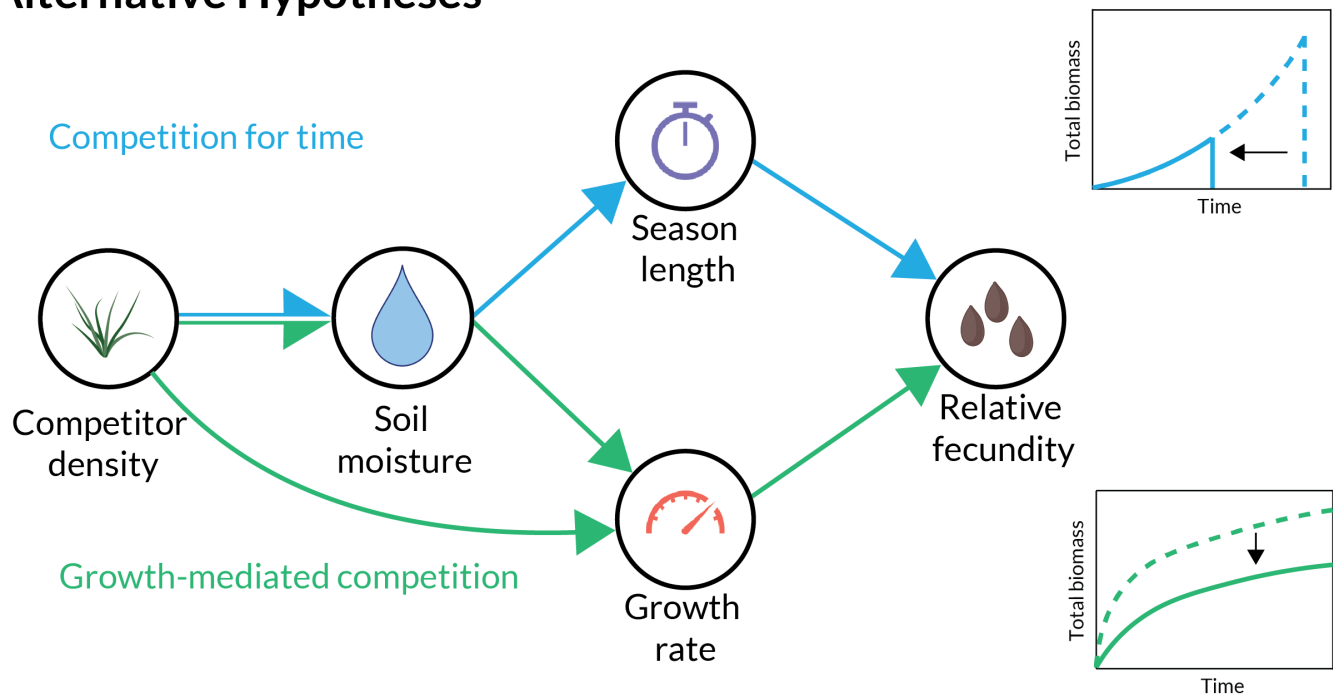
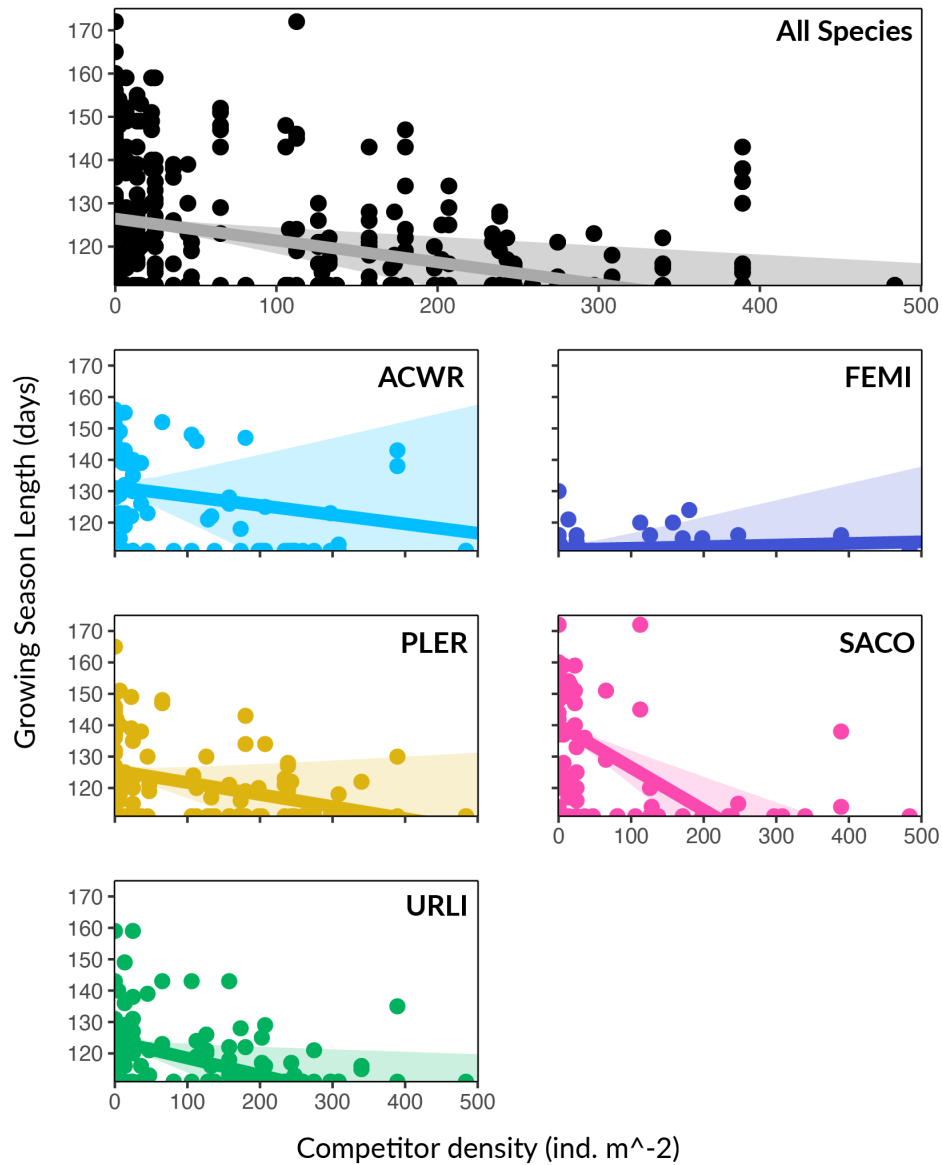


Figure 4 – A directed acyclic graph showing the alternative hypotheses tested in the competition for time experiment. The blue path (top) describes the causal pathway expected when Mediterranean annual plants compete for time: Increased competitor density results in lower soil water availability, which 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

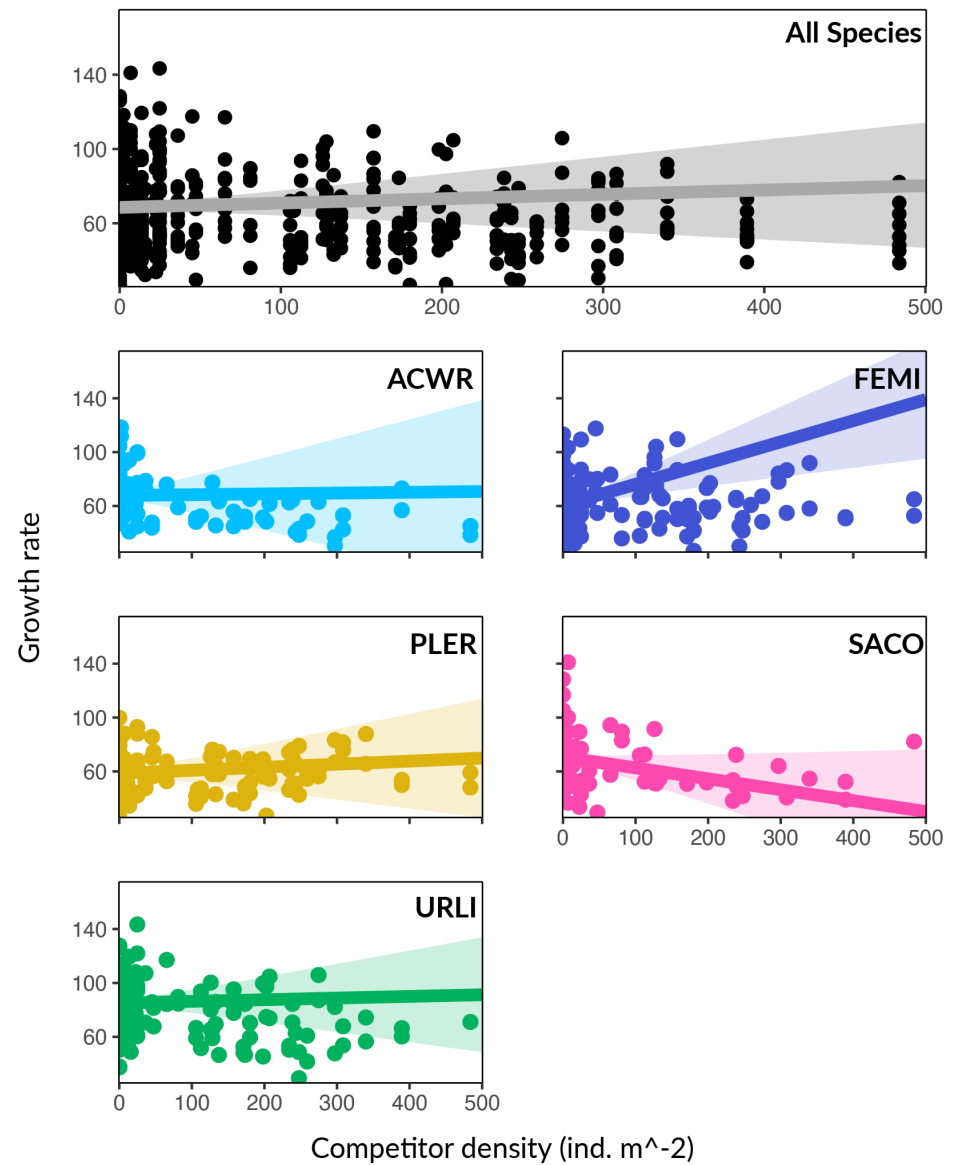
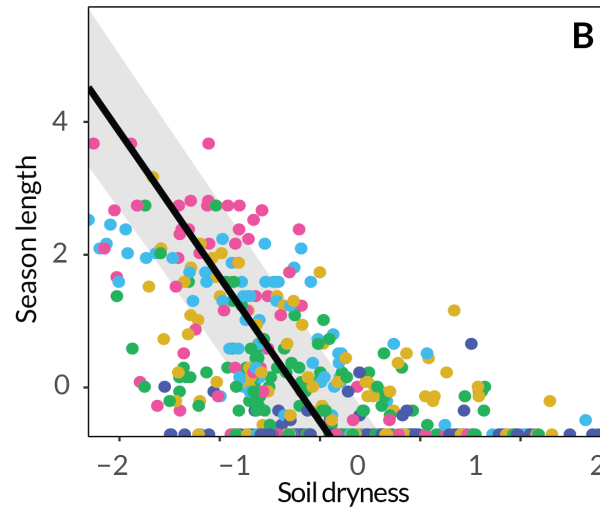
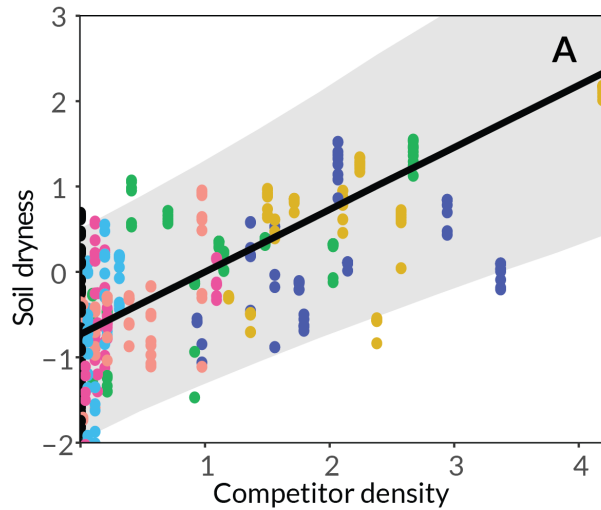


Figure 5 – Results of an analysis comparing the effect of competitor density on growing season length (competition for time, left panel) and the effect of competitor density on biomass growth rate (growth-mediated competition, right panel). The uppermost plot in each panel shows the overall



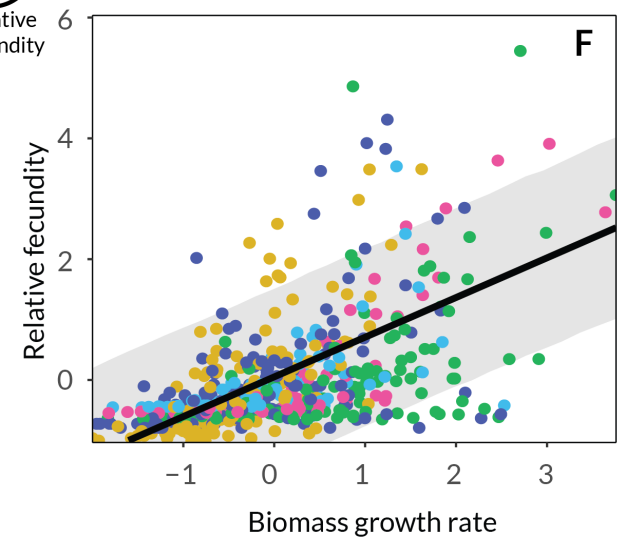
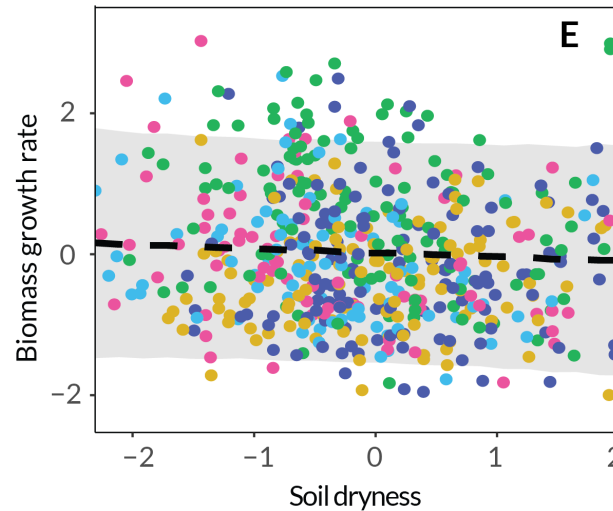
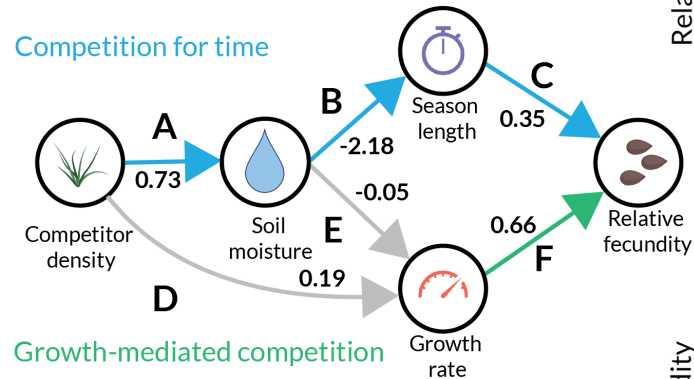
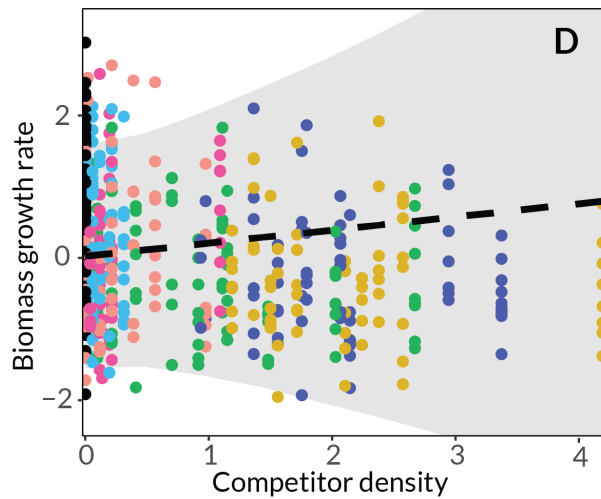
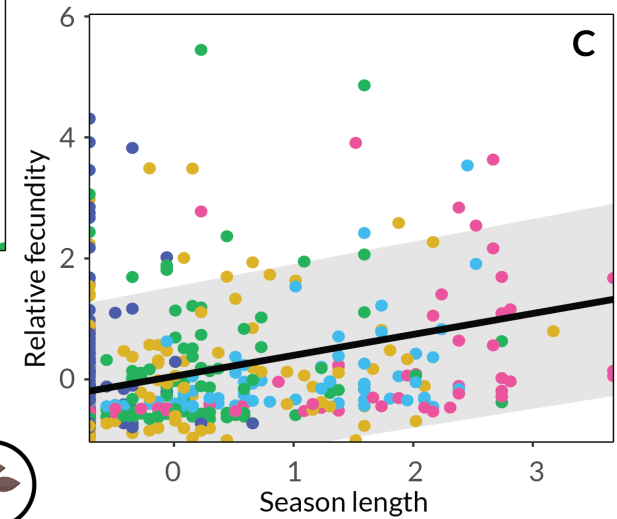
relationship across all competitor and focal species. The plots below show the relationship for each focal species, including data for all competitor species. Lines represent expected values as taken from the posterior distribution of the model, while shaded areas represent 95% credible intervals for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

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



Full path effects (competition for time):

$A+B+C$   
-0.54



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

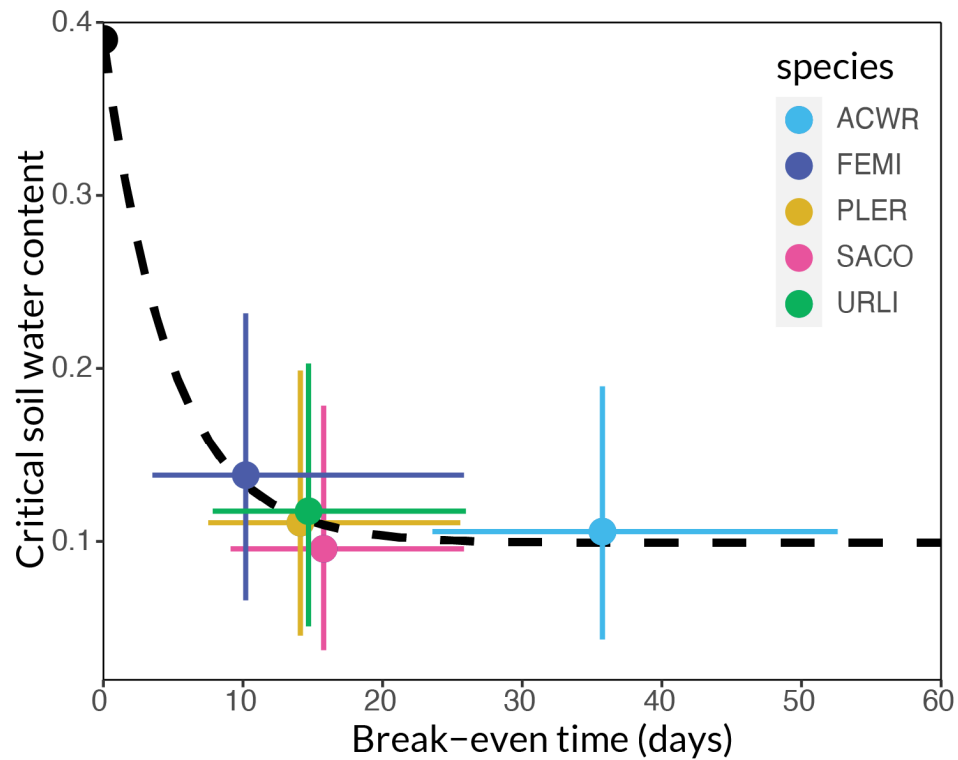


Figure 7 - The observed tradeoff between break-even time and critical soil water content. The points show the mean of the posterior predictions for each species' break-even time and critical soil water content, while lines show 95% credible intervals. The dashed line is a negative exponential fit by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