



# Coexistence in a variable environment: Eco-evolutionary perspectives



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## HIGHLIGHTS

- A periodic (seasonal) resource allows evolutionarily stable two species coexistence.
- Coexistence arises through evolutionary branching or non-local invasion.
- Coexistence depends on season length, fluctuation period, and tradeoffs.
- Evolution on ecological timescales sabotages otherwise stable coexistence.

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## ABSTRACT

A central question in community ecology is the means by which species coexist. Models of coexistence often assume that species have fixed trait values and consider questions such as how tradeoffs and environmental variation influence coexistence and diversity. However, species traits can be dynamic, varying between populations and individuals and changing over time as species adapt and evolve, at rates that are relevant to ecological processes. Consequently, adding evolution to ecological coexistence models may modify their predictions and stability in complex or unexpected ways. We extend a well-studied coexistence mechanism depending on resource fluctuations by allowing evolution along a tradeoff between maximum growth rate and competitive ability. Interactions between favorable season length and the period of fluctuations constrain coexistence, with two species coexistence favored by intermediate season length and arising through evolutionary branching or non-local invasion. However, these results depend on the relative rates of ecological and evolutionary processes: rapid evolution leads to a complete breakdown of otherwise stable coexistence. Other coexistence mechanisms should be evaluated from an evolutionary perspective to examine how evolutionary forces may alter predicted ecological dynamics.

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## 1. Introduction

Communities typically support many more species than classic theoretical models of competition that predict to stably coexist. Hutchinson (1961) highlighted this apparent violation of the competitive exclusion principle (Hardin, 1960) as the “paradox of the plankton”: the persistence of diverse plankton communities in seemingly homogeneous environments with few limiting resources. The resolution of this paradox has inspired much theoretical work identifying a variety of mechanisms promoting coexistence. Broadly speaking, these mechanisms require factors such as predators or other natural enemies (Holt, 1977; Holt and Lawton, 1994); mutualists (Gross, 2008; Lee and Inouye, 2010); spatial heterogeneity (Tilman, 1994; Amarasekare, 2003; Edwards

and Stachowicz, 2010; Berkley et al., 2010); or temporal variability (Levins, 1968, 1979; Armstrong and McGehee, 1980; Chesson and Warner, 1981; Abrams, 1984; Grover, 1990; Chesson, 1994; Huisman and Weissing, 1999; Litchman and Klausmeier, 2001; Abrams, 2004, 2006). The coexistence mechanism we investigate in this paper is a member of this last category.

Temporal variability is ubiquitous in ecological systems. It occurs at a range of scales and arises from multiple, often interacting, sources including exogenous and endogenous cycles and stochasticity. Because the competitive exclusion principle is equilibrium-based, non-equilibrium conditions have been suggested as a potential solution to the paradox of the plankton, beginning with Hutchinson (1961). Since then, mathematical models have shown that two or more species can coexist due to temporal variation, such as fluctuations in a single resource (Armstrong and McGehee, 1976; Levins, 1979; Hsu, 1980; Chesson and Warner, 1981; Tilman, 1982; Litchman and Klausmeier, 2001; Abrams, 2004). At its simplest, temporal variation can be incorporated into models by imposing switching between two distinct

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environmental states (in our model, growing and nongrowing seasons). Coexistence can occur when resource levels fluctuate if there is a tradeoff between the maximum growth rate and competitive ability of species (Hsu, 1980; Smith, 1981; Grover, 1991; Litchman and Klausmeier, 2001; Anderies and Beisner, 2000; Tachikawa, 2008; Xiao and Fussmann, this issue). This coexistence mechanism is termed relative nonlinearity by Chesson (1994). Fast growing species (“opportunists”) and strong resource competitors (“gleaners”) may coexist if the length of the good season where resource is available is neither too short (opportunists outcompete gleaners) nor too long (gleaners outcompete opportunists) (Litchman and Klausmeier, 2001). Empirically, temporal variation in factors including light, phosphorus, and temperature, promotes coexistence and enhances diversity (Sommer, 1984, 1985; Gaedeke and Sommer, 1986; Floder et al., 2002; Litchman, 1998, 2003; Jiang and Morin, 2007; Shurin et al., 2010).

There is increasing evidence that rapid evolution occurs widely and alters ecological dynamics (Yoshida et al., 2003; Hairston et al., 2005; Carroll et al., 2007; Fussmann et al., 2007; Pelletier et al., 2009; Post and Palkovacs, 2009; Ellner et al., 2011). Where this modifies interspecific interactions essential for coexistence, we must revisit our understanding of coexistence mechanisms from a new perspective (Egas et al., 2004; Shores et al., 2008; Lankau, 2010; Bolnick et al., 2011; Snyder and Adler, 2011; Abrams et al., 2012). Typically, coexistence models focus on a few (often two) species with static traits (or phenotypes). In reality, however, a continuous range of species trait values may be accessible through both evolutionary (standing genetic variation and novel mutation) and ecological (dispersal from the regional species pool) processes.

While immigration can increase local diversity and mutation is the ultimate source of diversity, these processes can also result in the exclusion of species otherwise capable of coexisting ecologically. First, a pair of distinct, stably coexisting species might be inviable by a species with an intermediate phenotype that displaces them both, while also resisting all other invaders (an evolutionarily stable strategy, or ESS) (Abrams, 1987). Given sufficient heritable genetic variation, such a strategy could result in convergent evolution and even species extinction (terHorst et al., 2010; Vasseur and Fox, 2011). Shores et al. (2008) noted this convergent evolution exacerbates the paradox of the plankton.

Second, mechanisms based on temporal niche partitioning between species with distinct trait values may be particularly sensitive to rapid evolution. If individual species are capable of shifting their trait values in response to changing environments they may closely track the temporally varying optimum, preempting any newly opened niches. For example, Abrams (2006) showed that rapid evolution destroyed the coexistence of ecologically distinct specialist and generalist species in a variable environment. We explore both of these phenomena in this paper, focusing on the resource competition in a variable environment.

The remainder of the paper adheres to the following structure: Section 2 details our ecological model of competition for fluctuating resources, describes how fitness is calculated, and summarizes the basic evolutionary modeling approach we employ (“adaptive dynamics” sensu Abrams, 2005). In Section 3 we determine the outcome of slow evolution (or community assembly) as a function of environmental and tradeoff parameters. This analysis is aided by analytical approximations from the limiting case where the period of fluctuations is infinite (successional state dynamics). In Section 4, we relax this infinite period approximation, exploring the outcome of slow evolution/community assembly under finite period lengths. In Section 5 we investigate the effect of more rapid evolution on species coexistence, relaxing the traditional separation of ecological and evolutionary timescales. Finally, in Section 6 we discuss our results and subsequent conclusions. For convenience, all parameter definitions and values are summarized (Table 1).

## 2. Competition, fitness, and evolution in a variable resource environment

### 2.1. Ecological model

In this paper, we extend an ecological model describing competition for a single, externally forced, fluctuating resource similar to one previously studied by Litchman and Klausmeier (2001) to include continuous trait variation. They parameterized the basic model for two particular phytoplankton species, a fast growing, poor competitor (*Nitzschia* sp.) and a slow growing, good competitor (*Sphaerocystis* sp.). Their results demonstrated that

**Table 1**  
Model parameters, definitions, and default values used in the text and figures, unless otherwise specified (refer also to values in Reynolds, 2006).

Parameter	Definition	Values
<i>State variables</i>		
$N$	Population density	–
$R$	Available resource	–
<i>Environmental parameters</i>		
$R_{in}$	Total resource during good season	1000
$T$	Period of the resource fluctuation	–
$\phi$	Proportion of period $T$ over which growth is possible (length of good season)	$0 \leq \phi \leq 1$
<i>Physiological parameters</i>		
$\mu$	Maximum growth rate	$\mu_{min} \leq \mu \leq \mu_{max}$
$\mu_{min}$	Smallest allowed maximum growth rate	$\mu_{min} = m = 0.1$
$\mu_{max}$	Largest allowed maximum growth rate	5
$K$	Half-saturation constant, depends on $\mu$	$K_{min} \leq K(\mu) \leq K_{max}$
$K_{min}$	Smallest allowed half-saturation constant	0.1
$K_{max}$	Largest allowed half-saturation constant	6
$c$	Exponent governing tradeoff between $\mu$ and $K$	2.5
$m$	Per capita death rate	0.1
<i>Evolutionary variables</i>		
$g$	Instantaneous fitness/ growth rate	–
$\bar{g}$	Average fitness over one period	–
$\sigma$	Phenotypic variance (rate of evolution)	0–0.7

when the resource is available either very briefly, or almost constantly, only a single species can persist (the fast growing species and the good resource competitor, respectively). However, with good seasons of intermediate length, both species were able to coexist, partitioning the resource in time. While this model is relatively simple, it provides realistic, well-understood ecological dynamics, including both competitive exclusion and multi-species coexistence, and provides a foundation for subsequently adding evolution.

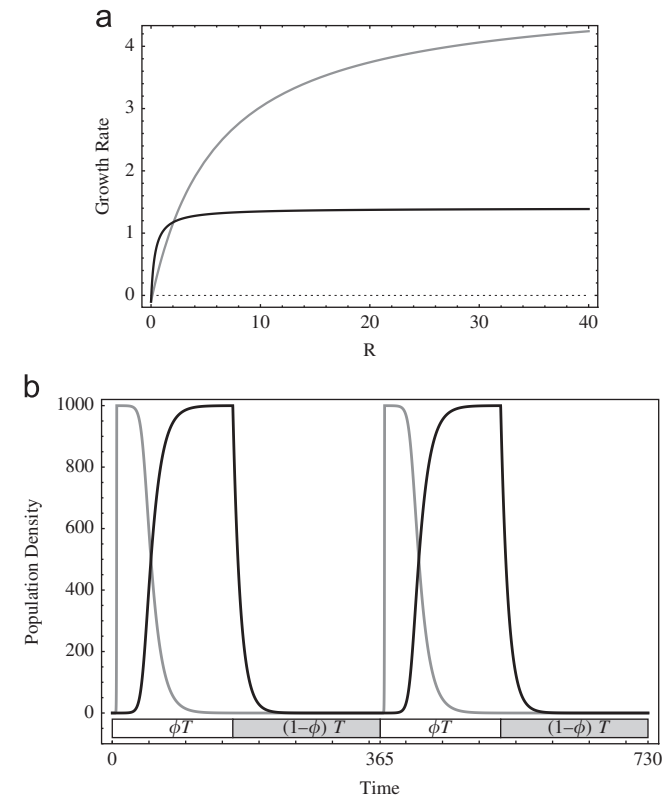
To describe the population dynamics of species  $i$  we consider how its density  $N_i$  changes due to growth and density-independent mortality (rate  $m$ ). Growth rates depend on the resource  $R$  following Michaelis–Menten–Monod kinetics (Fig. 1A), with maximum growth rate  $\mu_i$  and half-saturation constant  $K$

$$\frac{dN_i}{dt} = \left( \mu_i \frac{R}{R + K_i} - m \right) N_i = g(\mu_i; R) N_i \quad (2.1)$$

We define instantaneous fitness  $g$  as the per capita growth rate of species  $i$ , which depends on both the species trait  $\mu_i$  and the environmental variable  $R$ . Resource levels change as a function of biomass as well as external forcing, which is imposed with a period of length  $T$  and consists of alternating good and bad seasons

$$R(t) = \begin{cases} R_{in} - \sum_{i=1}^n N_i & \text{for } 0 \leq \text{mod}[t, T] < \phi T \\ 0 & \text{for } \phi T \leq \text{mod}[t, T] < T \end{cases} \quad (2.2)$$

In the good season, the level of available resource  $R$  is determined by the difference between total resource level (set to  $R_{in}$ )



**Fig. 1.** (a) Growth curves for a fast growing species (gray,  $\mu_1=4.99$ ,  $K_1=5.97$ ) and a slow growing species with low half-saturation constant (black,  $\mu_2=1.5$ ,  $K_2=0.36$ ). (b) Corresponding population dynamics illustrating the stable coexistence of species in (a). Resource is available (absent) in the intervals shown by the white (gray) boxes ( $\phi=0.45$ ,  $T=365$ ). Each period, the fast growing species dominates initially, then is replaced by the slow growing, better competitor as resources become limiting, followed by exponential death of both species during the bad season.

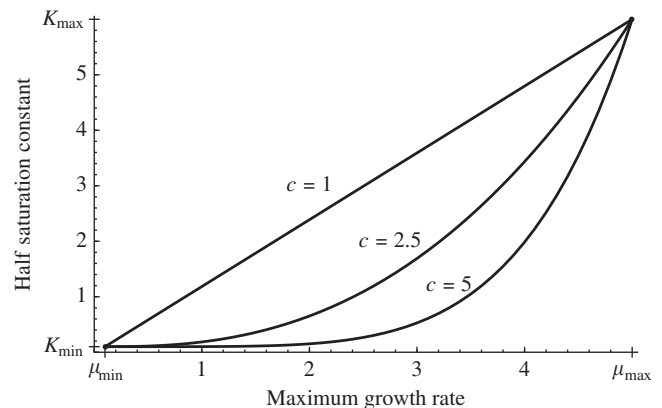
and the amount of resource made unavailable by the formation of biomass, which changes as growth, competition, and mortality occur. The good season lasts for a proportion  $\phi$  of the total period  $T$ . This parameter  $\phi$  is a key environmental variable controlling the length of time in each period where resource is available and growth is possible; it will be the focus of many of our results. At the end of the good season resource availability ceases, growth is impossible, and all species suffer mortality alike, declining exponentially in abundance for the duration of the bad season,  $(1-\phi)T$ . At this point, the cycle repeats with the return of the good season. For example, if we are considering fluctuations occurring on an annual scale ( $T=365$ ), and  $\phi=0.45$ , growth would be possible for only forty-five percent of each year, governed by resource availability (Fig. 1B). Biologically, this dynamic might correspond to a resource such as light, an essential resource for phytoplankton exhibiting strong diurnal and seasonal variation, or serve as a coarse approximation of the annual forcing temperate lakes experience due to many factors (temperature, lack of mixing, ice cover).

## 2.2. Growth rate–competitive ability tradeoff

It is well-known that when competing for a single, constantly supplied resource the species with the lowest break-even resource level  $R^*$ , defined as  $R^* = mK/(\mu - m)$  in this model, will outcompete all other species, rendering coexistence impossible (Tilman, 1982). Low values of  $K$  yield lower values of  $R^*$ , making species good competitors, favored to win when competing for a constant resource. However, minimizing  $K$  is often thought to come at the cost of lowering species' maximum growth rate  $\mu$ . This tradeoff sets up the potential for coexistence in environments where resource levels are not constant, as species with high maximum growth rates are able to quickly take advantage of a newly abundant resource (see Fig. 1 and Grover, 1990; Litchman and Klausmeier, 2001). We impose this tradeoff in our model by making  $K$  an increasing power function of  $\mu$

$$K(\mu) = K_{min} + (K_{max} - K_{min}) \left( \frac{\mu - \mu_{min}}{\mu_{max} - \mu_{min}} \right)^c \quad (2.3)$$

To restrict analysis to biologically relevant values, we also introduce bounds on  $\mu$  and  $K$  such that  $\mu_{min} \leq \mu \leq \mu_{max}$  and  $K_{min} \leq K(\mu) \leq K_{max}$  (Table 1). The strength of this tradeoff is controlled by parameter  $c$ , with  $c=1$  corresponding to a linear relationship between  $\mu$  and  $K$ , while  $c > 1$  results in an increasingly convex relationship (Fig. 2). Collectively, Eqs. (2.1)–(2.3) completely describe the ecological dynamics of species competing for a



**Fig. 2.** Tradeoff curve between maximum growth rate  $\mu$  and half-saturation constant  $K$ , bounded between biologically realistic values, for various values of shape parameter  $c$ .

fluctuating resource and constrained by a tradeoff between maximum growth rate and half-saturation constant.

### 2.3. Fitness in a periodic environment and invasion analyses

Prior to conducting evolutionary analyses, it is necessary to appropriately define the fitness of a species as a function of its traits and environment. We have previously defined a species' instantaneous fitness  $g$  in (2.1). However, in a fluctuating environment, the value of the instantaneous fitness  $g$  will vary over the course of a single period. The measure of fitness relevant for determining the long-term outcome of evolution and community assembly is  $\bar{g}$ , the time-average of instantaneous fitness over a period

$$\bar{g}(\mu_i) = \frac{1}{T} \int_0^T g(\mu_i; R(t)) dt \quad (2.4)$$

(Metz et al., 1992). This accounts for resource levels that vary through time due to external forcing and internal nutrient dynamics arising from growth and competition.

With this definition of fitness we can conduct invasion analyses, to determine the invasion rate of a population with trait  $\mu_{inv}$ . This invader can either arise through mutation from an existing species (giving it a similar trait value to its progenitor), or be introduced to the system through immigration (with no constraint on its trait value, as it comes from an unknown ecological and evolutionary environment). In either situation we specify that its initial abundance is rare (i.e.  $N_{inv} \approx 0$ ), which allows us to assume that resource dynamics remain unaffected by the invading species and are governed only by external forcing and the biotic effects of any resident species.

The invasion rate of a species with trait  $\mu_{inv}$  into an empty (or unoccupied) environment can be determined analytically

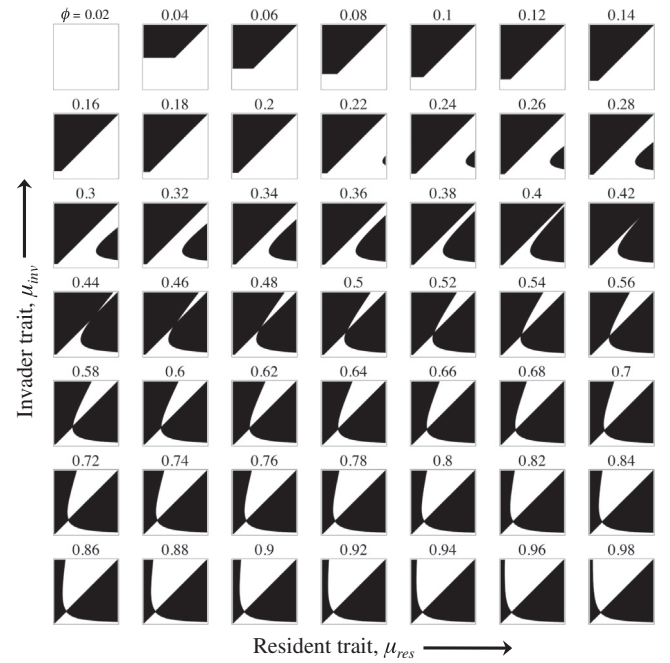
$$\bar{g}(\mu_{inv}) = \phi \mu_{inv} \frac{R_{in}}{R_{in} + K(\mu_{inv})} - m \quad (2.5)$$

as resource dynamics can be simplified such that  $R(t) = R_{in}$  during the good season and  $R(t) = 0$  otherwise (Litchman and Klausmeier, 2001). When  $\bar{g}(\mu_{inv}) > 0$ , the species has positive fitness and can increase in abundance, ultimately reaching its population dynamic attractor. If  $\bar{g}(\mu_{inv}) < 0$ , the species has negative fitness and is unable to persist even in the absence of competition. We can solve for the value of  $\phi$  where (2.5) changes sign for a species having the fastest permissible growth rate  $\mu_{max}$ ,

$$\phi_{min} = \frac{m}{\mu_{max}[R_{in}/(R_{in} + K_{max})]} \quad (2.6)$$

This value demarcates environments too severe for even single species to exist (Litchman and Klausmeier, 2001).

Now consider a novel phenotype invading an environment occupied by one or more resident species with traits given by the vector  $\vec{\mu}_{res}$ . We assume that invaders arise infrequently enough that resident communities reach their attractor between invasions and that multiple invasions do not occur simultaneously (separation of ecological and evolutionary timescales). Therefore we can consider the invasion rate  $\bar{g}(\mu_{inv}, \vec{\mu}_{res})$  to be a function only of the traits of the resident(s) and the invader. In general, it is impossible to determine the resident species attractor analytically, which prevents calculating the invasion rate explicitly. We can either locate the attractor by numerically solving (2.1) until  $|N_{res}(t) - N_{res}(t+T)| < \epsilon$  for some small  $\epsilon$ , or by an approximation valid for large period  $T$  (see Section 3). The population attractor then determines the relevant resource dynamics that an invader experiences, so we can calculate  $\bar{g}(\mu_{inv}, \vec{\mu}_{res})$ .



**Fig. 3.** Pair-wise invasibility plots (PIPs) across a range of values of  $\phi$ , obtained from SSD approximations. Positive (negative) invasion fitness is shown in black (white). As  $\phi$  increases across the panels evolutionary cases change: no species persists ( $\phi = 0.02$ ); single species global ESS at maximum trait value ( $\phi = 0.04$ – $0.2$ ); local but not global ESS ( $\phi = 0.22$ – $0.4$ ); branching point ( $\phi = 0.42$ – $0.82$ ); single species global ESS at low value of  $\mu$  ( $\phi = 0.84$ – $0.98$ ).

### 2.4. Modeling evolution with adaptive dynamics

Having defined the invasion fitness of a rare invader (mutant phenotype or immigrant species) as a function of its trait and those of the resident species, we can use the techniques of Adaptive Dynamics to analyze the outcome of evolution (or community assembly) for any given environment (Dieckmann and Law, 1996; Geritz et al., 1998, 2004; McGill and Brown, 2007). For a single resident species ( $\vec{\mu}_{res} = \mu_{res}$ ), the sign of  $\bar{g}(\mu_{inv}, \mu_{res})$  for all pairs of resident and invader traits across a range of values determines pair-wise invasibility plots (or PIPs), which can be used to graphically determine the outcome of single species (“monomorphic”) evolution (cf. Fig. 3 and Geritz et al., 1998). The fitness gradient  $\partial \bar{g}(\mu_{inv}, \mu_{res}) / \partial \mu_{inv} |_{\mu_{inv} = \mu_{res}}$  determines the direction of selection: positive (negative) values indicate that larger (smaller) trait values are favored. Singular strategies (evolutionary equilibria) can be found by solving for the value(s) of  $\mu_{inv}$  such that the fitness gradient is zero, corresponding to situations where there is no directional selection on the resident. The second derivative of the invasion fitness evaluated at the resident trait,

$$\partial^2 \bar{g}(\mu_{inv}, \mu_{res}) / \partial \mu_{inv}^2 |_{\mu_{inv} = \mu_{res}} \quad (2.7)$$

indicates whether the singular strategy experiences stabilizing or disruptive selection. Negative values of (2.7) indicate stabilizing selection where no invader with a nearby trait value will be able to invade the resident, leading to a local evolutionarily stable state (ESS). If it is also true that invasion fitness is negative for all values of  $\mu_{inv}$  (except  $\mu_{res}$  of course, and such that  $\mu_{min} \leq \mu_{inv} \leq \mu_{max}$ ), then we identify this ESS as a global ESS. However, in some cases values of  $\mu_{inv}$  sufficiently different from  $\mu_{res}$  can have positive invasion fitness. Then, through immigration or mutations of large effect, the single species ESS is invisable and may give way to two species coexistence. We describe this situation as a “local but not global evolutionarily stable state” (or LESS, see McGill and Brown, 2007). In contrast, if (2.7) is positive, corresponding to disruptive



selection, and convergence stability holds, a branching point is identified. Following the identification of a branching point (or a LESS), a two species singular strategy can be located by solving for the values of  $\vec{\mu}_{res} = (\mu_{res1}, \mu_{res2})$  such that the fitness gradient,  $\partial \bar{g}(\mu_{inv}, \vec{\mu}_{res}) / \partial \mu_{inv}$ , simultaneously equals zero when  $\mu_{inv}$  is evaluated at each element of  $\vec{\mu}_{res}$ . The stability of the resulting singular strategy is determined as before (refer to Eq. 2.7) and the process repeated until a global ESS state is determined. In this way, for any environment (given  $\phi$ ,  $T$ , or other parameters of interest), we can solve for both the number of species capable of arising and persisting stably through evolution and their associated trait values (Geritz et al., 1998, 2004).

Note that care must be taken in these calculations to maintain  $\mu$  between  $\mu_{min}$  and  $\mu_{max}$ . The lower value of  $\mu$  is effectively constrained by mortality rate  $m$ . However, in many cases, evolution would drive the maximum value of  $\mu$  above  $\mu_{max}$  despite the corresponding cost of high  $K$ . When this happens, we hold the species' trait at  $\mu_{max}$  as if it had reached a singular strategy, even if its fitness gradient was positive. In real biological systems, maximum growth rates may be constrained by additional factors such as metabolic tradeoffs, competitive abilities, predation, and temperature, preventing runaway selection for unrealistically high growth rates.

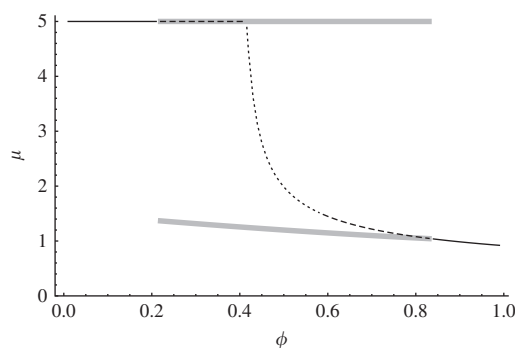
### 3. Slow evolution and coexistence using $T \rightarrow \infty$ approximation

#### 3.1. Successional state dynamics (SSD) approximation and motivation

Because the numerical evaluation of (2.1) is relatively costly, for our initial results we use an approximation method termed 'Successional state dynamics' (SSD, see Klausmeier, 2010), to arrive at analytically tractable expressions for population attractors (2.1) and invasion rates (2.4). This approach hinges on the observation that as  $T \rightarrow \infty$  in externally forced, piecewise, periodic systems, the dynamics consist entirely of discrete states, in which individual populations are either rare and exponentially increasing or decreasing in abundance, or common and at constant abundances. The transitions between these discrete states occur almost instantaneously relative to the length of a period  $T$ . We can determine the identity of these states as well as critical transition times between states. For specifics refer to the example of competition for a periodically available resource provided in detail in (Klausmeier, 2010). While the assumption of infinitely long periods may be initially disconcerting, it is often the case that numerical results from finite period environments converge rapidly on the SSD approximations as  $T$  increases (in our case, the results are indistinguishable from  $T=365$ ). We first present results using the SSD approach, and then investigate dynamics given finite values of  $T$ , indicating where these findings converge.

#### 3.2. Resource availability $\phi$ and trait bifurcation diagram

We now turn to examining how the length of the good season, governed by  $\phi$ , influences species coexistence and ESS trait values. Fig. 3 shows a sequence of PIPs across a range of  $\phi$  values, classified according to their stability (see Section 2.4 and Figs. 3 and A1A). This information can be condensed into a bifurcation diagram covering a continuous range of  $\phi$  values, showing simultaneously the trait values of one and two species singular strategies and categorizing the corresponding evolutionary regimes (Figs. 4 and A1B). This result shows that at either low or high values of  $\phi$  (near 0 or 1), only a single species can exist at the ESS (with high or low maximum growth rates, respectively). For intermediate values of  $\phi$ , two species coexistence is possible via



**Fig. 4.** Evolutionary equilibria and their stability as a function of  $\phi$ , the proportion of a period over which growth is possible. The black line follows the location of the one species singular strategy as  $\phi$  changes. The stability of the singular strategy transitions between global ESSs (solid line), local but not global ESSs (LESSs, dashed), and branching points (dotted). Gray lines indicate the traits of the two-species (dimorphic) ESS populations arising from LESSs or branching points. Whenever the fast growing strategy is favored it takes on the value of  $\mu_{max}=5$ .

evolutionary branching. Flanking either side of this range of  $\phi$  values are local but not global ESS (LESS) cases, where two species coexistence is possible, but can be attained only through immigration or mutations of large effect, rather than by small mutations (Fig. 4). These results are consistent with the findings of the ecological model of (Litchman and Klausmeier, 2001), with fast growing species dominating at low  $\phi$ , good competitors dominating at high  $\phi$ , and both strategies coexisting under intermediate resource availability. However, the range of values over which coexistence is possible is significantly larger when species trait values are optimized by evolution along our tradeoff, rather than given by the specific fixed parameters of Litchman and Klausmeier (2001). Additionally, we gain insight into the potential origin of coexisting species, and when the two species community can arise in situ through gradual evolutionary processes, or depends on a source of variation stemming from immigration or large mutations.

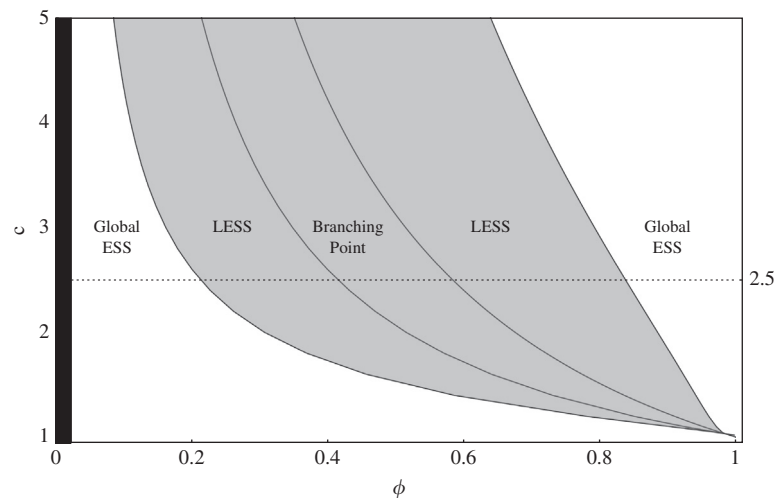
#### 3.3. Influence of tradeoff assumptions

Coexistence depends heavily on the assumed tradeoff between maximum growth rate  $\mu$  and half saturation constant  $K$ , the strength of which is governed by parameter  $c$  (Fig. 2). We examine the sensitivity of the preceding results to variation in this parameter (Fig. 5). When  $c=1$ , the relationship between  $\mu$  and  $K$  is linear, and the lowest value of  $R^*$  occurs at  $\mu_{max}$  (Fig. 2). As such, there is no competitive advantage to having a lower maximum growth rate and coexistence does not occur for any value of  $\phi$ . However, as  $c$  increases, coexistence becomes possible and the width of the coexistence region increases rapidly. As  $c$  increases further, the region of coexistence shifts gradually from higher to lower values of  $\phi$ , where the resource is available more briefly. Collectively these results illustrate another potential role for evolution in moderating coexistence, to the extent that tradeoffs may arise through evolutionary as well as physiological constraints.

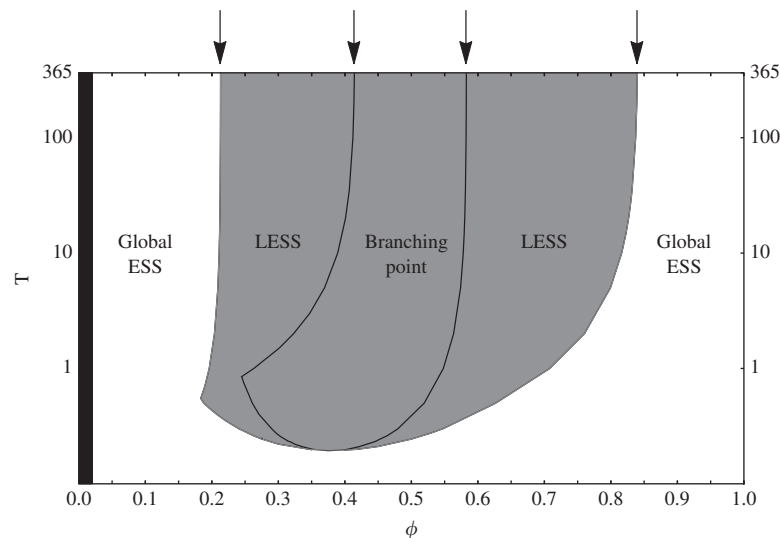
### 4. Slow evolution and coexistence under finite period fluctuations

#### 4.1. Evolutionary coexistence, length of the good season ( $\phi$ ), and period length ( $T$ )

Within aquatic environments, and across habitats, resources can be more or less ephemeral and fluctuate on different time scales (in other words, with periods of different lengths). Given the diversity of possible environments, it is important to understand



**Fig. 5.** As the strength of the tradeoff between maximum growth rate and half-saturation constant ( $c$ ) increases, the range of  $\phi$  value across which two species coexistence occurs increases (shaded gray region). The black rectangle indicates the region where  $\phi$  is so small that no allowable species persists. These results were obtained using the SSD approach. For comparison, the dashed line corresponds to  $c=2.5$ , the parameter value used in all other results.



**Fig. 6.** The relationship between evolutionary outcome and fluctuation regime parameters. The region of two species coexistence is shown in gray. Environments with brief resource availability ( $\phi < 0.2$ ) are dominated by fast growing species, while good resource competitors dominate in environments with consistent resources ( $\phi > 0.8$ ). For very short periods, no coexistence is possible, as resource fluctuations for any value of  $\phi$  occur too rapidly to allow temporal niche partitioning. Arrows indicate the predicted boundaries between evolutionary regimes obtained from the SSD approach; note that the results for  $T=365$  are practically indistinguishable from  $T=\infty$ . The black region at low  $\phi$  indicates environments too extreme for the survival of even a single species.

in which environments (with what kind of fluctuations) the coexistence of multiple species is possible based on the coexistence mechanism we study. In Section (3.2) we examined the effect of the length of the good season where resource is available (regulated by  $\phi$ ) on evolution and coexistence, assuming that  $T \rightarrow \infty$ . Now we relax this assumption, varying both  $\phi$  and  $T$ , while addressing the same questions (Fig. 6). As with the SSD results, increasing  $\phi$  produces a transition from a single fast growing species at the ESS to two species coexistence via a LESS, then branching, returning to LESS, and finally a single highly competitive species at the ESS. The SSD approximation is very accurate for the annual period of  $T=365$  days. However, as period length  $T$  becomes shorter, resource fluctuations become very rapid and coexistence collapses. When resource fluctuations occur rapidly relative to the rate species respond to their environment, individual species average their dynamics over the course of fluctuations, removing the potential for temporal niche partitioning.

## 5. Evolution on ecological timescales

We have demonstrated that evolutionarily stable two species coexistence can occur when ecological dynamics occur much more quickly than mutation and evolution (Fig. 4). However, population and trait dynamics may often occur on the same timescale, given the increasing recognition that phenotypic changes can occur rapidly through evolution (Hairston et al., 2005; Carroll et al., 2007; Pelletier et al., 2009; Ellner et al., 2011) or plasticity (Agrawal, 2001; Yoshida et al., 2003; Miner et al., 2005). Microbes, including phytoplankton, are known to evolve quickly and also exhibit plasticity, commonly in response to environmental stimuli that vary seasonally, including grazing and light availability (vanDonk, 1997; Stomp et al., 2008). Collectively, this suggests that species may often be capable of changing their phenotypes in response to shifting environmental conditions while fluctuations occur, potentially altering coexistence via temporal niche

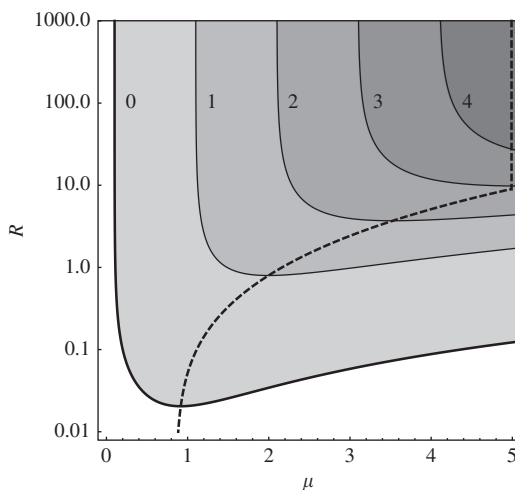
partitioning. We explore this possibility by first examining the extreme case of instantaneous evolution (fast evolution, slow ecology). Then we investigate the transition between instantaneous evolution and the usual Adaptive Dynamics limit (slow evolution, fast ecology) using two different approaches. Along the way, we highlight various obstacles these approaches face.

### 5.1. Fast evolution, slow ecology

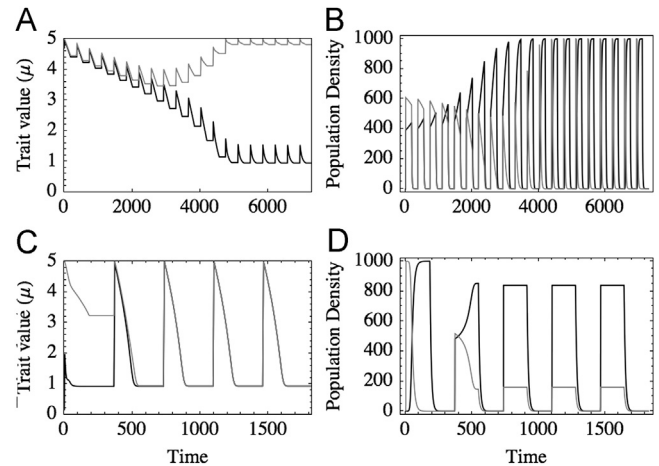
When evolution occurs infinitely rapidly relative to ecological processes, we can assume that a species will be able to adopt the trait value that maximizes its instantaneous fitness faster than any changes that occur in population density or resource availability. Such rapid adaptation is perhaps most intuitively interpreted as phenotypic or behavioral plasticity in response to the environment, rather than evolution in a classic sense. We can map instantaneous fitness  $g(\mu_{inv}; R)$  as a function of species trait and resource availability (Fig. 7). At any given resource level, instantaneous fitness is maximized at a single trait value. This suggests that in the case of extremely rapid evolution it is not possible for multiple species to coexist. This result holds for all values of  $\phi$ , as this parameter influences only the duration of various nutrient states, rather than the shape of the instantaneous fitness function  $g(\mu_{inv}; R)$ . A single species becomes, in effect, a Darwinian demon, capable of being either a fast grower or good resource competitor as resource levels dictate, and effectively no longer subject to a tradeoff between these abilities. In the next section, we study the transition between coexistence given slow evolution and competitive exclusion given rapid evolution.

### 5.2. Quantitative genetics (QG) approach

Adopting a modeling approach from quantitative genetics allows us to explicitly specify the rate at which species' traits respond to the strength of selection they experience. Variations of this approach have been derived several times (see Lande, 1976; Charlesworth, 1990; Iwasa et al., 1991; Taper and Case, 1992; Abrams et al., 1993; Abrams, 2001), and use a differential equation to track how a population's mean phenotypic trait responds to selection given available phenotypic variation. These



**Fig. 7.** Instantaneous fitness of a single species,  $g(\mu; R)$  from (2.1), as a function of available resource  $R$  and species trait  $\mu$ . Fitness increases with darker shading. The dashed line traces out the trait value corresponding to the strategy maximizing  $g$  at each given resource level  $R$ . A species capable of instantaneous adaptation would track the dashed line over the course of a period from right to left, jumping abruptly between the line's endpoints at the beginning of each period. The thick black line where fitness equals zero corresponds to the break-even nutrient concentration  $R^*$  for each distinct trait value.



**Fig. 8.** Examples of trait and population dynamics from the QG model for (A–B) low ( $\sigma=0.1$ ) and (C–D) high ( $\sigma=0.65$ ) rates of adaptation. At low adaptation rates, two species with very similar initial trait values ( $\mu_1=4.99$  and  $\mu_2=4.9$ ) diverge from one another, undergoing branching and coexisting using divergent strategies, while continuing to exhibit small-scale trait fluctuations during the period of resource variation (A–B). Contrastingly, when  $\sigma$  is large, even species with dramatically different initial trait values ( $\mu_1=4.99$  and  $\mu_2=0.15$ ) converge on a single shared trait trajectory, becoming effectively neutral (C–D). Differences in population abundances after trait convergence are generated by the species' distinct transient stages.

approaches can be used to describe trait evolution on ecological time scales in combination with equations describing population dynamics, such as (2.1); see derivation and comments in Abrams et al. (1993) and the Appendix of this paper. With respect to our model, this leads to a differential equation modeling change in species  $i$ 's mean trait  $\mu_i$  as a function of the direction and magnitude of its instantaneous fitness gradient, the traits of any other species present  $\vec{\mu} = (\mu_1, \mu_2, \dots, \mu_n)$ , and a rate parameter  $\sigma$ , describing phenotypic variation or mutation,

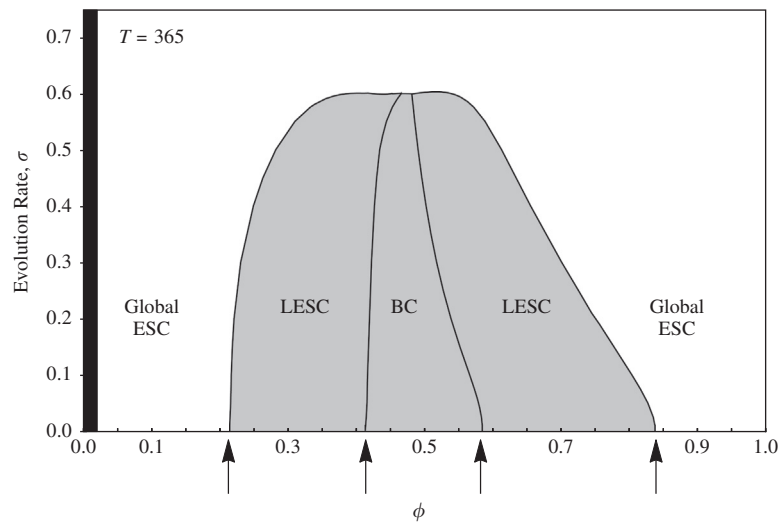
$$\frac{d\mu_i}{dt} = \sigma \left[ \frac{\partial g(\mu_{inv}, \vec{\mu})}{\partial \mu_{inv}} \right] \bigg|_{\mu_{inv} = \mu_i} \quad (5.1)$$

The sign of the fitness gradient indicates whether selection favors increased (or decreased) values of  $\mu_i$ . Numerically, constraints on the range of  $\mu_i$  are achieved using Heaviside step functions to prevent evolution beyond the trait values  $\mu_{min}$  (if the fitness gradient is negative) or  $\mu_{max}$  (if the fitness gradient is positive). The rate at which trait  $\mu_i$  responds to selection depends entirely on parameter  $\sigma$  and the magnitude of selection. An alternative interpretation of (5.1) is that it models the dynamics of phenotypic plasticity (Abrams, 2005) which places no upper limit on  $\sigma$ .

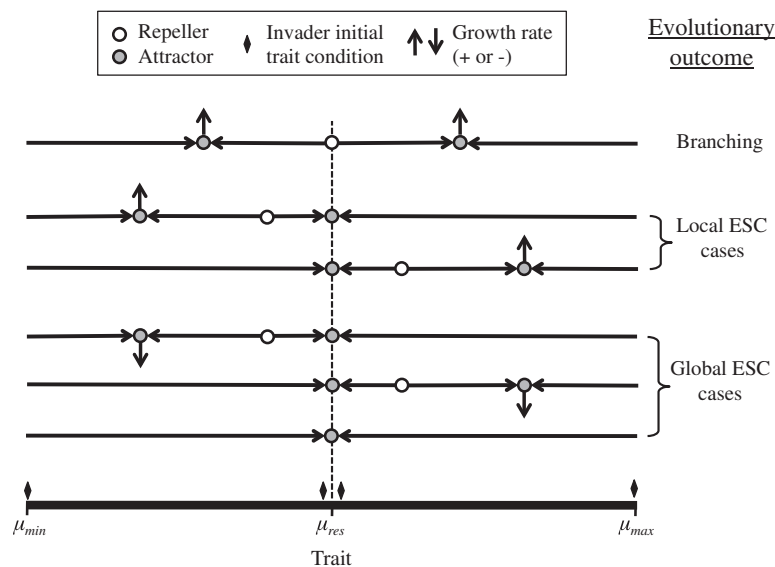
As  $\sigma \rightarrow 0$ , trait change declines to zero and the trait becomes effectively constant. However, competitive dynamics still play out between species having different, near-stationary trait values, potentially leading to invasion, competitive exclusion, and the replacement of residents. In this way, as  $\sigma \rightarrow 0$  we effectively recreate the Adaptive Dynamics limit, where ecological and evolutionary timescales are separated (Abrams, 2005). In this limit, all of the results obtained previously hold; in particular, for intermediate values of  $\phi$ , two species arranged along the fast grower to good competitor tradeoff coexist.

### 5.3. Intermediate evolutionary rates (QG approach)

We can begin to investigate the collapse of two species coexistence with the increase of evolution rates by combining Eqs. (2.1) and (5.1). Together, these equations can describe the population and trait dynamics of one or more competing species



**Fig. 9.** As the rate of adaptation ( $\sigma$ ) increases, the potential for coexistence collapses (shaded area corresponds to the region of two species coexistence). At  $\sigma \rightarrow 0$ , the coexistence and evolutionary boundaries converge on those predicted for the same period ( $T=365$ ) by the Adaptive Dynamics approach, shown by the arrows (Fig. 6). A small region of the parameter space where coexistence collapses contains a variety of esoteric dynamics (not shown here).



**Fig. 10.** Assessing evolutionary stability of singular cycles in the QG model. Horizontal arrows indicate the net direction of change of a rare invader's trait dynamics over one cycle, given a resident singular cycle with initial trait  $\mu_{res}$ . Gray nodes represent invader trait attractors, while white nodes correspond to repellers, separating basins of attraction of invader trait dynamics. Vertical arrows indicate the time-averaged growth rate of an invader at an invader trait attractor. Finally, diamonds indicate initial invader trait conditions used to ascertain GESCs, LESCOs, and branching cycles.

in our seasonally forced environment. Evolution enables species to adapt over the course of a period, rather than maintaining constant trait values. Consequently, trait values typically increase at the beginning of a period to allow rapid growth when the resource is plentiful, then decrease again as the resource becomes limiting. Despite this variation in traits on a short time scale, two species can still exhibit distinct trait attractors, consistent with multispecies coexistence (Fig. 8A and B). However, this coexistence collapses when  $\sigma$  is high (Fig. 8C and D); despite having dramatically different initial trait values, two species rapidly converge on the same trait dynamics. Essentially,  $\sigma$  becomes so large that any species is able to rapidly approach the trait values optimizing its fitness over the course of the resource fluctuations and no niche space remains for ecologically distinct species. Once competitively

neutral, the addition of any demographic stochasticity would lead to the eventual exclusion of one species or the other. The collapse of coexistence agrees with our previous finding regarding the limit of fast evolution and slow ecology (Section 5.1 and Fig. 7).

We can map out how coexistence and evolutionary regimes change with increasing  $\sigma$  (and across variation in  $\phi$ ). For non-zero values of  $\sigma$ , species' trait values vary through time, rendering typical Adaptive Dynamics approaches that assume constant trait values inapplicable. Population and trait attractors (denoted  $\hat{N}_i(t)$  and  $\hat{\mu}_i(t)$ ), and consisting of their dynamics over the course of one period,  $T$ ) must be determined numerically, solving the system of equations described by (2.1) and (5.1) until both  $|\hat{N}_i(t) - \hat{N}_i(t+T)| < \epsilon$  and  $|\hat{\mu}_i(t) - \hat{\mu}_i(t+T)| < \epsilon$  for small  $\epsilon$  and all  $i$  species under consideration. We then proceed to identify singular cycles, branching cycles,



and evolutionarily stable cycles (ESCs) in these systems by performing numerical invasion experiments (see graphical schematic in Fig. 10).

First, we locate one-species singular cycles by solving for  $\hat{\mu}(t)$  and  $\hat{N}(t)$  until a stable cycle is reached. To determine the uniqueness of this singular cycle, we identify  $\hat{\mu}(t)$  separately given different initial trait conditions ( $\mu_{\min}$  and  $\mu_{\max}$ ). If the resulting attractors are identical, we conclude that the singular strategy  $\hat{\mu}(t)$  is both unique and convergence stable in the trait range  $[\mu_{\min}, \mu_{\max}]$ . All of the singular cycles identified while examining this model were unique. Second, we determine the evolutionary stability of singular cycles (Fig. 10). We solve for the trait equation of an invading species assumed to be rare (to have no impact on resource dynamics) and forced by the singular cycle solution, starting from a variety of initial trait values. Once the invader's trait attractor is reached, we calculate its time-averaged growth rate. We can identify three different types of singular cycles: global evolutionarily stable cycles (GESCs), local but not global evolutionarily stable cycles (LESCs), and branching cycles (Fig. 10). GESCs arise in two ways: (1) the invader trait dynamics converge on the resident trait attractor whether its initial trait value is  $\mu_{\min}$  or  $\mu_{\max}$ , or (2) the invader trait dynamics converge on the resident attractor for initial conditions close to the resident attractor, while converging on a distinct, non-local trait attractor when starting at  $\mu_{\min}$  or  $\mu_{\max}$ ; however, the average growth rate of the invader at this new trait attractor is negative, so that the invader cannot persist. LESCs represent a very similar case to (2) above, with the distinction that the average growth rate of an invader at a non-local trait attractor is positive instead of negative. Finally, branching cycles occur when invaders with initial trait values similar to the resident diverge from the resident trait attractor, settling on two distinct trait attractors with positive average invader growth rates. These outcomes are analogous to the three different types of singular strategies from traditional Adaptive Dynamics.

Using this approach, we outline the environments producing these three distinct regimes provided in Fig. 9 as a function of the length of the good season  $\phi$  and evolution rate  $\sigma$ . Collectively, GESC's, LESCs, and branching cycles represent the overwhelming majority of evolutionary outcomes observed in our model. However, we do note the presence of a variety of more baroque alternatives arising in a small area of parameter space where these evolutionary regimes converge at high  $\sigma$  (not shown, but see Fig. A4); for simplicity we do not discuss these here. For  $\sigma \rightarrow 0$ , boundaries between evolutionary regimes identified with this quantitative genetics model agree closely with those obtained from Adaptive Dynamics (see arrows in Fig. 9). As expected, however, the region of coexistence declines with increasing  $\sigma$ , deteriorating completely around  $\sigma=0.6$ . At this value, species are able to respond rapidly enough to variation in resource levels over the course of a single period to be both fast growing initially and highly competitive as resources become limiting. The exact evolutionary rate permitting this to occur varies with the overall length of each fluctuation period, which controls the amount of time a species has to adapt to resource conditions. Ultimately, these results show that rapid evolution can sabotage the coexistence of species otherwise able to persist in a purely ecological model with constant trait values.

#### 5.4. Limitations of QG approach

Eq. (5.1), describing trait evolution, is derived from a Taylor series approximation of the effect of selection on the mean phenotypic trait of a population (see Appendix and Abrams et al., 1993). The population is assumed to exhibit Gaussian phenotypic variation governed by a constant variance parameter proportional to  $\sigma$ , which governs the rate of trait change in

response to selection (Taper and Case, 1992; Abrams et al., 1993). The validity of this approximation is limited when the fitness function is highly nonlinear or the phenotypic variance parameter is sufficiently large (Abrams et al., 1993). Additional terms from the Taylor series approximation are required to avoid this source of error as phenotypic variance increases. This observation is significant to our results (and the results of several recent papers in this field, for example Yamauchi and Yamamura, 2005; Mougi, 2012), as we are explicitly interested in how eco-evolutionary regimes are altered by increasing  $\sigma$ . The collapse of two species coexistence occurs for increasingly lower evolution rates as higher order terms are included in (5.1), but the qualitative results of Fig. 9 remain unchanged (see Appendix, Fig. A2).

When phenotypic axes are constrained or bounded, additional issues arise. Interactions between the distribution of phenotypic values within a population and trait constraints can lead to departures from assumptions of normality and constant phenotypic variance. Eqs. (5.1), (A.1), and (A.3), all typically assume that phenotypic variation follows a normal distribution. It remains unclear if (5.1) remains valid when modeling the rapid evolution of a bounded trait regardless of how many higher order terms are included. To confirm our results while avoiding this assumption, we also model rapid evolution as a mutation/diffusion process, as described in the Appendix. This approach reinforces our previous finding that two species coexistence at intermediate values of  $\phi$  collapses as mutation rates, and hence evolution rates, increase (Fig. A3). While the exact point at which coexistence collapses is difficult to pinpoint, collectively our results from a variety of approaches demonstrate that sufficiently rapid evolution precludes coexistence by temporal niche partitioning.

## 6. Discussion & conclusions

This paper is motivated by our desire to understand how classic coexistence models at the heart of community ecology behave when species traits can evolve. Other recent papers have begun to consider this same question (Egas et al., 2004; Lankau, 2010; Snyder and Adler, 2011; Abrams et al., 2012). In particular, we have focused here on studying an existing ecological model of competition and coexistence that relies on temporal variation in resource levels. Concentrating on discovering when coexistence is evolutionarily stable and how it might arise, we have explored the significance of various kinds of environmental variation as well as the tradeoff essential for coexistence. We have also carefully studied how our results depend on the way in which evolution is modeled, paying particularly close attention to the dependence of coexistence on the rate at which evolution occurs relative to ecological dynamics.

In general, when evolution occurs slowly, our results agree qualitatively with existing ecological models of this mechanism of coexistence (Litchman and Klausmeier, 2001). For example, two species coexistence was only possible when resource fluctuations were not too rapid ( $T$  sufficiently large) and resource was neither too briefly nor too constantly available (Fig. 6). The proportion of each period when resource was available ( $\phi$ ) had a strong effect on the occurrence of two species coexistence, but a weak effect on the specific traits comprising two species ESSs (gray lines in Fig. 4 is almost constant). Thus in this case evolution (or community assembly) expanded the region of coexistence relative to Litchman and Klausmeier (2001) by identifying a more broadly successful pair of gleaner and opportunist traits, as opposed to driving trait adaptation across a gradient in  $\phi$ . Identifying boundaries separating evolutionary regimes, and more importantly the possibility of coexistence, as a function of environmental parameters may prove important, as shifts in the environment could lead to abrupt

changes in species diversity (e.g., transitioning between two and one species ESS's, see Fig. 6).

By analyzing this model from an evolutionary perspective, we also gained insight into differences in the development of two species coexistence across environments. In some cases two species coexistence can arise in situ through evolutionary branching or disruptive selection (branching point region in Fig. 6). In others, coexistence cannot arise from local evolutionary processes reliant on small trait changes (low mutational variance), but can develop if large trait changes or immigration are possible (LESS regions in Fig. 6). This sets up the potential for complex, higher-level interactions between ecology and evolution, with evolution generating trait diversity through adaptive processes occurring across heterogeneous environments, and dispersal influencing the exchange of diversity between habitats.

Tradeoffs are an essential part of coexistence mechanisms. Their exact nature and origin are rarely determined, yet their forms can dramatically influence the number of species that coexist in given environment. While a tradeoff between maximum growth rate and half-saturation constant is often assumed, we know little about its actual shape. For this reason, we explored how variation in its strength influences coexistence in our model (Fig. 5). While the coexistence of at least five species was demonstrated in (Litchman and Klausmeier, 2001), we never observed the coexistence of more than two species in any of our results. We attribute this to the realistic constraints on trait ranges that we impose, as the diversity achieved in Litchman and Klausmeier (2001) required variation in trait values across orders of magnitude.

In addition to exploring the effects of ecological parameters governing resource fluctuations and trait tradeoffs, we also explored the rate of evolutionary responses to the environment, rather than assuming only slow evolution. This was a pressing question, both because ever more examples of rapid evolution are being documented (Yoshida et al., 2003; Hairston et al., 2005; Carroll et al., 2007; Fussmann et al., 2007; Pelletier et al., 2009; Ellner et al., 2011), and because the coexistence mechanism we focused on depends critically on differences in species' growth rates leading to temporal niche partitioning. We argue that the expected consequence of extremely rapid evolution (or high plasticity) is the collapse of coexistence, even in environments otherwise capable of supporting multiple species (Section 5 and Figs. 7–9). We also show, using a variety of methods, how coexistence collapses as rates of evolutionary response increase. This occurs well before the limit of an instantaneously adapted species is reached, as species need only to become flexible enough in their trait strategies to prevent niche partitioning in order to preclude coexistence. The precise value of the evolutionary rate leading to competitive exclusion will vary depending on the timescale of the fluctuations enabling coexistence, as well as species' growth rates. In general, empirical rates of adaptation are not well quantified, although for phytoplankton, as with other microbes, evolution rates are potentially quite high, given short generation times. Collectively, these results suggest that attention must be paid to the rates at which species can adapt and evolve before temporal variation is invoked as the mechanism responsible for coexistence in any particular system. However, it remains an open question whether or not other coexistence mechanisms are equally sensitive to rapid evolution.

Several theoretical developments were required in these analyses. First, we applied the SSD approximation (Klausmeier, 2010) to Adaptive Dynamics methods (Geritz et al., 1998), a combination which offers the potential to facilitate numerical and analytical study of a variety of models and coexistence mechanisms involving environmental fluctuations. Second, we developed an approach for classifying evolutionary outcomes in systems where

trait dynamics fluctuate according to the QG-type differential equations in forced environments. These techniques extend the notion of ESS to evolutionary cycles and should be applicable to other non-equilibrium models with evolution on ecological time scales. Finally, methods for modeling rapid evolution using QG models with large trait variances have important limitations, recognized by Abrams et al. (1993). We have explored these limitations, and an alternative approach, contributing to a better understanding of how to appropriately, transparently, and efficiently model rapid evolution (Appendix, Figs. A2 and A3).

There are a number of potential extensions to this work. While we generally conceive of our model as describing phytoplankton competing for a variable resource, its basic structure, including the alternation of discrete environmental states, may be applicable to other biological systems. For example, Hamelin et al. (2011) used an analogously structured model to explore the evolutionary divergence of plant parasite traits, leading to the coexistence of species that differed in their over-winter mortality and infectivity rates. Other extensions include considering competition between species with different evolution rates or levels of plasticity (values of  $\sigma$ ), which can arise due to fundamental differences in biology, genetics, and reproductive system. Different rates of adaptation control the sensitivity and response of organisms to environmental fluctuations, and may incur different costs. These factors could generate additional, interesting behaviors in our model (Sniegowski et al., 1997; de Visser, 2002). We primarily considered the mechanism driving trait change in this work to be evolution (or community assembly). However, physiological plasticity or behavior are both plausible factors endowing individuals and species with the ability to change their trait strategies in response to their environment. Indeed either of these expand the capacity of species to respond to selective pressures more rapidly than population dynamics might respond. These phenomenon, and their interplay, may have the potential to modify ecological dynamics and coexistence mechanisms (for example, see Cortez, 2010).

Temporal variation abounds in nature. Using a well-established model of competition in a variable environment, we have shown that evolution can modify species coexistence, with important roles for fluctuation regime, tradeoffs between traits, and evolutionary rates. Other coexistence mechanisms should be similarly evaluated from an evolutionary perspective. Such investigations can improve our understanding of the role of evolution in driving diversity patterns in community ecology.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.jtbi.2013.05.005>.

## References

- Abrams, P.A., 1984. Variability in resource consumption rates and the coexistence of competing species. *Theor. Popul. Biol.* 25, 106–124.

- Abrams, P.A., 1987. Alternative models of character displacement and niche shift. 2. Displacement when there is competition for a single resource. *Am. Nat.* 130, 271–282.
- Abrams, P.A., 2001. Modelling the adaptive dynamics of traits involved in inter- and intraspecific interactions: An assessment of three methods. *Ecol. Lett.* 4 (2), 166–175.
- Abrams, P.A., 2004. When does periodic variation in resource growth allow robust coexistence of competing consumer species? *Ecology* 85 (2), 372–382.
- Abrams, P.A., 2005. 'Adaptive Dynamics' vs. 'adaptive dynamics'. *J. Evol. Biol.* 18 (5), 1162–1165, <http://dx.doi.org/10.1111/j.1420-9101.2004.00843.x>.
- Abrams, P.A., 2006. The prerequisites for and likelihood of generalist-specialist coexistence. *Am. Nat.* 167 (3), 329–342, <http://dx.doi.org/10.1086/499382>.
- Abrams, P.A., Harada, Y., Matsuda, H., 1993. On the relationship between quantitative genetic and ESS models. *Evolution* 47 (3), 982–985.
- Abrams, P.A., Tucker, C.M., Gilbert, B., 2012. Evolution of the storage effect. *Evolution* 67 (2), 315–327.
- Agrawal, A.A., 2001. Phenotypic plasticity in the interactions and evolution of species. *Science* 294 (5541), 321–326, <http://dx.doi.org/10.1126/science.1060701>.
- Amarasekare, P., 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecol. Lett.* 6 (12), 1109–1122.
- Andersen, J.M., Beisner, B.E., 2000. Fluctuating environments and phytoplankton community structure: a stochastic model. *Am. Nat.* 155 (4), 556–569, <http://dx.doi.org/10.1086/303336>.
- Armstrong, R.A., McGehee, R., 1976. Coexistence of two competitors on one resource. *J. Theor. Biol.* 56 (2), 499–502.
- Armstrong, R.A., McGehee, R., 1980. Competitive exclusion. *Am. Nat.* 115 (2), 151–170.
- Berkley, H.A., Kendall, B.E., Mitarai, S., Siegel, D.A., 2010. Turbulent dispersal promotes species coexistence. *Ecol. Lett.* 13 (3), 360–371, <http://dx.doi.org/10.1111/j.1461-0248.2009.01427.x>.
- Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C., Vasseur, D.A., 2011. Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* 26 (4), 183–192, <http://dx.doi.org/10.1016/j.tree.2011.01.009>.
- Carroll, S.P., Hendry, A.P., Reznick, D.N., Fox, C.W., 2007. Evolution on ecological time-scales. *Func. Ecol.* 21 (3), 387–393, <http://dx.doi.org/10.1111/j.1365-2435.2007.01289.x>.
- Charlesworth, B., 1990. Optimization models, quantitative genetics, and mutation. *Evolution* 44 (3), 520–538.
- Chesson, P.L., Warner, R.R., 1981. Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.* 117 (6), 923–943.
- Chesson, P.L., 1994. Multispecies competition in variable environments. *Theor. Popul. Biol.* 45 (3), 227–276.
- Cortez, M.H., 2010. Comparing the qualitatively different effects rapidly evolving and rapidly induced defences have on predator–prey interactions. *Ecol. Lett.* 14 (2), 202–209, <http://dx.doi.org/10.1111/j.1461-0248.2010.01572.x>.
- de Visser, J.A.G.M., 2002. The fate of microbial mutators. *Microbiology* 148 (5), 1247–1252.
- Dieckmann, U., Law, R., 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.* 34 (5–6), 579–612.
- Edwards, K.F., Stachowicz, J.J., 2010. Multivariate trade-offs, succession, and phenological differentiation in a guild of colonial invertebrates. *Ecology* 91 (11), 3146–3152.
- Egas, M., Dieckmann, U., Sabelis, M.W., 2004. Evolution restricts the coexistence of specialists and generalists: the role of trade-off structure. *Am. Nat.* 163 (4), 518–531, <http://dx.doi.org/10.1086/382599>.
- Ellner, S.P., Geber, M.A., Hairston Jr., N.G., 2011. Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. *Ecol. Lett.* 14 (6), 603–614, <http://dx.doi.org/10.1111/j.1461-0248.2011.01616.x>.
- Floder, S., Urabe, J., Kawabata, Z., 2002. The influence of fluctuating light intensities on species composition and diversity of natural phytoplankton communities. *Oecologia* 133 (3), 395–401, <http://dx.doi.org/10.1007/s00442-002-1048-8>.
- Fussmann, G.F., Loreau, M., Abrams, P.A., 2007. Eco-evolutionary dynamics of communities and ecosystems. *Funct. Ecol.* 21 (3), 465–477, <http://dx.doi.org/10.1111/j.1365-2435.2007.01275.x>.
- Gaedeke, A., Sommer, U., 1986. The influence of the frequency of periodic disturbances on the maintenance of phytoplankton diversity. *Oecologia* 71 (1), 25–28, <http://dx.doi.org/10.1007/BF00377315>.
- Geritz, S.A.H., Kisdi, É., Meszéna, G., Metz, J.A.J., 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* 12 (1), 35–57.
- Geritz, S.A.H., Kisdi, É., Meszéna, G., Metz, J.A.J., 2004. Adaptive dynamics of speciation: ecological underpinnings. In: Dieckmann, U., Doebeli, M., Metz, J.A.J., Tautz, D. (Eds.), *Adapt. Spec.*. Cambridge University Press, New York, NY, pp. 54–75.
- Gross, Kevin, 2008. Positive interactions among competitors can produce species-rich communities. *Ecol. Lett.* 11 (9), 929–936, <http://dx.doi.org/10.1111/j.1461-0248.2008.01204.x>.
- Grover, James P., 1990. Resource competition in a variable environment: phytoplankton growing according to Monod's model. *Am. Nat.* 136 (6), 771–789.
- Grover, James P., 1991. Resource competition in a variable environment: phytoplankton growing according to the variable-internal-stores model. *Am. Nat.* 138 (4), 811–835.
- Hairston Jr., N.G., Ellner, S.P., Geber, M.A., Yoshida, T., Fox, J.A., 2005. Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.* 8 (10), 1114–1127.
- Hamelin, F.M., Castel, M., Poggi, S., Andrivon, D., Maillet, L., 2011. Seasonality and the evolutionary divergence of plant parasites. *Ecology* 92 (12), 2159–2166.
- Hardin, G., 1960. The competitive exclusion principle. *Science* 131 (3409), 1292–1297, <http://dx.doi.org/10.1126/science.132.3419.96-a>.
- Holt, R.D., 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Popul. Biol.* 12 (2), 197–229.
- Holt, R.D., Lawton, J.H., 1994. The ecological consequences of shared natural enemies. *Annu. Rev. Ecol. Syst.* 25, 495–520.
- Hsu, S.B., 1980. A competition model for a seasonally fluctuating nutrient. *J. Math. Biol.* 9 (2), 115–132.
- Huisman, J., Weissing, F.J., 1999. Biodiversity of plankton by species oscillations and chaos. *Nature* 402 (6760), 407–410, <http://dx.doi.org/10.1038/46540>.
- Hutchinson, G.E., 1961. The paradox of the plankton. *Am. Nat.* 95, 137–145.
- Iwasa, Y., Pomiankowski, A., Nee, S., 1991. The evolution of costly mate preferences II. The 'handicap' principle. *Evolution* 45 (6), 1431–1442.
- Jiang, L., Morin, P.J., 2007. Temperature fluctuation facilitates coexistence of competing species in experimental microbial communities. *J. Anim. Ecol.* 76 (4), 660–668, <http://dx.doi.org/10.1111/j.1365-2656.2007.01252.x>.
- Klausmeier, C.A., 2010. Successional state dynamics: a novel approach to modeling nonequilibrium foodweb dynamics. *J. Theor. Biol.* 262 (4), 584–595, <http://dx.doi.org/10.1016/j.jtbi.2009.10.018>.
- Lande, R., 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30 (2), 314–334.
- Lankau, R., 2010. Rapid evolution and mechanisms of species coexistence. *Ann. Rev. Ecol. Syst.* 42 (1), 335–354, <http://dx.doi.org/10.1146/annurev-ecolsys-102710-145100>.
- Lee, C.T., Inouye, B.D., 2010. Mutualism between consumers and their shared resource can promote competitive coexistence. *Am. Nat.* 175 (3), 277–288, <http://dx.doi.org/10.1086/650370>.
- Levins, R., 1968. *Evolution in Changing Environments*. Princeton University Press, Princeton, NJ.
- Levins, R., 1979. Coexistence in a variable environment. *Am. Nat.* 114 (6), 765–783.
- Litchman, E., 1998. Population and community responses of phytoplankton to fluctuating light. *Oecologia* 117 (1), 247–257.
- Litchman, E., 2003. Competition and coexistence of phytoplankton under fluctuating light: experiments with two cyanobacteria. *Aquat. Microb. Ecol.* 31 (3), 241–248.
- Litchman, E., Klausmeier, C.A., 2001. Competition of phytoplankton under fluctuating light. *Am. Nat.* 157 (2), 170–187.
- McGill, B.J., Brown, J.S., 2007. Evolutionary game theory and adaptive dynamics of continuous traits. *Ann. Rev. Ecol. Syst.* 38 (1), 403–435, <http://dx.doi.org/10.1146/annurev.ecolsys.36.091704.175517>.
- Metz, J.A.J., Nisbet, R.M., Geritz, S.A.H., 1992. How should we define 'fitness' for general ecological scenarios? *Trends Ecol. Evol.* 7 (6), 198–202.
- Miner, B.G., Sultan, S.E., Morgan, S.G., Padilla, D.K., Relyea, R.A., 2005. Ecological consequences of phenotypic plasticity. *Trends Ecol. Evol.* 20 (12), 685–692.
- Mougi, A., 2012. Predator–prey coevolution driven by size selective predation can cause anti-synchronized and cryptic population dynamics. *Theor. Popul. Biol.* 81 (2), 113–118, <http://dx.doi.org/10.1016/j.tpb.2011.12.005>.
- Pelletier, F., Garant, D., Hendry, A.P., 2009. Eco-evolutionary dynamics. *Philos. Trans. Roy. Soc. B: Biol. Sci.* 364, 1483–1489.
- Post, D.M., Palkovacs, E.P., 2009. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philos. Trans. Roy. Soc. B: Biol. Sci.* 364, 1629–1640, <http://dx.doi.org/10.1098/rstb.2009.0012>.
- Reynolds, C., 2006. *The Ecology of Phytoplankton*. Cambridge University Press, New York, NY.
- Shoresh, N., Hegreness, M., Kishony, R., 2008. Evolution exacerbates the paradox of the plankton. *Proc. Natl. Acad. Sci.* 105 (34), 12365–12369, <http://dx.doi.org/10.1073/pnas.0803032105>.
- Shurin, J.B., Winder, M., Adrian, R., Keller, W.B., Matthews, B., Paterson, A.M., Paterson, M.J., Pinel-Alloul, B., Rusak, J.A., Yan, N.D., 2010. Environmental stability and lake zooplankton diversity – contrasting effects of chemical and thermal variability. *Ecol. Lett.* 13 (4), 453–463, <http://dx.doi.org/10.1111/j.1461-0248.2009.01438.x>.
- Smith, H.L., 1981. Competitive coexistence in an oscillating chemostat. *SIAM. J. Appl. Math.* 40 (3), 498–522.
- Snieszko, P.D., Gerrish, P.J., Lenski, R.E., 1997. Evolution of high mutation rates in experimental populations of *E. coli*. *Nature* 387 (6634), 703–705, <http://dx.doi.org/10.1038/42701>.
- Snyder, R.E., Adler, P.B., 2011. Coexistence and coevolution in fluctuating environments: can the storage effect evolve? *Am. Nat.* 178 (4), E76–E84, <http://dx.doi.org/10.1086/661905>.
- Sommer, U., 1984. The paradox of the plankton: fluctuations of phosphorus availability maintain diversity of phytoplankton in flow-through cultures. *Limnol. Oceanogr.* 29 (3), 633–636.
- Sommer, U., 1985. Comparison between steady state and non-steady state competition: experiments with natural phytoplankton. *Limnol. Oceanogr.* 30 (2), 335–346.
- Stomp, M., van Dijk, M.A., van Overzee, H.M.J., Wortel, M.T., Sigon, C.A.M., Egas, M., Hoogveld, H., Gons, H.J., Huisman, J., 2008. The timescale of phenotypic plasticity and its impact on competition in fluctuating environments. *Am. Nat.* 172 (5), E169–E185, <http://dx.doi.org/10.1086/591680>.

- Tachikawa, M., 2008. Fluctuation induces evolutionary branching in a mathematical model of ecosystems. *PLoS One* 3 (12), e3925, <http://dx.doi.org/10.1371/journal.pone.0003925>.
- Taper, M.L., Case, T.J., 1992. Models of character displacement and the theoretical robustness of taxon cycles. *Evolution* 46 (2), 317–333.
- terHorst, C.P., Miller, T.E., Powell, E., 2010. When can competition for resources lead to ecological equivalence? *Evol. Ecol. Res.* 12 (7), 843–854.
- Tilman, D., 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.
- Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75 (1), 2–16.
- vanDonk, E., 1997. Defenses in phytoplankton against grazing induced by nutrient limitation, UV-B stress and infochemicals. *Aquat. Ecol.* 31 (1), 53–58.
- Vasseur, D.A., Fox, J.W., 2011. Adaptive dynamics of competition for nutritionally complementary resources: character convergence, displacement, and parallelism. *Am. Nat.* 178 (4), 501–514, <http://dx.doi.org/10.1086/661896>.
- Yamauchi, A., Yamamura, N., 2005. Effects of defense evolution and diet choice on population dynamics in a one-predator-two-prey system. *Ecology* 86 (9), 2513–2542.
- Xiao, X., and G.F. Fussmann. 2013. Armstrong-McGehee mechanism revisited: competitive exclusion and coexistence of nonlinear consumers. *J. Theor. Biol.* (special issue).
- Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F., Hairston, N.G., 2003. Rapid evolution drives ecological dynamics in a predator–prey system. *Nature* 424 (6946), 303–306.