

# LIFE HISTORY EVOLUTION IN A COMMUNITY CONTEXT

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August 28, 2023

## Abstract

Life histories are predicted to evolve when the age schedules of mortality shift due to top-down forces such as predation. Theory on how competitive interactions alter the life history is rare. We use an explicit consumer-resource model to show that changes in the way organisms interact with their resources and changes in the properties of those resources can alter the optimal life history of a consumer. When older/larger organisms are better competitors, delayed maturity can be favored. When older/larger individuals are better competitors but also shift their resource use with age or size, alternative life histories are possible. We further show that when two species compete for shared resources, selection tends to make the life histories of the two competitors more similar. These results, some of which are opposite to predictions from traditional theory, illustrate the importance of incorporating explicit interactions between trophic levels into models for life history evolution.

# **LIFE HISTORY EVOLUTION IN A COMMUNITY CONTEXT**

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**Running title:** Life histories and communities

**Keywords:** Life history evolution, species coexistence, consumer-resource models, species interactions.

**Type of article:** Letter

**Number of words in:**

**Abstract: 150, Main text: 5036**

**Number of references: 43**

**Number of:**

**Figures: 4, Tables: 1**

**Statement of authorship:** RDB conceived the research. RDB and EJ developed and analyzed the models, and RDB wrote the first draft of the manuscript. All authors discussed the results and contributed to the final draft.

**Statement of data accessibility:** No new data were used in this manuscript. All R Code used in the manuscript are available at: <https://github.com/rdb0057/Life-history-in-a-community-context>.

## **Abstract**

Life histories are predicted to evolve when the age schedules of mortality shift due to top-down forces such as predation. Theory on how competitive interactions alter the life history is rare. We use an explicit consumer-resource model to show that changes in the way organisms interact with their resources and changes in the properties of those resources can alter the optimal life history of a consumer. When older/larger organisms are better competitors, delayed maturity can be favored. When older/larger individuals are better competitors but also shift their resource use with age or size, alternative life histories are possible. We further show that when two species compete for shared resources, selection tends to make the life histories of the two competitors more similar. These results, some of which are opposite to predictions from traditional theory, illustrate the importance of incorporating explicit interactions between trophic levels into models for life history evolution.

## Introduction

A long-standing hypothesis is that the life histories of organisms are shaped by natural selection to balance the benefits and costs of maturing at a particular age or expending a particular amount of reproductive effort at a specific age (Gadgil & Bossert 1970; Law 1979; Michod 1979; Stearns 1992; Charlesworth 1994; Stearns 2000; Roff 2002). Ecological factors, such as age- or size-dependent predation risk, shift patterns of mortality across the life cycle and thereby change the balance between these costs and benefits. The optimal life history is one that balances costs and benefits at each age to maximize some measure of fitness over the lifetime.

This perspective of the life history can be analyzed using mathematical models that incorporate life history trade-offs and summarize the ecological factors that alter mortality patterns across the life cycle (Stearns 1992; Charlesworth 1994; Roff 2002). The most familiar models summarize the effects of top-down agents of mortality like predation or parasitism. Most models summarize these effects as density-independent, age- or stage-specific changes in the mortality of the target organism (but see DeAngelis, Kitchell & Post 1985; Day, Abrams & Chase 2002; Gardmark, Dieckmann & Lundberg 2003).

Bottom-up forces like resource limitation have received less attention. Unlike top-down factors, bottom-up factors like resource limitation create complex feedbacks between the consumer and its resources (Abrams 2022). To alleviate these complexities, bottom-up forces are typically summarized in mathematical models using interaction coefficients that vary in strength across different ages or stages of the life cycle. This simplification has generated insight into the differences between the effects of density-independent and density-dependent selection (Travis *et al.* In press). However, it has also precluded us from gaining general insights into how resource use alone can alter the balance of costs and benefits of different life history strategies

and whether bottom-up and top-down forces will interact in a meaningful fashion. Simply put, we cannot answer the question of whether the agent of mortality matters for the evolution of the life history.

Bottom-up factors are also viewed as important determinants of community level organization. For example, the resource niche of a species has long been predicted to determine whether it can stably coexist with another species (Hutchinson 1961; MacArthur & Levins 1967). It has also been predicted to evolve so as to limit the similarity between competing species (Brown & Wilson 1956). Species also often change their resource niche as they age or grow in size (Corbet 1980; Werner & Gilliam 1984; Reñones, Polunin & Goni 2002; Wallace & Leslie 2008; Briones *et al.* 2012) and these changes can facilitate coexistence with other species under some circumstances (Miller & Rudolf 2011; Nakazawa 2015; Bassar, Travis & Coulson 2017; Anaya-Rojas *et al.* 2021; Anaya-Rojas *et al.* 2023). If the life history of an organism is in part determined by this resource use and how it changes throughout its life, then we can expect the life history to evolve along with the evolution of the resource niche. Conversely, if coexistence itself is a function of the life history, then species coexistence becomes both a function of the resource use of the two species and the evolutionary state of the life history of both species. It is far from clear whether life history evolution can strengthen or weaken the likelihood of species coexistence and whether there are combinations of life histories that are more plausible in ecological communities than others. As a result, the study of the evolution of life histories has yet to be fully integrated with other related questions of community diversity and how they change over time.

Here we initiate an integration between theories of the evolution of life histories and community ecology. We do so by developing a model of the life history that depends explicitly

on multispecies interactions. We replace the traditional interaction coefficient approach with explicit competitive interactions within and between species that occur when resources are shared. Doing so allows us to ask how the structure of the underlying community and how differences in age- or size-specific competitive ability affect the evolution of the life history. We first formulate these questions using simple age-dependent models and describe a similar size-dependent model in the Online Supplement.

### **The Consumer-Resource Model**

The age-dependent model is a discrete time consumer-resource model of a community with resources ( $R$ ) structured by trophic level ( $T$ ) and a consumer species ( $C$ ) structured by age ( $a$ ).

The dynamic equation for the resource is:

$$R(T, t + 1) = R(T, t) \frac{\lambda(T)}{1 + \frac{\lambda(T) - 1}{K(T)} R(T, t) + \sum_{a=1} \theta_a(T) \gamma_a(T) C_a(t)}, \quad 1$$

The resource dynamics are modeled after a modified Beverton-Holt model that includes predation by the consumer (Streipert, Wolkowicz & Bohner 2022). The function  $R(T, t)$  describes the number of individuals of trophic level  $T$  at time  $t$ .  $K(T)$  is the carrying capacity as a function of trophic level, or the maximum number of individuals of a given trophic level the environment can support. The function  $\lambda(T)$  represents the multiplicative growth rate of a species at trophic level  $T$ . Inside the summation, the functions  $\theta_a(T)$  and  $\gamma_a(T)$  describe the proportion of resources that constitute the diet of the consumer and the feeding rate of the consumer, respectively, as a function of age  $a$  and trophic level  $T$ . The function  $C_a(t)$  describes the number of individual consumers of age  $a$  at time  $t$ .

The equation for the consumer is a standard discrete time projection model that translates the number of individuals in age class  $a$  at time  $t$  into the number of individuals in age class  $a + 1$  at time  $t + 1$  as a function of births and deaths of the consumer.

$$\mathbf{C}_{(t+1)} = \mathbf{A}\mathbf{C}_{(t)}. \quad 2$$

The vector  $\mathbf{C}_{(t)}$  is structured by age with elements that describe the number of individuals of age  $a$  at time  $t$ . The projection matrix  $\mathbf{A}$  contains elements that describe the per-capita birth and survival probabilities of the different ages. We assume that offspring are born immediately prior to the census such our projection has the form:

$$\mathbf{A} = \begin{bmatrix} M_1S_1 & M_2S_2 & M_3S_3 & M_4S_4 & M_5S_5 & M_6S_6 \\ S_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_5 & S_6 \end{bmatrix}. \quad 3$$

The elements  $S_a$  are the age-dependent probabilities of surviving from age class  $a$  at time  $t$  to age class  $a + 1$  at time  $t + 1$  and the  $M_a$  elements are the age specific fertilities. Although much of life history theory utilizes the characteristic equation to translate this system of equations into a summation across ages (Stearns 1992; Charlesworth 1994; Roff 2002), the characteristic equation is less tractable away from equilibrium and when the survival to age function ( $l_a$  in the characteristic equation) for each age depends on age-specific competitive effects. Nevertheless, the two formulations are equivalent and interchangeable.

Both survival and reproduction of the consumer depend upon the amount and types of resources individuals of each age class can acquire and utilize efficiently.

$$S_a = \frac{1}{\left[1 + e^{\left(-\left(s_0 + \kappa_{a,s}(1 - \eta_a)\delta_a \int B(T)\gamma_a(T)\theta_a(T)R(T,t)dT\right)\right)}\right]}, \quad 4$$

$$M_a = 0.5\kappa_{a,m}\eta_a\delta_a \int B(T)\gamma_a(T)\theta_a(T)R(T,t)dT. \quad 5$$

The functions and parameters within the integrals describe the interaction between the consumer and its resources. Three functions describe the net resource acquisition of each consumer. First, the function  $\theta_a(T)$  indicates the proportion of the diet made up of each trophic level. Second, the function  $\gamma_a(T)$  indicates the feeding rate of the consumer as a function of the trophic level on which it is feeding. Third, the function  $\theta_a(T)$  is a probability distribution that describes the proportion the resource makes up in the diet of the consumer (Table 1). The remaining function,  $B(T)$ , describes the net benefit acquired by the consumer as a function of type of resource. If  $B(T)$  is independent of  $T$ , then resources are perfectly substitutable in their profit per unit resource for the consumer. However, if  $B(T)$  is an increasing function of trophic level, then resources at higher trophic levels yield a greater benefit per resource unit to the consumer.

The quantities outside the integrals describe how ingested resources are used by the consumer. The parameter  $\delta_a$  describes the efficiency with which the acquired resources are turned into useable energy, is bound to be between 0 and 1, and may be a function of the age of the consumer. The next functions describe the allocation of this energy to competing functions. The parameter  $\eta_a$  is the fraction of energy that is devoted to reproduction; energy not devoted to reproduction ( $1 - \eta_a$ ) is allocated to survival. This then forms the fundamental life history trade-off for age at maturity and reproductive effort at each age. The  $\kappa$  functions are scaling factors that translate energy gained into new offspring or survival probabilities. The parameter  $s_0$  yields

the background mortality rate in the absence of any resources for the consumer and the fertility function is multiplied by 0.5 to reflect that this is a female-only model. Table 1 summarizes the functional forms and parameter values and in the Online Supplement we describe a version of the model that is based explicitly on body size instead of age.

### *Model Properties*

For any given demographic rate, the equation describing its value at a given age addresses two basic questions: how does the organism obtain resources and what do they do with it once obtained? The first question speaks to the ecology of the organism. The second question is fundamentally about the configuration of the life history. This dichotomy can be seen, for example, in the equation for fertility. In this equation, the functions under the integral pertain to how the organism acquires resources and the characteristics of the resources—its ecology. The remaining functions determine what the organism does with the resources once they have been obtained—how much can be converted to usable energy ( $\delta_a$ ), how much of this is available for use for reproduction versus maintenance  $\eta_a$ , and how this is converted to a demographic rate  $\kappa_{a,m}$ . We can therefore simplify the notation by replacing parameters related to allocation (i.e. the life history) with  $A_{a,m} = 0.5\kappa_{a,m}\eta_a\delta_a$  and those related to the ecology with  $E_a(T) = \gamma_a(T)\theta_a(T)$  so that

$$M_a = A_{a,m} \int B(T)E_a(T)R(T, t)dT. \quad 6$$

Thinking in these terms is useful because it summarizes the demographic outcome, e.g. fertility, as the product of processes occurring at two levels. organismal biology, or the life history, captured in  $A_{a,m}$ , and ecology, captured by the integral. Because they are multiplied together, there is a fundamental interaction between them.

Because fertility and survival both contain  $\eta_a$  in their allocation functions, they are connected through a tradeoff: increased allocation towards survival ( $A_{a,s}$ ) requires a decrease in allocation towards fecundity ( $A_{a,m}$ ). Allocation tradeoffs such as these reflect the general life history problem—what is the best way to allocate limited resources towards different fitness components (demographic rates) across the lifetime?

### **Age at maturity in a community context**

We use our general model to ask whether changes in the structure of the resource community and how the consumer interacts with the community can change the optimal age at maturity. We analyze the model in 16 combinations of conditions, four different structures of the resource community crossed with four different ways the consumer can interact with the community.

We assume that the way the consumers interact with the resource community can change in age-dependent ways, analogous to the size-dependent changes in (Bassar *et al.* 2016; Bassar, Travis & Coulson 2017; Bassar, Coulson & Travis 2023) . We assume that the feeding rate can increase with age such that  $\gamma_a = e^{\phi_0 + \phi_a a}$ , where  $\phi_0$  is the baseline feeding rate and  $\phi_a$  describes how this changes with age. Likewise, we assume that the mean of the trophic niche of the consumer can move to higher trophic levels with increasing age. Because most food chains have lower and upper limits in their length, we describe the trophic niche of the consumer using a beta distribution such that

$\theta_a(T) = \frac{\Gamma(\beta + P_a)}{\Gamma(\beta)\Gamma(P_a)} T^{\beta-1} (1 - T)^{(P_a-1)}$ . Where  $P_a$  describes the mean of the trophic niche and is a function of age such that  $P_a = \rho_0 + \rho_a a$ . Higher mean trophic niches with increased age are described by a positive value of  $\rho_a$ .

In the first examples, we assume all resources are perfectly substitutable. That is, they do not differ in their growth rates ( $\lambda$ ), carrying capacities ( $K$ ), or their benefit to the consumer ( $B$ ). Within this context, we look at four scenarios: 1) assume that all ages of the consumer interact with the environment in the same way (i.e.  $\phi_a = 0$  and  $\rho_a = 0$ ); 2) that older individuals consume more resources ( $\phi_a > 0$ ); 3) that individuals shift the mean of their resource niche towards higher trophic levels as they age ( $\rho_a > 0$ ); and 4) scenarios 2) and 3) combined, in which older individuals both consume more resources and shift their resource niche with age.

We then repeat this set of consumer interactions for cases in which resources are not perfectly substitutable. In case 1, higher trophic levels benefits consumers more than lower trophic levels but all trophic levels are equally abundant ( $B(T)$  an increasing function of  $T$ ;  $K(T)$  constant). In case 2, all trophic levels benefit the consumer in the same way but higher trophic levels are less abundant ( $B(T)$  constant;  $K(T)$  a decreasing function of  $T$ ). Case 3 combines the previous two cases; higher trophic levels benefit the consumer more than lower trophic levels but are less abundant. In each of the 16 situations, we find the age at maturity that is expected to evolve using evolutionary invasion analysis.

### *Resources perfectly substitutable*

In this example resources are equally abundant in the absence of the consumer. In other words, the carrying capacity and growth rate of resources are not functions of  $T$  and have the same benefit to the consumer ( $K$  and  $B$  is independent of  $T$ ). When all individuals interact with the resources in the same way (equal feeding rates and same resource niches), the evolutionary stable strategy (ESS) is to mature at age 1 (Figure 1A). However, when older individuals acquire more resources, the ESS age at maturity is later in life (Figure 1B). This occurs because the

acquisition of more resources at later ages increases the survival of the older individuals (Figure 2A). At the same time, having older individuals that consume more of the same resources decreases the survival of younger individuals. In contrast, when older individuals shift to higher trophic levels such that they compete less with younger individuals, this does not provide a benefit for delaying maturity (Figure 1C).

When the older individuals both acquire more resources and shift to higher trophic levels, this provides a benefit to delayed maturation in a similar fashion as simply acquiring more resources (Figure 1D). However, this comes with a twist. In this case, later age at maturity is not the only possible outcome; a new, unstable equilibrium emerges at age 3. The meaning of this is that the life history could evolve towards maturing at either age 1 or age 6, depending upon the starting point. This creates an evolutionary hysteresis wherein large perturbations are required to move between the two strategies.

The shifts in the optimal age at maturity occur because changes in the way that the consumer interacts with the resources are analogous in their action to changes in age-dependent mortality due to predators or parasites. In both cases where we observed delayed maturation, it resulted from an increase in adult survival relative to juvenile survival (Figure 2A and C).

#### *Increased benefits to the consumer of foraging at higher trophic levels*

When higher trophic levels are equally abundant but yield an increased benefit to the consumer (i.e.  $B(T)$  is an increasing function of trophic level,  $T$ ), the ESS age at maturity is still age 1 when all individuals interact with the environment in the same way (Figure 1E) and is later in life when older individuals consume more resources (Figure 1F). However, in contrast to when resources are perfectly substitutable, changes in the resource niche as the organism ages

also led to delayed maturation (Figure 1G). When older individuals shift their resource use with age and consume more resources, this eliminates the mixed life history strategy observed when the resources were completely substitutable (Figure 1H vs D).

The increased benefit of the higher trophic levels does not affect the ESS life history when older individuals simply consume more resources without shifting their resource use with age because it does not change the survival curves at equilibrium (Figure 2D compared to Figure 2A). However, the delay in maturity that occurs when older individuals shift their resource niche arises from an increase in the survival at equilibrium for pre-reproducing, but not reproducing age classes (Figure 2E). The pattern of survival when older individuals both shift their resource niche and consume more resources is similar to when they simply shift their resource use with age (Figure 2F vs Figure 2E).

#### *Higher trophic levels are less abundant*

When higher trophic levels are less abundant than lower trophic levels, but yield the same benefit to the consumer, a delayed age at maturation is predicted only when older individuals consume more resources without shifting their resource use with age (Figure 1I-L). Again the effect of the structure of the community had no effect on the age-dependent pattern of survival of the consumer when feeding rate increased with age (Figure 2G vs Figure 2A), but resulted in decreased survival of older individuals whenever they shifted their consumption towards higher trophic levels (Figure 2H and I vs Figure 2B and C).

*Higher trophic levels are less abundant but yield larger benefits to the consumer*

Finally, when resources at higher trophic levels are less abundant but yield a greater per-unit resource benefit to the consumer, the expected life history changes are similar to the case where resources are perfectly substitutable (Figure 1M-P). In this case, the similarity of the predicted changes in the ESS age at maturity was caused by a similarity in the patterns of survival of the consumer at the ESS (Figure 2). This implies that the effects of increasing benefits of feeding at higher trophic levels are cancelled by their being less of them for the consumer to acquire. However, this may depend on the particular parameters used for the benefit to the consumer ( $B(T)$ ) and the carrying capacity of the resource ( $K(T)$ ).

### **Life histories, competition, and species coexistence**

Two age or size structured species that are competitors are expected to coexist when one species shifts its resource use with increased age or size and the other species is a better competitor for the resources they share (Bassar, Travis & Coulson 2017). As the above results show, these conditions may also lead to contrasting life histories of the two species—the species that shifts its niche with increased size should mature earlier and the species that is the better competitor should mature later (Figure 1B and C). This pattern suggests that species with different patterns of resource use should also have different life histories, leading to the idea that complimentary life histories can facilitate coexistence (Lancaster, Morrison & Fitt 2017; Jops & O'Dwyer 2023). However, this observation does not include how competing for resources alters the evolution of the life history itself. Below we ask does coexistence with a competitor alter the expected life history? This question is important because it provides predictions for how the life

history of two species may evolve jointly when they experience species interactions beyond predation or parasitism.

For all cases we assume that the two species can initially stably coexist: one species increases its feeding rate on the resource with increased age and the other shifts its resource niche to higher trophic levels with increased age (Bassar, Travis & Coulson 2017). Then for each species we ask if the presence of the other competing species alters the expected age at maturity (Figures 3, 4) compared to when the competitor was not present (Figure 1 second and third columns).

In each of the ecological scenarios, the presence of a competitor that shifts its resource use with age had no effect on the age at maturity that is expected to evolve in the species that increases its feeding rate with increased age (Figure 3 A, C, E, G compared to Figure 1B, F, J, N). Demographically, this was because the presence of the niche shifting competitor did not change the distribution of mortality across the life cycle compared to when the species was alone (Figure 4A, C, E, and G) and hence does not change the costs or benefits of later maturation.

The result is quite different when we consider the effects of a competitor on the species that shifts its resource niche with increased age. Here, competition with the species that increases its feeding rate with age caused a delay in the age at maturation in all ecological scenarios except when resources at higher trophic levels occur at lower abundance (Figure 3B, D, F, H). In this case, few of the life history strategies are able to invade and the species goes extinct. In those cases where the model predicts a delay in maturation, the changes are caused by shifts in the costs and benefits of later maturation through changes in the age schedule of mortality (Figure 4).

## Discussion

Our results show that the way that organisms interact with their resources can lead to a change in the predicted age at maturity (columns in Figure 1), that the properties of the resource community can modulate these effects (rows in Figure 1), and that these predicted changes occurred due to changes in the age-dependent survival functions (Figure 2). Specifically, we predicted delayed maturation whenever older age classes experienced increased survival and younger age classes experienced lower survival. This is analogous to the predicted response of age at maturity when age-dependent survivorship changes due to predation or parasitism, but arises due to resource competition, verifying the general principle that it is age- or stage- or size-specific mortality that drives life history evolution, regardless of the source of mortality.

However, these results also illustrate how small changes in parameters change the optimum life history (Figure 1C vs G and D vs P) and how the same LH is optimal under very different ecological assumptions (Figure 1B, G, H or A, K, L). Understanding age-specific mortality is necessary for the correct prediction but understanding the ecology is necessary to make the correct prediction for the right reason. In the Online Supplement, we show that these predicted changes in the consumer-resource model can be predicted in an interaction coefficient model, but only when resources are perfectly substitutable and both the density-independent and density-dependent parameters of the model are altered concordantly to reflect changes in the nature of the organismal interactions with the environment.

When we modelled two coexisting species competing for similar resources, we showed that competition with a species with a contrasting way of interacting with the resources leads to the evolution of more similar life histories. This occurs because interspecific competition makes the patterns of age-specific survival more similar between the two species (Figure 4).

### *Single predictions or alternative life histories?*

Some of the more interesting results of our models are where changes in the way the consumer interacts with the environment can lead to alternative life history strategies. These alternative life history strategies occurred in both the age-dependent and size-dependent consumer models (see Online Supplement) and always involved an age-dependent shift in resource use. This could be a shift towards feeding at higher trophic levels with age or an increase in feeding rates with increased age (Figure 1). In the Online Supplement we show that these alternative life histories show up in a model where ecological interactions are based on size, but occur under different conditions (Figure S 1). Such alternative life history strategies have been difficult to predict theoretically (Coulson *et al.* 2022). These scenarios are accompanied by increases in mortality in the middle age or size classes, as has been observed in other studies (Ratner & Lande 2001; Day, Abrams & Chase 2002; Gardmark & Dieckmann 2006; Taborsky, Heino & Dieckmann 2018). Given that a great many animal species display increases in the feeding rate or trophic niche with age or size are common in nature (Werner & Gilliam 1984; Reñones, Polunin & Goni 2002; Wallace & Leslie 2008; Briones *et al.* 2012), our models suggest that the evolution of alternative life histories may happen often.

### *Community interactions that cause life history evolution*

Our results strengthen the general predictions from demographic theories of the life history that age or size specific mortality shapes the life history. However, changes in demographic attributes due to predation or parasitism do not always have the same selective effect as those due to the effects of low resource levels. This is because predation and parasitism

affect the survival functions directly and can only affect the other demographic rates through indirect effects (i.e. changes in the population size and hence availability of resources for prey). In the absence of any indirect effects, changes in mortality of the prey are then the only demographic factor that can shape the balance of costs and benefits of earlier (or smaller) vs later (or larger) age (or size) at maturity. In contrast, resource limitation affects all of the demographic rates directly and is the intermediary through which indirect effects of predation act. Changes in the age (or size) dependent ways organisms interact with their resources and the properties of those resources then have the potential to additionally shape the costs and benefits of earlier or later maturation through survival, but also age-dependent changes in fecundity. Thus explicitly examining how interactions with an organism's resources and its competitors alters the life history expands the range of factors that affect the balance of costs and benefits of different life history strategies.

### *Life histories and species coexistence*

Another intriguing result from our work is that we predicted the life histories of two competing and coexisting species to converge towards similar life histories. This occurs because resource competition tends to make the shapes of the mortality schedules of the two species more similar to each other. Other authors have identified some cases where competition may make species more different in their life histories, particularly if competition is size dependent with the primary life history trade-off between survival and growth (Lancaster, Morrison & Fitt 2017).

If resource competition can cause the evolution of the life history, can the evolution of the life history in turn change the outcome of resource competition? Some work in this area suggests that it can (Bonsall, Jansen & Hassell 2004; Lancaster, Morrison & Fitt 2017), but such

life history evolution is rarely directly incorporated into theory on species coexistence. Most work on species coexistence with resource competition has taken a phenomenological approach with interaction coefficients that does not incorporate the actual biotic interactions (Abrams 2022; Spaak, Adler & Ellner 2023) or life history differences between the competing species. However, as we have shown here, density-dependent model components should be viewed as functions of both the interactions with the environment and organismal patterns of allocation to different competing functions. Thus, when interaction coefficients are viewed through the lens of describing only differences in the resource niche, there is the implicit assumption that the life histories of the organisms are the same. Our results showing that the life histories of two competing species are predicted to become more similar imply that this may be a reasonable assumption, but this is far from definitive.

#### *Model assumptions and future directions*

Our work, and others that incorporate dynamics of resources or predators along with those of the focal species (e.g. DeAngelis, Kitchell & Post 1985; Abrams & Rowe 1996; Day, Abrams & Chase 2002; Gardmark, Dieckmann & Lundberg 2003), represent answers to Stearns' (2000) call for more ecologically realistic models of life history evolution. Even still, more realism is warranted.

Our examples used a Type I functional response for simplicity. Type I functional responses of the consumer combined with resource carrying capacities generally lead to damped oscillations towards stable equilibria between the consumer and the resource as we observed here. Incorporating Type II functional responses, while often providing more realism, complicate the analysis by introducing more complex dynamics. In particular, they can lead to the paradox

of enrichment, in which increasing the carrying capacity of the resource can lead to the extinction of the consumer (Rosenzweig 1971). It is currently unknown how phenomena such as the paradox of enrichment alter the types of life histories that should evolve. This could be investigated using the framework we outline here.

More realism could also be added if the feeding rate of the consumer depended on trophic level. If the difference in the feeding among different trophic levels is caused by differences in the handling time, then this could be incorporated by letting the parameters of the Type II functional response vary with trophic level. Our intuition is this should make higher trophic levels functionally less abundant and push the results towards the scenario in which higher trophic levels are less abundant than lower trophic levels. This conjecture remains to be studied.

Our models also do not include any indirect effects of the resources on each other. Such indirect effects are clearly important in structuring communities at different trophic levels and have an unknown effect on the optimal life history. These types of ecological dynamics in particular are unlikely to be clearly resolved by interaction coefficient approaches because it is not clear how indirect effects affect interaction coefficients.

We have also not included the effects of predation on the consumer in these models. This means that our models could be viewed as those for top predators or for prey that are not tightly coupled with their predators (*sensu* Day, Abrams & Chase 2002). Models with tight coupling between predators and their prey and where the prey competes for a single resource show that many different types of potential outcomes are possible, depending on the strength of the indirect effect of predation (Abrams & Rowe 1996; Day, Abrams & Chase 2002). Further work on life history evolution in the context of interactions among three trophic levels is an important horizon for new research.

## Conclusions

The results of our models show that bottom-up factors can do more than act as indirect modifiers of changes in top-down factors on mortality schedules. Indeed, the nature of the interactions with resources and the assumptions of the structure of the resource community can have a broad impact on the life history that mirror how changes in predation-driven mortality change the life history in both direction and magnitude. Overall, these results provide a clear picture of how these common ecological situations can also be diversifying agents of the life history.

## ACKNOWLEDGEMENTS

We would like to thank Tomos Potter and Tim Coulson for valuable comments on previous drafts of the manuscript. Model development and analyses presented here were funded by a USA NSF grant (2100163).

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Table 1. Parameters definitions, demographic rate functions, and parameter values used in the age dependent model.

| Description   | Equation   |
|---|--|
| <i>Resources</i>  |  |
| Carrying capacity of resources in absence of consumer     | $K(T) = 26e^{-0.01\left(T - \frac{\max(T)}{2}\right)}$   |
| Intrinsic rate of increase of resources                   | $r(T) = 0.82e^{-0.01\left(T - \frac{\max(T)}{2}\right)}$   |
| Limits of resource trophic levels $\min(T)$ and $\max(T)$ | 0 to 100   |
| <i>Consumer interactions with resources</i>               |  |
| Feeding rate of the consumer                              | $\gamma_a = e^{\phi_0 + \phi_a a}$   |
| Resource use distribution of consumer                     | $\theta_a(T) = \frac{\Gamma(\beta + P_a)}{\Gamma(\beta)\Gamma(P_a)} T^{\beta-1} (1-T)^{(P_a-1)}$ |
| Resource use distribution of consumer                     | $P_a = \rho_0 + \frac{\rho_a a}{T}$  |
| Consumer benefit  | $B(T) = \frac{T}{1 + 0.1T}$  |
| Baseline feeding rate                                     | $\phi_0 = -0.25$   |
| Feeding change with age                                   | $\phi_a = 0 \text{ or } 0.05$  |
| Baseline mean resource niche                              | $\rho_0 = 20$  |
| Change in mean resource niche with age                    | $\rho_a = 0 \text{ or } 0.20$  |
| Conversion efficiency                                     | $\delta = 0.15$  |
| <i>Life history</i>                                       |  |
| Fraction of energy devoted to reproduction                | $\eta_a = \begin{cases} 0; & \text{if } a < a^* \\ 0.5; & \text{if } a \geq a^* \end{cases}$     |
| Age at maturity   | $a^* = \{1, 2, 3, 4, 5, 6\}$   |
| Offspring per resource                                    | $\kappa_m = 6.5^{-1}$  |
| Survival unit per resource                                | $\kappa_{a,s} = 5(6 + 4(a - 1))^{-10}$   |



**Figure 1.** Pairwise invasibility plots for the optimal life history as a function of the properties of the resources (rows) and organismal interactions with their resources (columns). White areas of the plots are regions where the invading strategy can invade (i.e. grow in numbers) while competing with the resident strategy. Gray areas are those regions where they cannot invade. The evolutionary stable strategies (ESS) are denoted with a black dot. Unstable equilibria are marked with an open dot.

**Figure 2.** Age-dependent survival at the ESS. Black dots correspond to the baseline survival in Figure 1A, E, I, and M. Blue dots correspond to the survival at the ESS as a function of the properties of the resources (rows) and organismal interactions with the resources (columns) as in Figure 1.

**Figure 3.** Pairwise invasibility plots for the optimal life history as a function of the properties of the resources (rows) and organismal interactions with their resources when competing for resources with another species (columns). The invasion plots in the first column are for a species that increases its feeding rate with increased age (compare with column 2 of Figure 1). The invasion plots for the second column are for a species that shifts its resource niche to higher trophic levels with increased age (compare with column 3 of Figure 1). White areas of the plots are regions where the invading strategy can invade (i.e. grow in numbers) while competing with the resident strategy. Gray areas are those regions where they cannot invade. The evolutionary stable strategies (ESS) are denoted with a black dot. Unstable equilibria are marked with an open dot.

**Figure 4.** Age-dependent survival at the ESS. Black dots correspond to the baseline survival in Figure 1A, E, I, and M. Blue dots correspond to the survival at the ESS as a function of the properties of the resources (rows) and organismal interactions with the resources (columns) as in Figure 1.

**Figure 1**

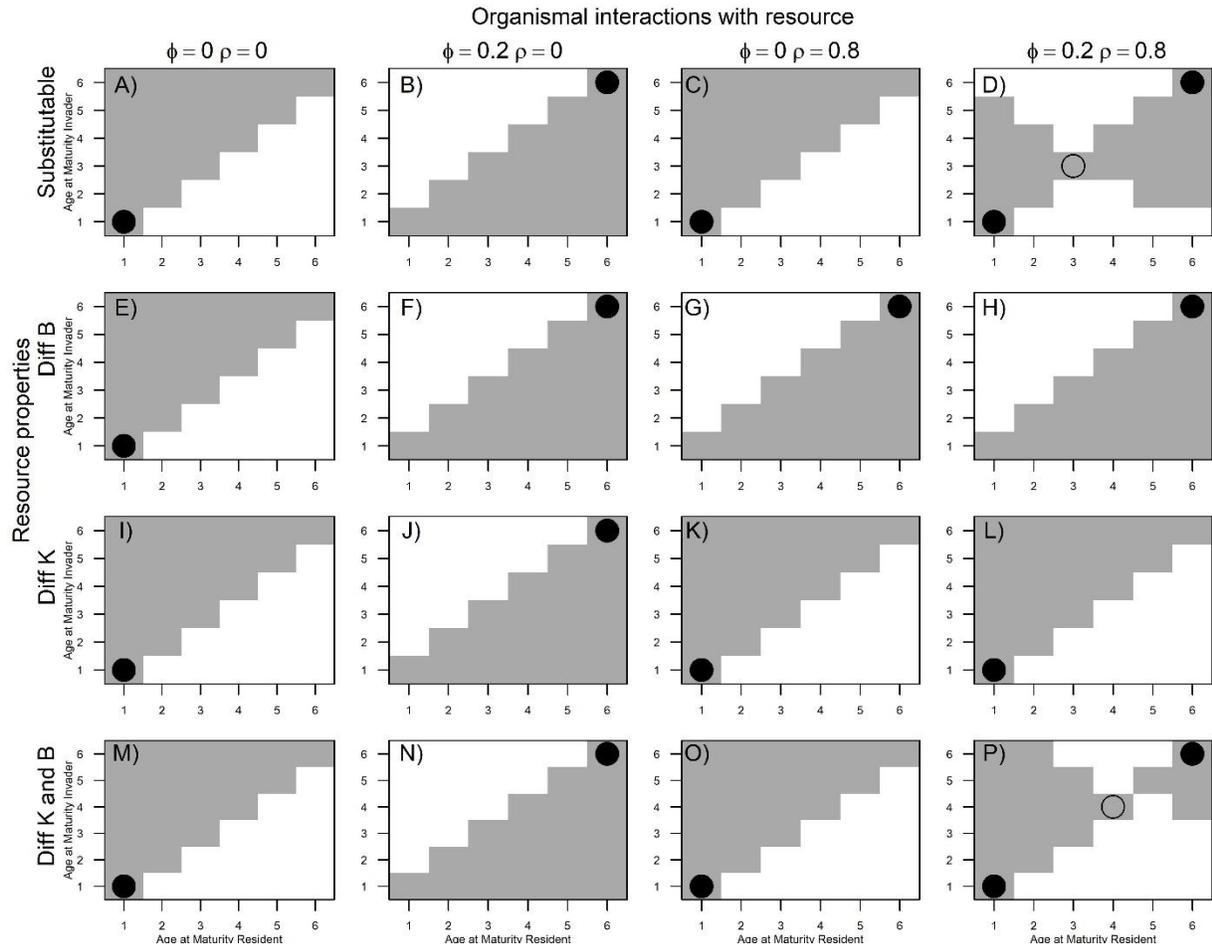
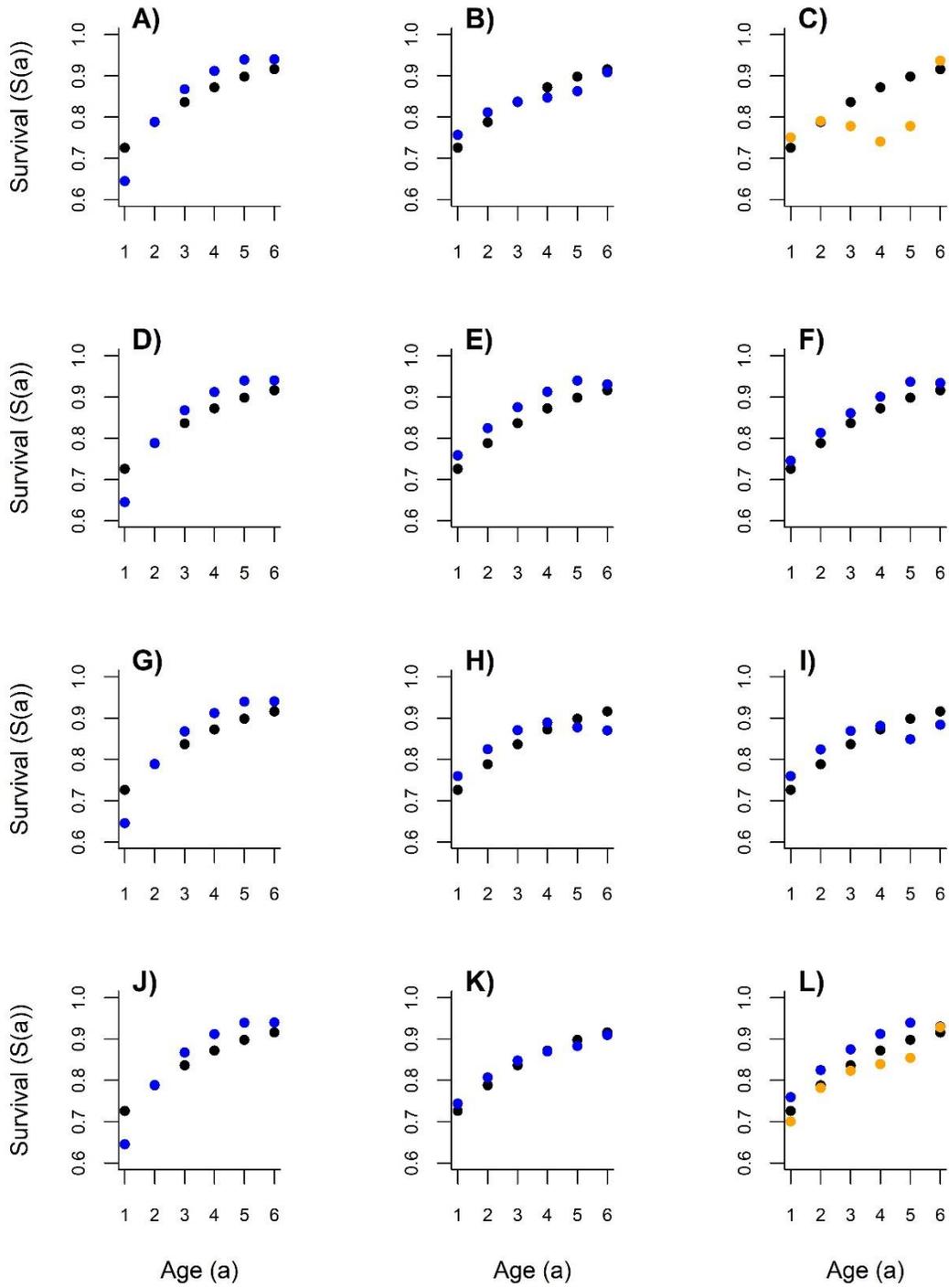


Figure 2



**Figure 3**

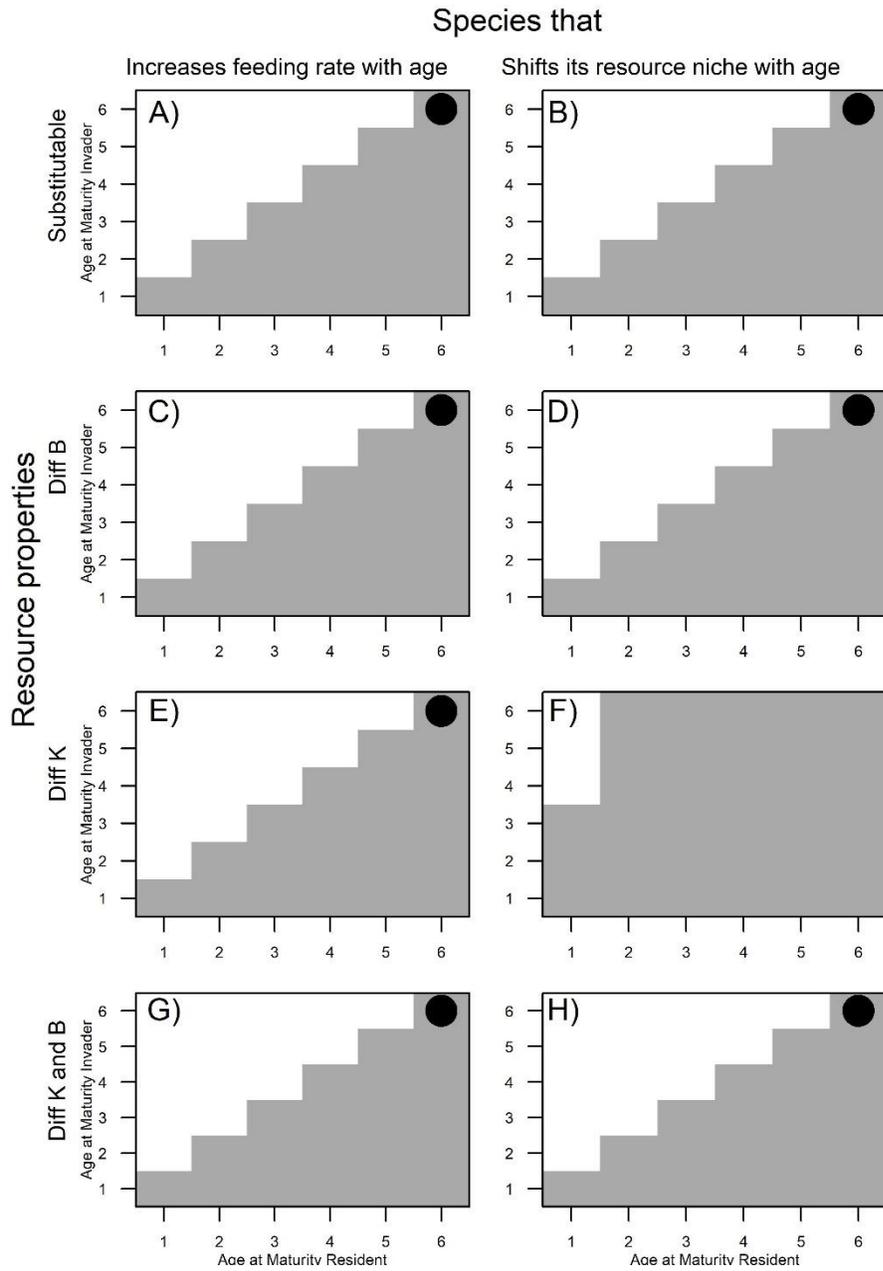


Figure 4

