COEXISTENCE IN TEMPORALLY VARIABLE ENVIRONMENTS: ECO-EVOLUTIONARY PERSPECTIVES

By

Colin T. Kremer

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ABSTRACT

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Ecological systems are rarely constant through time. The abundances of predators & prey and competitors & mutualists fluctuate, driven by biotic interactions and underlying variation in precipitation, nutrients, and temperature. This reality challenges our ability to study ecology and disentangle its underlying mechanisms, both empirically and theoretically. Temporal variation is more than just a nuisance: it contributes to creating and maintaining the diversity of ecological communities, as changing environmental conditions favor different species at different times. Tradeoffs limit the ability of individual species to perform optimally in every situation; as a consequence, times that are the best for some species are likely to be the worst for others. Temporal variation can also drive evolution by imposing selective pressures on the traits that allow species to succeed under particular conditions. Together, the interaction of ecological and evolutionary processes influences how many species can coexist and their identity and traits. To better understand the diversity, composition, and function of communities, I adopt a synthetic, eco-evolutionary approach to studying coexistence in temporally variable environments. I seek to understand how evolution modifies the functioning of ecological communities and under what conditions this is possible. My work includes both theoretical investigations, applying mathematical tools and approximations to the dissection, analysis, and interpretation of models, and efforts to create models that generate testable predictions.

For my parents.

ACKNOWLEDGEMENTS

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INTRODUCTION

> *"It was the best of times, it was the worst of times, it was the age of wisdom, it was the age of foolishness, […] it was the season of Light, it was the season of Darkness, it was the spring of hope, it was the winter of despair […]"*
>
> Charles Dickens, A Tale of Two Cities

Ecological systems are rarely constant through time. The abundances of predators & prey and competitors & mutualists fluctuate, driven by biotic interactions and underlying variation in precipitation, nutrients, and temperature. This reality challenges our ability to study ecology and disentangle its underlying mechanisms, both empirically and theoretically. Temporal variation is more than just a nuisance: it contributes to creating and maintaining the diversity of ecological communities, as changing environmental conditions favor different species at different times. Tradeoffs limit the ability of individual species to perform optimally in every situation; as a consequence, times that are the best for some species are likely to be the worst for others. Temporal variation can also drive evolution by imposing selective pressures on the traits that allow species to succeed under particular conditions. Together, the interaction of ecological and evolutionary processes influences not only how many species can coexist, but also their identity and traits. To better understand the diversity, composition, and function of communities, we must adopt a synthetic, eco-evolutionary approach to the study of temporally variable environments.

My dissertation focuses on exploring coexistence mechanisms that depend on temporal variation from a perspective that integrates ecology and evolution. I seek to understand how evolution modifies the functioning of ecological communities and under what conditions this is possible. My work includes both theoretical investigations, applying mathematical tools and approximations to the dissection, analysis, and interpretation of models, and efforts to create models that turn theoretical ideas to the task of generating testable predictions. Biologically, my research is motivated by studying the ecology of phytoplankton. For the empirically motivated theoretician, they are ideal organisms: their rapid generation times, predominantly asexual reproduction, quantifiable mechanistic traits and size make them comparatively simple to model, assay, and manipulate in laboratory experiments. They are also considerably important within ecosystems, including both lakes and oceans, where they overwhelmingly comprise the foundation of food webs and are intimately involved in nutrient cycling. However, many of the theoretical results that I present can readily be applied or generalized to other organisms and systems.

In Chapter 2, I investigate a coexistence mechanism that depends on fluctuating resource availability (Kremer & Klausmeier 2013). Fluctuating resources can support coexistence when there is a trade-off between how quickly a species can grow (when nutrients are plentiful) and how good of a nutrient competitor it is (when nutrients are scarce). This mechanism is well studied from an ecological perspective but virtually unexplored in an evolutionary context, prompting my research. In particular, I ask whether evolution permits species with distinct competitive strategies to arise and persist. I show that the properties of resource fluctuations (duration and period) play an essential role in determining when and how coexisting pairs of species occur. Increasingly extreme tradeoffs between growth rate and competitive ability widen the range of fluctuations permitting coexistence. Finally, I show that the time scale of evolution (trait change) governs whether coexistence is possible: rapid evolution allows species to respond quickly to changing resource conditions, preventing coexistence.

Temperature is an important regulating factor in many ecosystems. Chapter 3, explores how marine phytoplankton adapt to ocean temperature variation over space and time. This work represents the combined efforts of myself and Mridul K. Thomas, resulting in a jointly first-authored publication (Thomas et al. 2012). This synergistic project combines data gleaned from the literature (by MKT) and theoretical models (developed by CTK) to elucidate patterns of adaptation to ocean temperatures across a diverse set of species. Together, we show that the optimum temperatures of phytoplankton are strongly related to mean annual temperatures. An eco-evolutionary model that I developed, driven by realistic temperature fluctuations and physiology, largely recapitulates this relationship. This represents one of the first applications of eco-evolutionary models to the task of predicting trait distributions across environmental gradients; connecting these predictions to empirical data is even less common. Finally, looking into the future, we explored how phytoplankton communities adapted to contemporary ocean environments may be affected by continued global warming. The fundamental range of most species will shift towards the poles, prompting declines in diversity in the tropics. Addressing these and related questions is central to understanding the future of global biogeochemical cycles and marine food webs reliant on phytoplankton producers.

In my last Chapter (4), I explore how complex patterns of coexistence and community structure emerge from simple models of species competition in periodically varying environments. This represents a generalization of the more targeted eco-evolutionary model employed in Chapter 3. In this model periodic variation in an environmental factor, such as temperature, determines the growth rates of species, each of which specializes on a particular temperature but is identical in all other respects. Given competition between species with different temperature preferences and various kinds of temperature fluctuations, I seek to determine the diversity and composition of communities of coexisting species that are evolutionarily stable (ESS). Unsurprisingly, I find that weak fluctuations support little or no diversity. As the amplitude of fluctuations increases, however, the diversity of evolutionarily stable communities rises. Unexpectedly, I discovered that alternate, stable ESS communities are both possible and common across many fluctuations. This challenges our ability to predict unique trait distributions across habitats. I also show that temporal variation cannot support unlimited levels of diversity under most situations; extreme fluctuations present too harsh of an environment for diverse sets of species to persist. Finally, I demonstrate that the choice of a particular periodic function describing environmental variation has underappreciated effects on patterns of diversity across a range of fluctuation amplitudes.

Overall, the work I present in this dissertation is significant because: 1) it improves our knowledge of several basic theoretical models, showing how trait evolution can have dramatic effects on temporally varying ecological systems, 2) it illustrates the use of techniques that can employed in studying other models containing both temporal variation and evolution, adding to a still limited field, and 3) it applies eco-evolutionary theory to explaining and predicting empirical patterns. Collectively, these contributions advance our understanding of fundamental, general ecological mechanisms and shed light on the role of these mechanisms play in a specific system (marine phytoplankton) of considerable environmental and social importance.

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CHAPTER 2

COEXISTENCE IN A VARIABLE ENVIRONMENT: ECO-EVOLUTIONARY PERSPECTIVES

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.

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 & Lawton 1994); mutualists (Gross 2008, Lee & Inouye 2010); spatial heterogeneity (Tilman 1994, Amarasekare 2003, Edwards & Stachowicz 2010, Berkley et al. 2010); or temporal variability (Levins 1968, 1979, Armstrong & McGehee 1980, Chesson & Warner 1981, Abrams 1984, Grover 1990, Chesson 1994, Huisman & Weissing 1999, Litchman & Klausmeier 2001, Abrams 2004, 2006). The coexistence mechanism we investigate in this chapter 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 & McGehee 1976, Levins 1979, Hsu 1980, Chesson & Warner 1981, Tilman 1982, Litchman & Klausmeier 2001, Abrams 2004). At its simplest, temporal variation can be incorporated into models by imposing switching between two distinct environmental states (in our model, growing and non-growing 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 & Klausmeier 2001, Anderies & Beisner 2000, Tachikawa 2008, Xiao &

Fussmann 2013). 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 & Klausmeier 2001). Empirically, temporal variation in factors including light, phosphorus, and temperature, promotes coexistence and enhances diversity (Sommer 1984, 1985, Gaedeke & Sommer 1986, Floder et al. 2002; Litchman 1998, 2003, Jiang & 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 & 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, Shoresh et al. 2008, Lankau 2010, Bolnick et al. 2011, Snyder & 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 invasible 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 & Fox 2011). Shoresh 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 chapter, focusing on the resource competition in a variable environment.

The remainder of the chapter 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 or 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 2.1).

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

2.1. Ecological model

In this chapter, we extend an ecological model describing competition for a single, externally forced, fluctuating resource similar to one previously studied by Litchman & Klausmeier (2001) to include continuous trait variation. They parameterized the basic

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

Table 2.1. Model parameters, definitions, and default values used in the text and figures, unless otherwise specified (refer also to values in Reynolds 2006).

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 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. 2.1, A), with maximum growth rate μ_i and half-saturation constant K

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

We define instantaneous fitness g as the per capita growth rate of species *i*, which depends on both the species trait μ_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:

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

In the good season, the level of available resource R is determined by the difference between total resource level (set to R_{in}) 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 φ of the total period T. This parameter φ 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, $(1-\varphi)T$. 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 $\varphi = 0.45$, growth would be possible for only forty-five percent of each year, governed by resource availability (Fig. 2.1, B). 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).

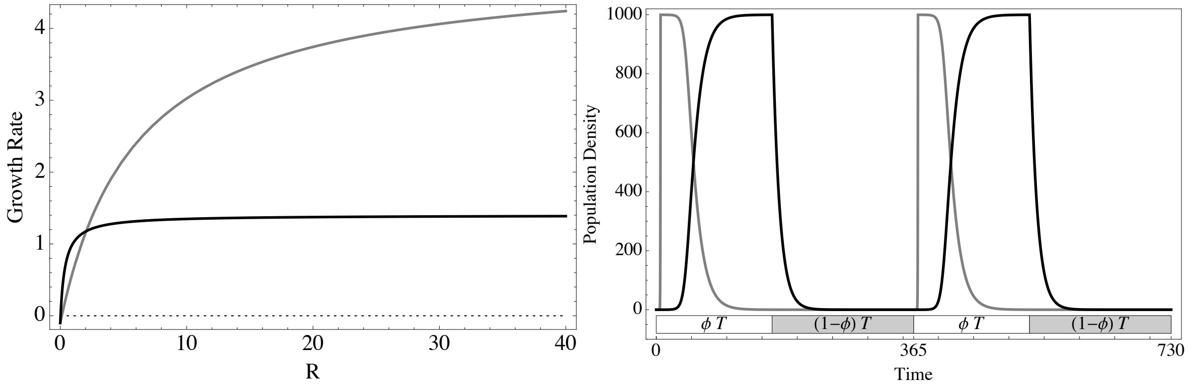

Figure 2.1 Growth curves & population dynamics. A) Growth curves for a fast growing species (gray, $\mu_1 = 4.99$, $K_1 = 5.97$) and a slow growing species with low half-saturation constant (black, $\mu_2 = 1.5$, $K_2 = 0.36$). **B)** Corresponding population dynamics illustrating the stable coexistence of species in **A**. Resource is available (absent) in the intervals shown by the white (grey) 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.

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 μ. 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 & Klausmeier 2001). We impose this tradeoff in our model by making K an increasing power function of μ:

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

To restrict analysis to biologically relevant values, we also introduce bounds on μ and K such that $\mu_{min} \leq \mu \leq \mu_{max}$ and $K_{min} \leq K(\mu) \leq K_{max}$ (Table 2.1). The strength of this tradeoff is controlled by parameter c, with $c = 1$ corresponding to a linear relationship between μ and K, while $c > 1$ results in an increasingly convex relationship (Fig. 2.2). Collectively, equations (2.1)–(2.3) completely describe the ecological dynamics of species competing for a 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

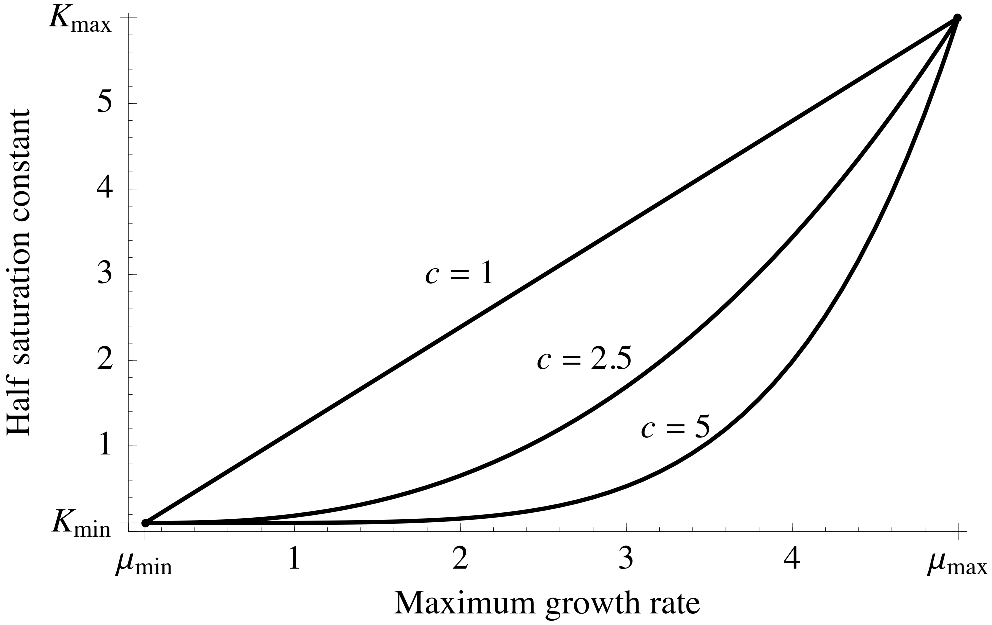

Figure 2.2 Tradeoff curve between maximum growth rate and half-saturation constant, bounded between biologically realistic values, for various values of shape parameter *c*.

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:

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

(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 μ_{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 μ_{inv} into an empty (or unoccupied) environment can be determined analytically:

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

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 φ where (2.5) changes sign for a species having the fastest permissible growth rate μ_{max},

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

This value demarcates environments too severe for even single species to exist (Litchman & 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 $|N_{res}(t) - N_{res}(t+T)| < \varepsilon$ for some small ε, 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 $\bar{g}(\mu_{inv}, \vec{\mu}_{res})$.

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 & Law 1996, Geritz et al. 1998, Geritz et al. 2004, McGill & 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. 2.3 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 μ_{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,

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

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

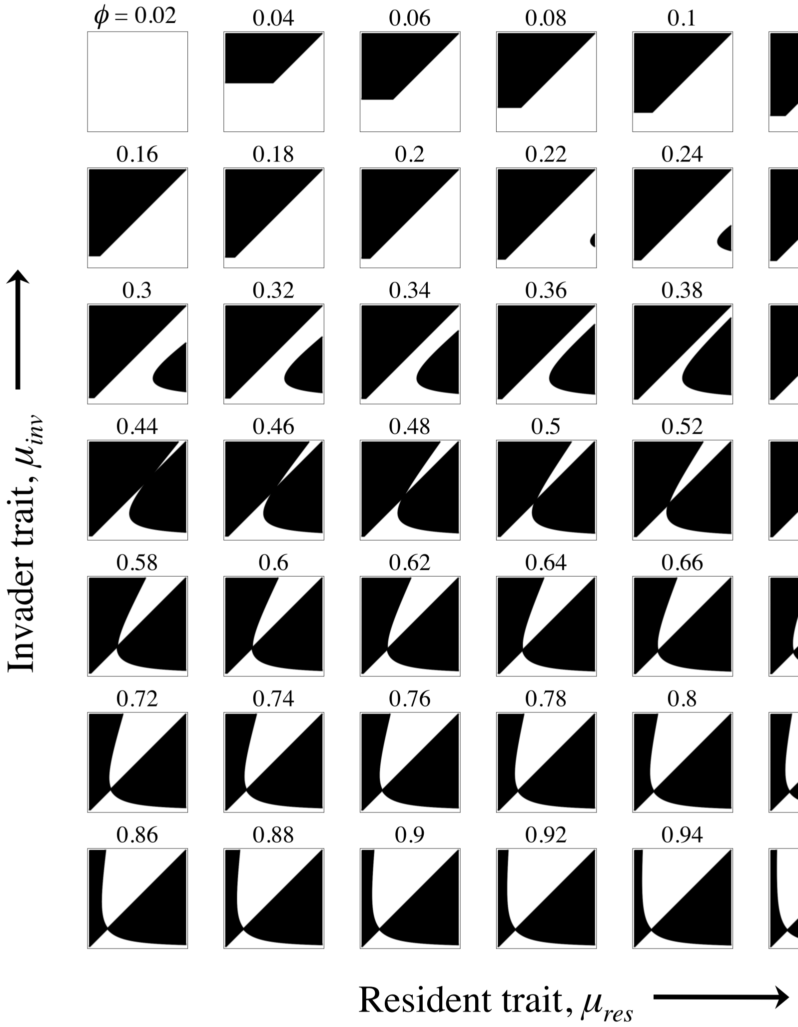

Figure 2.3 Pair-wise invasibility plots (PIPs) across a range of values of ϕ, obtained from SSD approximations. Positive (negative) invasion fitness is shown in black (white). As ϕ increases across the panels evolutionary cases change: no species persists ($\phi = 0.02$); single species global ESS at maximum trait value ($\phi = 0.04$ to 0.2); local but not global ESS ($\phi = 0.22$ to 0.4); branching point ($\phi = 0.42$ to 0.82); single species global ESS at low value of μ ($\phi = 0.84$ to 0.98).

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 μ_{inv} (excepting μ_{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 μ_{inv} sufficiently different from μ_{res} can have positive invasion fitness. Then, through immigration or mutations of large effect, the single species ESS is invasible 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 & 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 μ_{inv} is evaluated at each element of $\vec{\mu}_{res}$. The stability of the resulting singular strategy is determined as before (refer to equation 2.7) and the process repeated until a global ESS state is determined. In this way, for any environment (given φ, 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, Geritz et al. 2004).

Note that care must be taken in these calculations to maintain μ between μ_{min} and μ_{max}. The lower value of μ is effectively constrained by mortality rate m. However, in many cases, evolution would drive the maximum value of μ above μ_{max} despite the corresponding cost of high K. When this happens, we hold the species' trait at μ_{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 $T \to \infty$ 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 $T \to \infty$ 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 φ and trait bifurcation diagram

We now turn to examining how the length of the good season, governed by φ, influences species coexistence and ESS trait values. Figure 3 shows a sequence of PIPs across a range of φ values, classified according to their stability (see section 2.4 and Figs. 2.3 and 2.A.1, A). This information can be condensed into a bifurcation diagram covering a

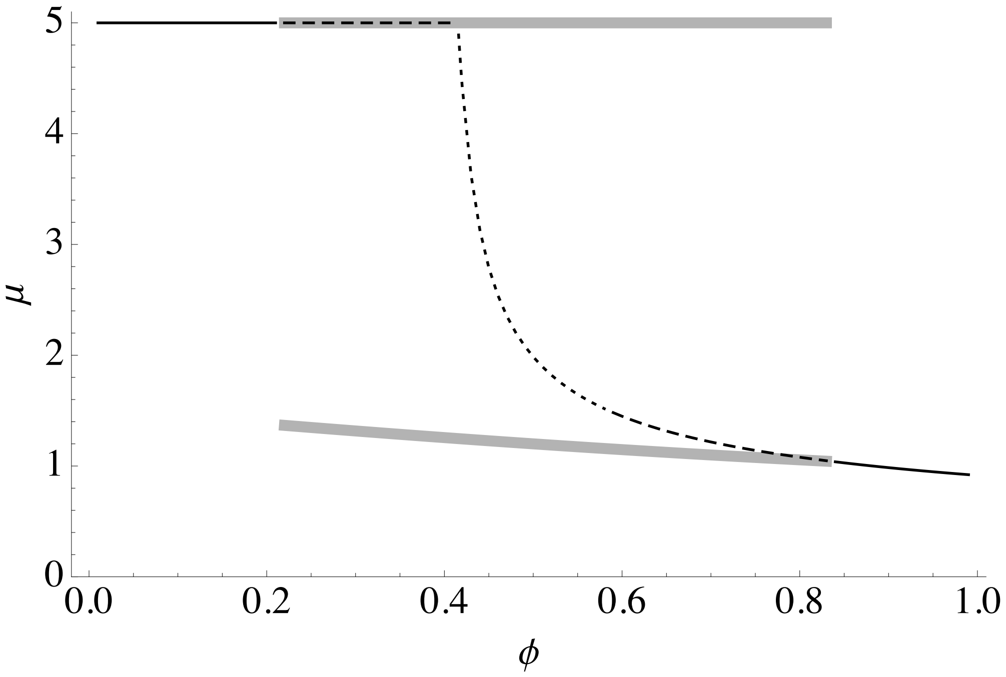

Figure 2.4 Evolutionary equilibria and their stability as a function of φ, the proportion of a period over which growth is possible. The black line follows the location of the one species singular strategy as ϕ changes. The stability of the singular strategy transitions between global ESSs (solid line), local but not global ESSs (LESSs, dashed), and branching points (dotted). Grey 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 μ_{max} = 5.

continuous range of φ values, showing simultaneously the trait values of one and two species singular strategies and categorizing the corresponding evolutionary regimes (Figs. 2.4 and 2.A.1, B). This result shows that at either low or high values of φ (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 φ, two species coexistence is possible via evolutionary branching. Flanking either side of this range of φ 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. 2.4). These results are consistent with the findings of the ecological model of (Litchman & Klausmeier

2001), with fast growing species dominating at low φ, good competitors dominating at high φ, 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 & 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 μ and half saturation constant K, the strength of which is governed by parameter c (Fig. 2.2). We examine the sensitivity of the preceding results to variation in this parameter (Fig. 2.5). When $c = 1$, the relationship between μ and K is linear, and the lowest value of R^* occurs at μ_{max} (Fig. 2.2). As such, there is no competitive advantage to having a lower maximum growth rate and coexistence does not occur for any value of φ. 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 φ, 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.

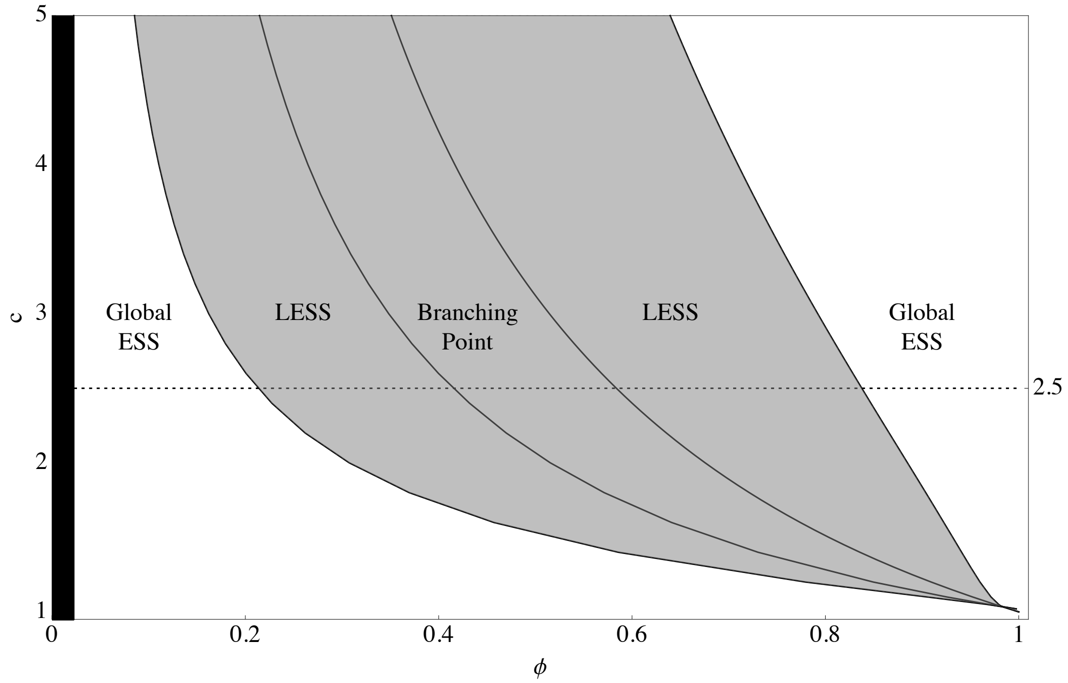

Figure 2.5 As the strength of the tradeoff between maximum growth rate and half-saturation constant (c) increases, the range of ϕ value across which two species coexistence occurs increases (shaded grey region). The black rectangle indicates the region where ϕ is so small that no allowable species persists. 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.

4. Slow evolution and coexistence under finite period fluctuations

4.1 Evolutionary coexistence, length of the good season (φ), 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 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 φ) on evolution and coexistence, assuming that $T \to \infty$. Now we relax this assumption, varying both φ and T, while addressing the same questions (Fig. 2.6). As with the SSD results, increasing φ 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.

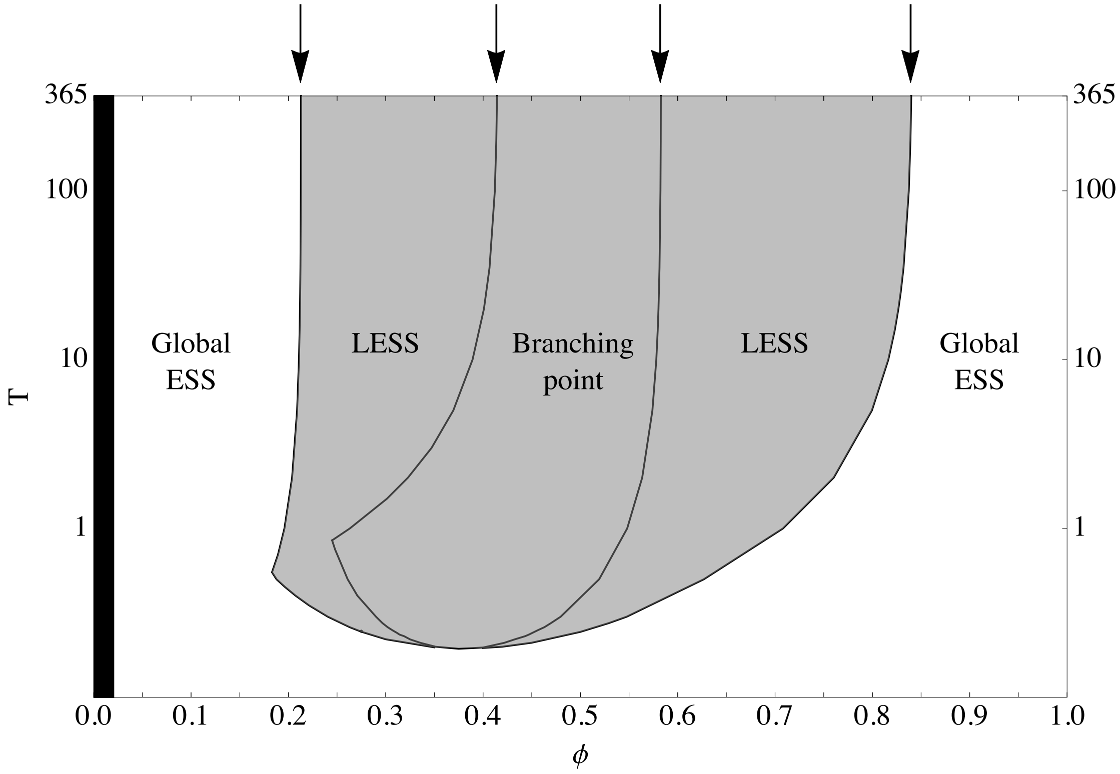

Figure 2.6 The relationship between evolutionary outcome and fluctuation regime parameters. The region of two species coexistence is shown in grey. Environments with brief resource availability ($\phi < 0.2$) are dominated by fast growing species, while good resource competitors dominate in environments with consistent resources ($\phi > 0.8$). For very short periods, no coexistence is possible, as resource fluctuations for any value of ϕ 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 ϕ indicates environments too extreme for the survival of even a single species.

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. 2.4). 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 (van Donk 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 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

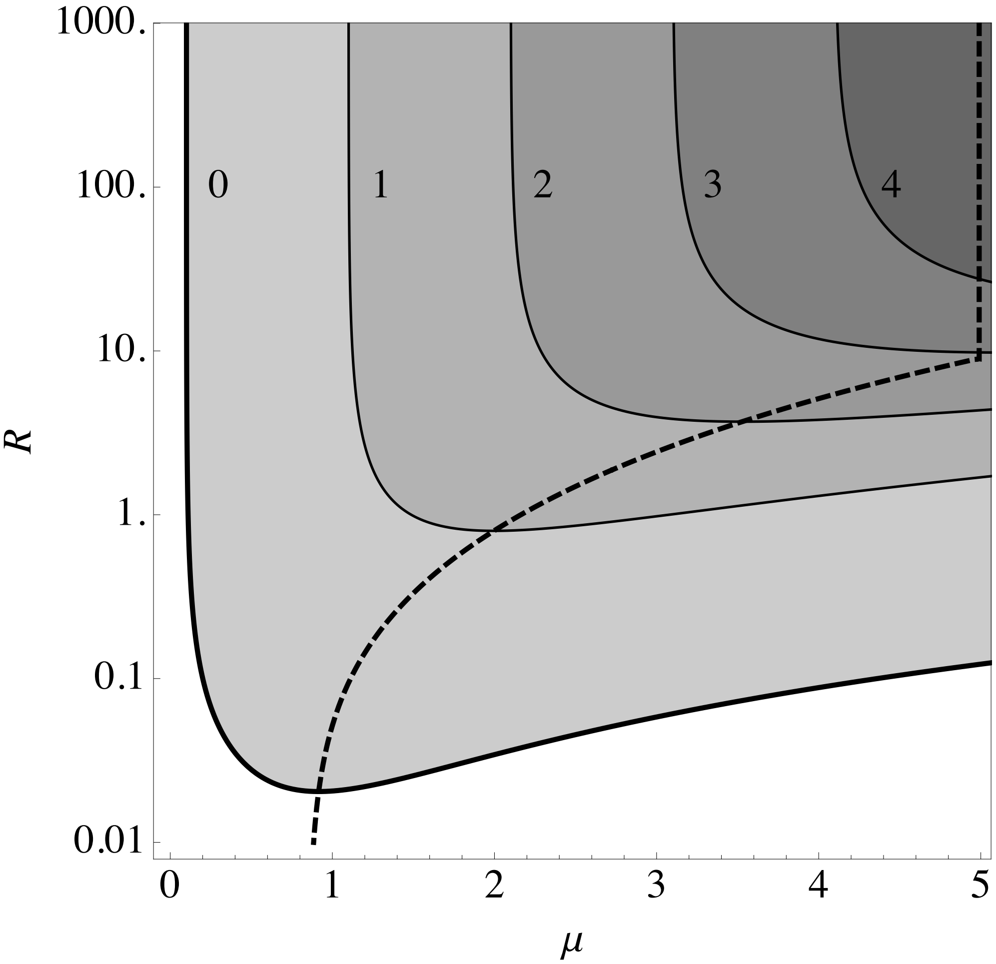

Figure 2.7 Instantaneous fitness of a single species, g(μ; *R*) from (2.1), as a function of available resource *R* and species trait μ. Fitness increases with darker shading. The dashed line traces out the trait value corresponding to the strategy maximizing *g* at each given resource level *R*. A species 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. 2.7). 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 φ, 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 & 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 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 supplement of this chapter. With respect to our model, this leads to a differential equation modeling change in species *i*'s mean trait μ_i as a function of the direction and magnitude of its instantaneous fitness gradient, the traits of any other species present $\vec{\mu} = (\mu_1, \mu_2, \ldots, \mu_n)$, and a rate parameter σ, describing phenotypic variation or mutation,

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

The sign of the fitness gradient indicates whether selection favors increased (or decreased) values of μ_i. Numerically, constraints on the range of μ_i are achieved using Heaviside step functions to prevent evolution beyond the trait values μ_{min} (if the fitness gradient is negative) or μ_{max} (if the fitness gradient is positive). The rate at which trait μ_i responds to selection depends entirely on parameter σ 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 σ.

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 re-create 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 φ, 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 equations (2.1) and (5.1). Together, these equations can describe the population and trait dynamics of one or more competing species 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. 2.8, A and B). However, this coexistence collapses when σ is high (Fig. 2.8, C and D); despite having dramatically different initial trait values, two species rapidly converge on the same trait dynamics. Essentially, σ 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. 2.7).

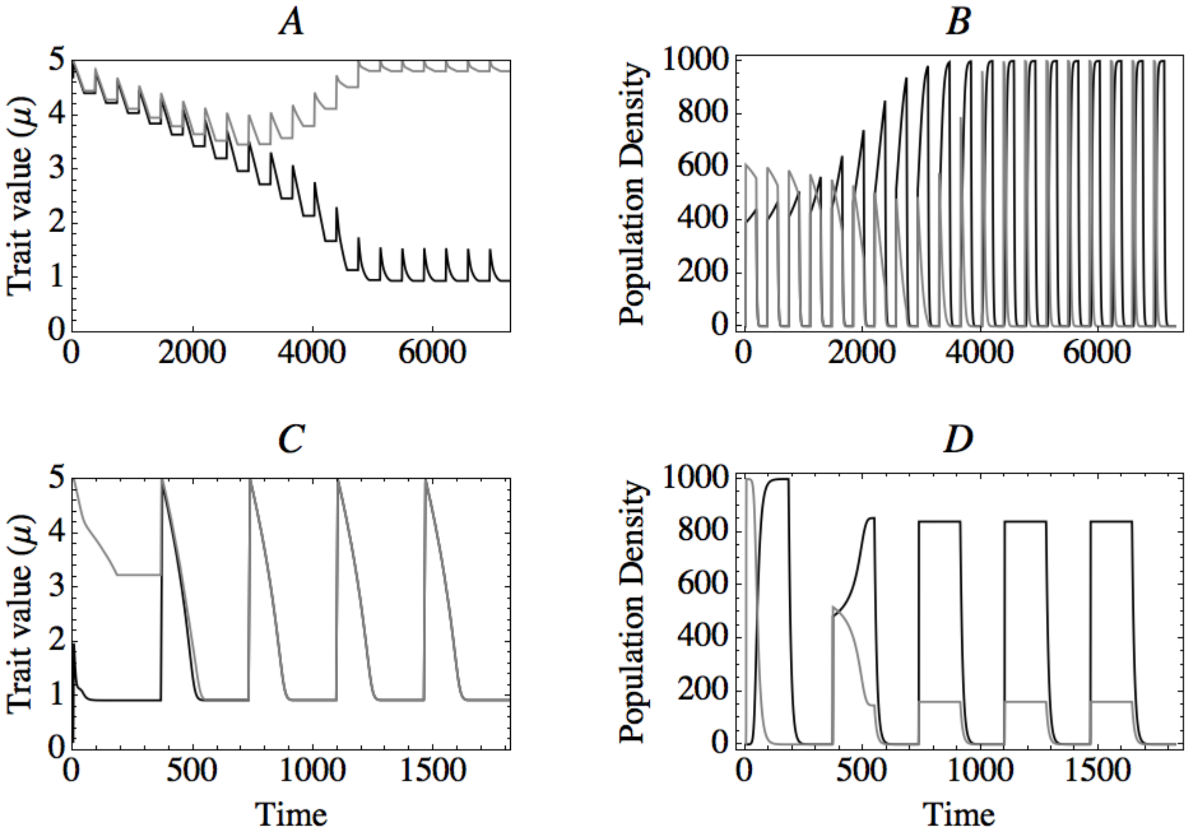

Figure 2.8 Examples of trait and population dynamics from the QG model for (***A***–***B***) low ($\sigma = 0.1$) and (***C***–***D***) high ($\sigma = 0.65$) rates of adaptation. At low adaptation rates, two species with very similar initial trait values ($\mu_1 = 4.99$ and $\mu_2 = 4.9$) diverge from 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 σ 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.

We can map out how coexistence and evolutionary regimes change with increasing σ (and across variation in φ). For non-zero values of σ, 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 $|N_i(t) - N_i(t+T)| < \varepsilon$ and $|\mu_i(t) - \mu_i(t+T)| < \varepsilon$ for small ε 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. 2.9).

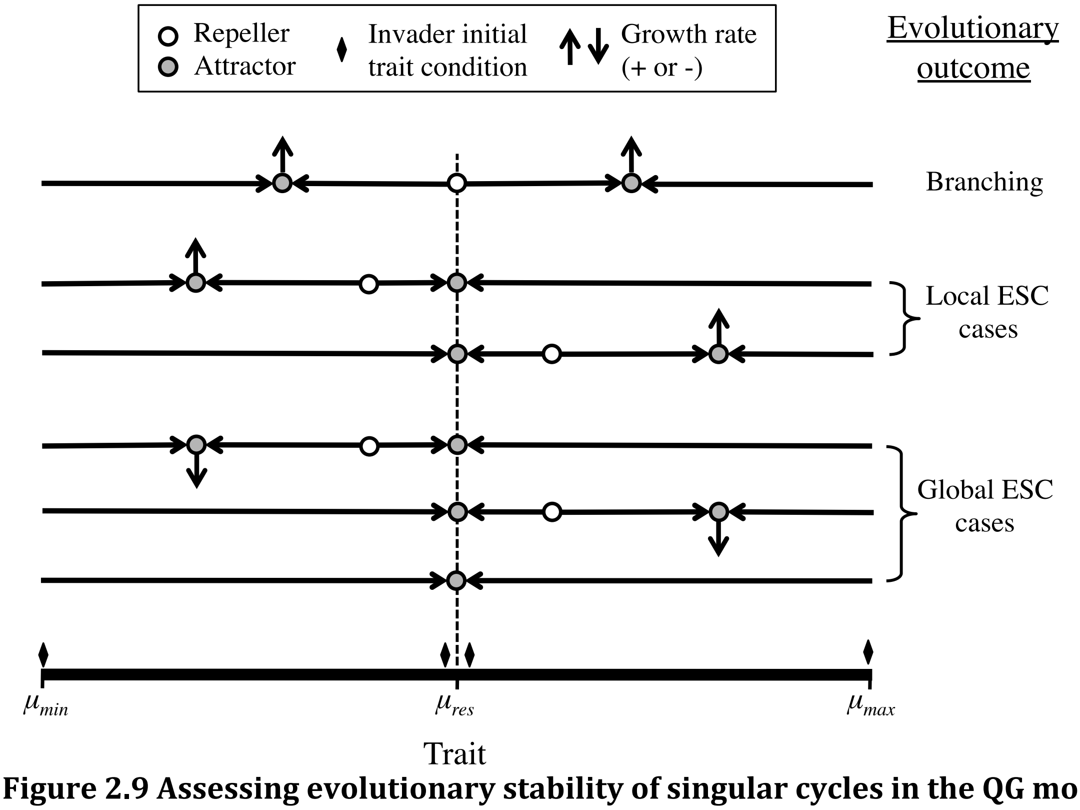

Figure 2.9 Assessing evolutionary stability of singular cycles in the QG model. Horizontal arrows indicate the net direction of change of a rare invader's trait dynamics over one cycle, given a resident singular cycle with initial trait μ_{res}. Grey nodes represent invader trait attractors, while white 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, LESCs, and branching cycles.

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 (μ_{min} and μ_{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 [μ_{min}, μ_{max}]. All of the singular cycles identified while examining this model were unique. Second, we determine the evolutionary stability of singular cycles (Fig. 2.9). 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. 2.9). GESC's arise in two ways. 1) The invader trait dynamics converge on the resident trait attractor whether its initial trait value is μ_{min} or μ_{max}. 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 μ_{min} or μ_{max}; however, the average growth rate of the invader at this new trait attractor is negative, so that the invader cannot persist. LESC's 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.

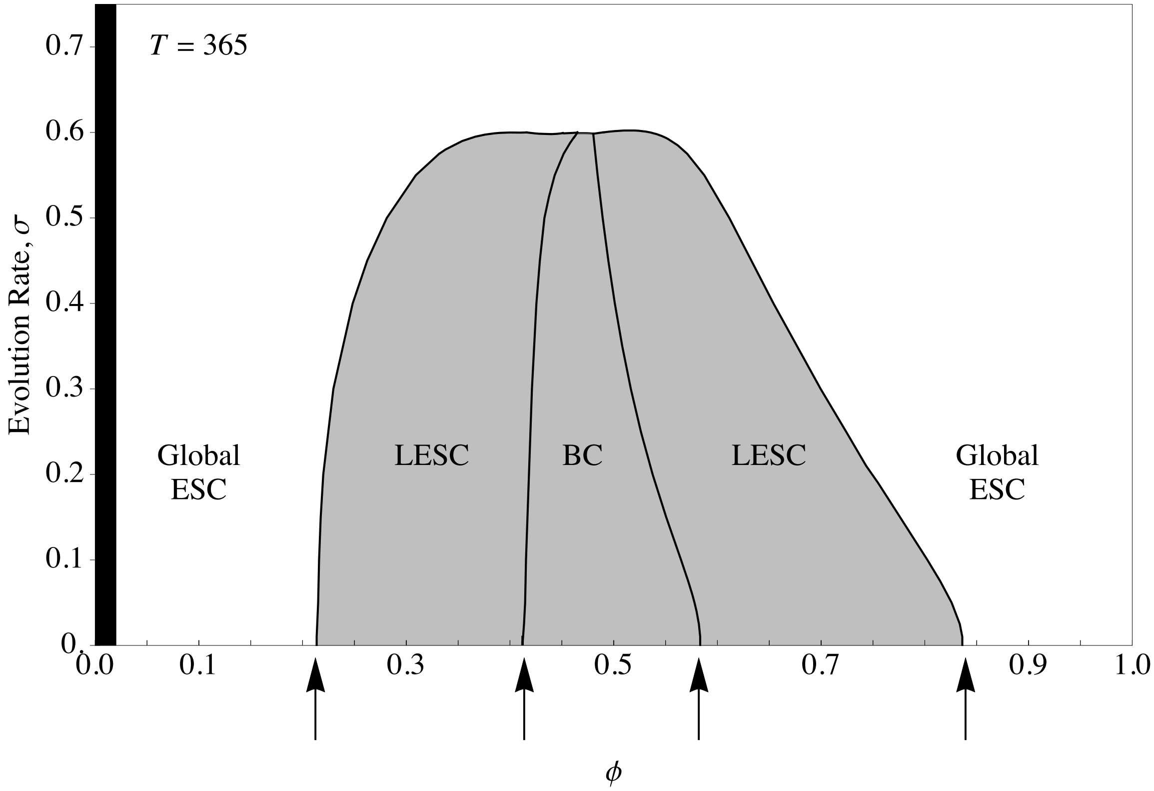

Figure 2.10 As the rate of adaptation (σ) increases, the potential for coexistence collapses (shaded area corresponds to the region of two species coexistence). At $\sigma \rightarrow 0$, the coexistence and evolutionary boundaries converge on those predicted for the same period (T = 365) by the Adaptive 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).

Using this approach, we outline the environments producing these three distinct regimes provided in Fig. 2.10 as a function of the length of the good season φ and evolution rate σ. Collectively, GESC's, LESC's, 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 σ (not shown, but see Fig. 2.A.4); 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. 2.10). As expected, however, the region of coexistence declines with increasing σ, deteriorating completely around σ = 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 (see Fig. 2.A.2). 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

Equation (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 supplement and Abrams et al. 1993). The population is assumed to exhibit Gaussian phenotypic variation governed by a constant variance parameter proportional to σ, which governs the rate of trait change in response to selection (Taper & 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 & Yamamura 2005, Mougi 2012), as we are explicitly interested in how eco-evolutionary regimes are altered by increasing σ. 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. 2.10 remain unchanged (see supplement, Fig. 2.A.2).

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. Equations (5.1), (A.1), and (A.3), all typically assume that phenotypic variation follows a normal distribution. It is 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 supplement. This approach reinforces our previous finding that two species coexistence at intermediate values of φ collapses as mutation rates, and hence evolution rates, increase (Fig. 2.A.3). 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 chapter 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 & Adler 2011, Abrams et al. 2013). 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 on this mechanism of coexistence (Litchman & Klausmeier 2001). For example, two species coexistence was only possible when resource fluctuations were not too rapid (T sufficiently large) and resource neither too briefly nor too constantly available (Fig. 2.6). The proportion of each period when resource was available (φ) had a strong effect on the occurrence of two species coexistence, but a weak effect on the specific traits comprising two species ESSs (grey lines in Fig. 2.4 are almost constant). Thus in this case evolution (or community assembly) expanded the region of coexistence relative to Litchman & Klausmeier (2001) by identifying a more broadly successful pair of gleaner and opportunist traits, as opposed to driving trait adaptation across a gradient in φ. 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. 2.6).

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. 2.6). 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. 2.6). 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. 2.5). While the coexistence of at least five species was demonstrated in (Litchman & 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 & 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 Fig. 2.7, 2.8 and 2.10). 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 (supplement, Fig. 2.A.2 and 2.A.3).

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 σ), 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 phenomena, 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.

7. Supplement A: Modeling rapid evolution

7.A.1 Derivation and application of QG model

As described by Abrams et al. (1993) and derived by Lande (1982), the rate of change of the mean phenotypic trait of a species can be modeled by the following:

$$\frac{d\mu^*}{dt} = \frac{\sigma_a}{\sigma}\int \left[(\mu-\mu^*)\, g(\mu;\mu^*)\, p(\mu)\right] du \tag{A.1}$$

Here μ^* is the mean trait value. The additive and total phenotypic variances are denoted by σ_a and σ, respectively. The distribution of phenotypic values around the mean is given by $p(\mu)$, which is typically assumed to be a normal distribution, such that:

$$p(\mu) \sim \text{Gaussian}\left(\text{mean} = \mu^*, \text{variance} = \sigma\right) \tag{A.2}$$

The integral in equation (A.1) can then be simplified using a Taylor series approximation, after Abrams et al. (1993), providing us with:

$$\begin{aligned}\int \left[(\mu-\mu^*)\, g(\mu;\mu^*)\, p(\mu)\right] du \approx\, & \sigma\left(\partial g/\partial\mu\right)\big|^* \\ & + \left(\sigma^2/2\right)\left(\partial^3 g/\partial\mu^3\right)\big|^* \\ & + \left(\sigma^3/8\right)\left(\partial^5 g/\partial\mu^5\right)\big|^* \\ & + \ldots\end{aligned} \tag{A.3}$$

where σ is the variance of the phenotypic distribution and $|^*$ indicates evaluation at $\mu = \mu^*$. When the value of σ is sufficiently small and/or the values of higher order derivatives are small (g function is not strongly nonlinear), the first term of (A.3) adequately approximates the value of the integral. As phenotypic variance increases, increasing the rate of evolution, the quality of the approximation decreases and the inclusion of higher order terms is required to maintain accuracy.

Assuming that $\sigma_a = \sigma$, equations (A.1) and (A.3) reproduce equation (5.1), depending on the number of higher order terms retained:

$$\frac{d\mu^*}{dt} = \sigma\left(\partial g/\partial\mu\right)\big|^* + \left(\sigma^2/2\right)\left(\partial^3 g/\partial\mu^3\right)\big|^* + \ldots \tag{A.4}$$

In our investigation of the evolutionary stability of coexistence as evolutionary rates increase on the timescale of ecological dynamics, we explicitly manipulate the value of σ. By increasing this value to speed up evolution, we risk invalidating the Taylor series approximation that provided (5.1). We repeated the calculations described in sections 5.3 and 5.4, and shown in figure 9, using the first two terms of equation (A.4) instead of (5.1). This second order approach yielded qualitatively similar patterns, with the region of coexistence collapsing as σ increases, although the precise value of σ at which this occurs decreases somewhat (Figs. 2.A.2 and 2.10). Additionally, the second order approach does not prevent the occurrence of unusual dynamical outcomes observed as coexistence collapses. It remains possible that even the second order approximation is insufficient for the task at hand. We deemed avoiding the approximation by implementing (A.1) in full to be too computationally intensive, and took an alternative approach to confirm our qualitative findings.

7.A.2 Alternative to QG model

Instead of modeling trait evolution by deriving explicit expressions for $d\mu/dt$, we can instead consider the dynamics of a set of populations, spaced evenly along the phenotypic axis. We treat mutation as a diffusion process between populations that are adjacent in trait space. This approach has several advantages, including avoiding the Taylor series approximation issue described in the previous section, and does not require an explicit assumption about the shape of the phenotypic distribution. The system of differential equations describing this approach is as follows:

$$\begin{aligned}
\frac{dN_1}{dt} &= g(\mu_1;R)N_1 + \frac{\sigma_m}{\delta^2}\left(-N_1 + N_2\right)\\
\frac{dN_2}{dt} &= g(\mu_2;R)N_2 + \frac{\sigma_m}{\delta^2}\left(N_1 - 2N_2 + N_3\right)\\
\ldots &= \ldots\\
\frac{dN_i}{dt} &= g(\mu_i;R)N_i + \frac{\sigma_m}{\delta^2}\left(N_{i-1} - 2N_i + N_{i+1}\right)\\
\ldots &= \ldots\\
\frac{dN_n}{dt} &= g(\mu_n;R)N_n + \frac{\sigma_m}{\delta^2}\left(N_{n-1} - N_n\right)
\end{aligned} \tag{A.5}$$

for μ_1, μ_2, …, μ_n given n number of species, and $\mu_i = \mu_{min} + (i\text{-}1)\delta$ with $\delta = (\mu_{max}\text{-}\mu_{min})/(n\text{-}1)$. In other words, δ is the distance in trait space between adjacent populations N_i. In this model, σ_m is a scaling parameter controlling the rate at which mutation moves population density between populations that are adjacent in trait space, and is qualitatively analogous to σ in our preceding analyses. As $\delta \to 0$, system A.5 could be represented as a partial differential equation, but is more computationally tractable as stated.

With this model we wish to manipulate mutation rate (σ_m) to observe its effect on the stable coexistence of species exhibiting distinct gleaner-opportunist strategies. We set up two duplicate sets of ODE's following (A.5), and denoting the populations of each set as

N and *M*. All N_i's and M_i's are linked by the consumption of the shared resource, but not capable of mutation between systems (i.e., between any N_i and M_i). We start each of the ODE sets with different initial conditions (where initial abundances of *N* and *M* are 0.1 at μ_{min} or μ_{max}, respectively, and 0 elsewhere). This is the case even if the environmental fluctuation is sufficient to support distinct gleaner and opportunist strategies. To observe whether or not these two ODE systems converge rapidly on the same trait/population distribution, indicative of selection for a single preferred strategy, or first converge on distinct distributions (despite converging in the long term), we followed their dynamics for 100 periods. We then measure the propensity of the system to have converged (characteristic of a one species solution), or remain divergent (two species solution), by calculating

$$\frac{1}{2}\sum_{i=1}^{n}\left|N_i/N_{tot}-M_i/M_{tot}\right| \tag{A.6}$$

where $N_{tot}=\sum N_i$ and $M_{tot}=\sum M_i$ are the total abundances of *N* and *M* summed across trait values. When the distributions of N and M are completely disjunct, (A.6) achieves a maximum value of 1, whereas when N and M have completely converged, (A.6) approaches 0. Figure 2.A.3 uses this metric to demonstrate the collapse of the coexistence of distinct gleaner and opportunist strategies with increasing evolution rate. While this approach gives us qualitatively similar results to Figures 2.10 and 2.A.2, σ and σ_m are not quantitatively comparable, and it is not possible to differentiate between evolutionary regimes (such as LESCs or branching cycles).

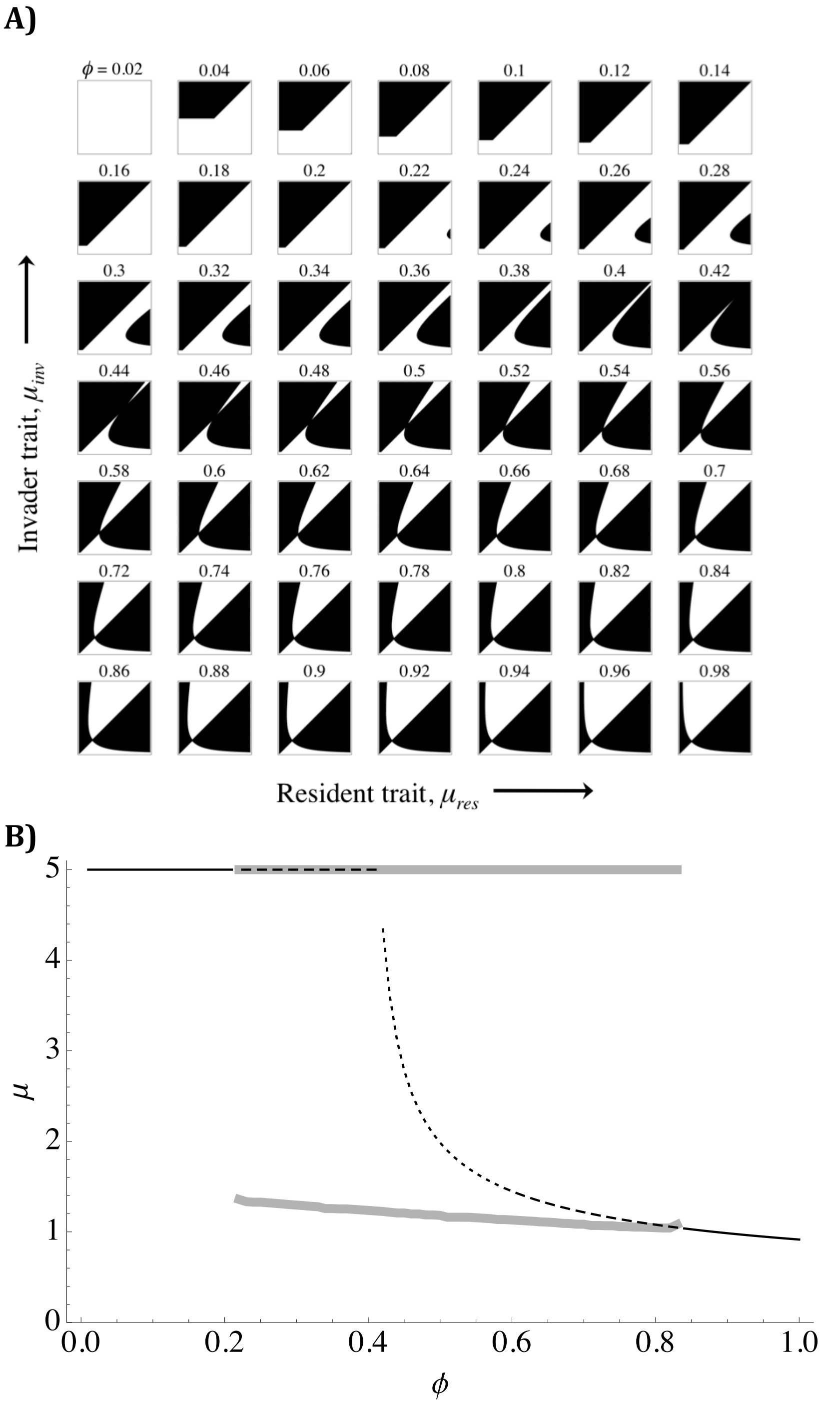

Figure 2.A.1 A) PIP array and corresponding B) bifurcation plot (see Figs. 2.3 and 2.4) for T = 365.

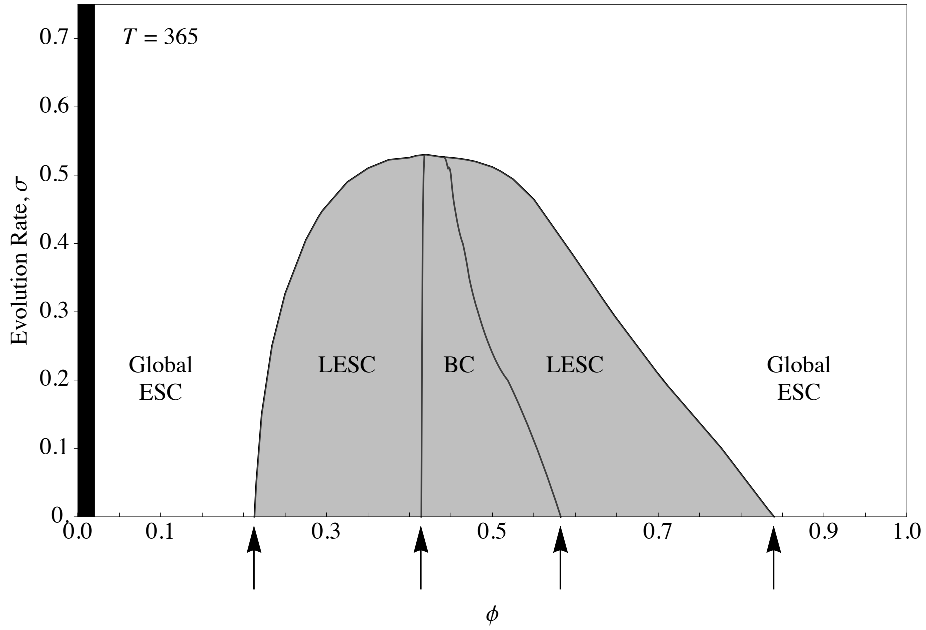

Figure 2.A.2 Comparison of evolutionary outcomes as a function of σ and ϕ, using a second order approximation, as given in equation (A.4), for comparison with Fig. 2.10.

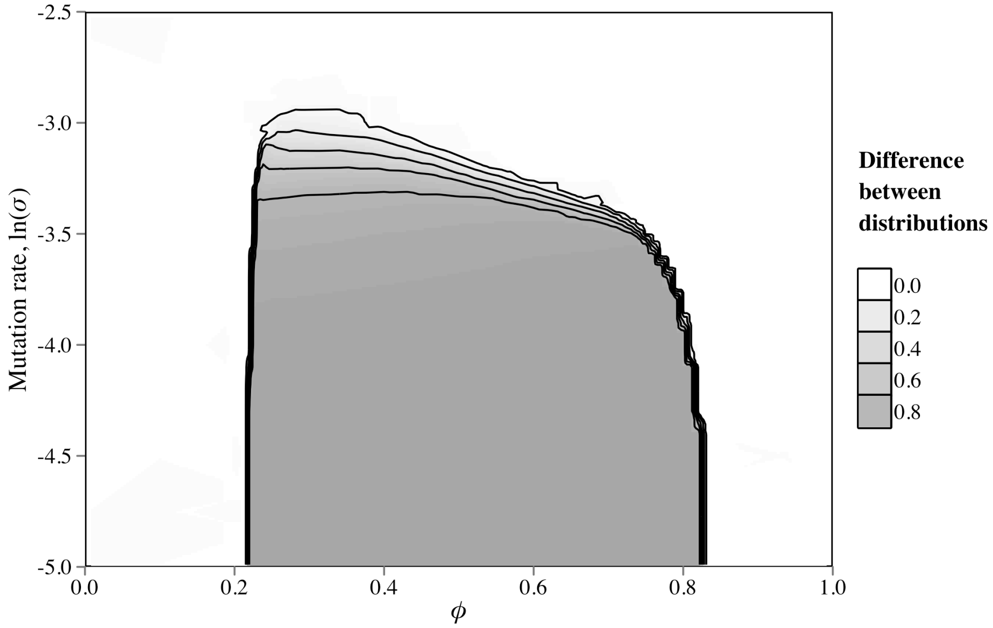

Figure 2.A.3 Demonstrating the difference between trait distributions of two guilds with opposing initial trait values after 100 periods. White areas correspond to regions where both guilds converged on the same trait distribution, while dark grey areas indicate that distinct trait distributions have been maintained despite mutation. At high mutation rates, distinct trait distributions collapse, for all values of ϕ = proportion of period that is 'good'.

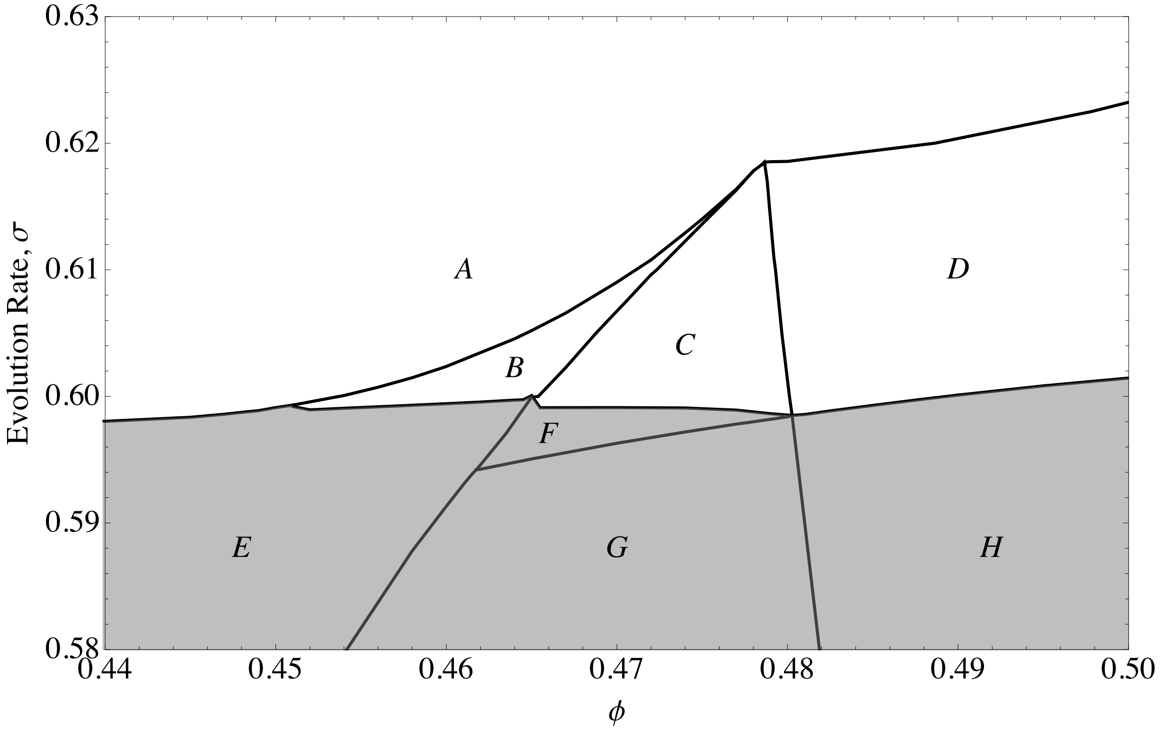

Figure 2.A.4 Close up version of Fig. 2.10, in the region where esoteric dynamics occur. A similar region exists in the second order approximation (Fig. 2.A.2). Two species results are indicated by grey shading. Additional complexity is added by the formation of local maxima in the fitness gradient at which invasion rates remain negative. These represent local attractors for the trait dynamics of potential invaders, yet do not endow them with positive growth rates, situations that we refer to as 'sea mounts'. The distinct cases we identified are labeled A-H, may not be exhaustive, and consist of the following: A) single species, global ESS, B) initial growth of non-local invader, followed by convergence on resident strategy, C) branching point leads to sea mount and the extinction of one species, D) single species, global ESS but seamount present, E) local ESS, F) branching point resulting in either a seamount (1 species) or an ESS (2 species), depending on initial invader population size, G) evolutionary branching point, H) local ESS.

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CHAPTER 3

A GLOBAL PATTERN OF THERMAL ADAPTATION IN MARINE PHYTOPLANKTON

ABSTRACT

Rising ocean temperatures will alter the productivity and composition of marine phytoplankton communities, thereby affecting global biogeochemical cycles. Predicting the effects of future ocean warming on biogeochemical cycles depends critically on understanding how existing global temperature variation affects phytoplankton. Here we show that variation in phytoplankton temperature optima over 150 degrees of latitude is well explained by a gradient in mean ocean temperature. An eco-evolutionary model predicts a similar relationship, suggesting that this pattern is the result of evolutionary adaptation. Using mechanistic species distribution models, we find that rising temperatures this century will cause poleward shifts in species' thermal niches and a sharp decline in tropical phytoplankton diversity in the absence of an evolutionary response.

1. Introduction

Marine phytoplankton are responsible for nearly half of global primary productivity (Field et al. 1998). They play essential roles in food webs and global cycles of carbon, nitrogen, phosphorus, and other elements (Redfield 1958, Falkowski et al. 1998). Empirical studies have shown that recent ocean warming has driven changes in productivity (Behrenfeld et al. 2006), population size (Boyce et al. 2010), phenology (Edwards & Richardson 2004), and community composition (Moran et al. 2010). Global ocean circulation models predict further temperature-driven reductions in phytoplankton productivity this century, with con- sequent decreases in marine carbon sequestration (Bopp et al. 2001, Steinacher et al. 2010). The main mechanism that these studies have identified is indirect: Rising temperatures drive an increase in ocean stratification, which in turn leads to a decrease in nutrient supply to surface waters. However, most models do not consider the direct effects of rising temperatures on individual phytoplankton species, which experience sharp declines in growth rate above their optimum temperatures for growth. They may, therefore, underestimate the effects of warming on ecosystems.

To understand how ocean warming will directly affect marine and estuarine phytoplankton, we examined growth responses to temperature in 194 strains belonging to more than 130 species from the major phytoplankton groups (See methods in Thomas et al. 2012). Temperature-related traits, such as the optimum temperature for growth and the thermal niche width (the temperature range over which growth rate is positive), are among the most important in ectothermic species, especially given predictions of global warming (Kingsolver 2009). We estimated these traits from >5000 growth rate measurements, synthesized from 81 papers published between 1935 and 2011. The strains were isolated from 76°N to 75°S, giving us exceptionally broad cover-age of the latitudinal and temperature gradients (Fig. S1 in Thomas et al. 2012).

Growth responses to changes in temperature are characterized by thermal tolerance curves (reaction norms). Two features of these curves are common to all ectotherms: unimodality and negative skewness (i.e., a sharper decline in fitness above the optimum temperature than below) (Fig. S2 in Thomas et al. 2012, see also Kingsolver 2009, Eppley 1972). The latter condition makes ectotherms living at their optimum temperature more sensitive to warming than cooling, with important consequences for their performance in the environment (Martin & Huey 2008). Furthermore, there is an exponential increase in the maximum growth rate attainable with increasing temperature (across species). These curves may be described using three principal traits: maximum growth rate, optimum temperature for growth, and thermal niche width. We estimated these traits for each strain by fitting a thermal tolerance function to the data (Norberg 2014) and examined their relationships with environmental and taxonomic covariates (See methods in Thomas et al. 2012).

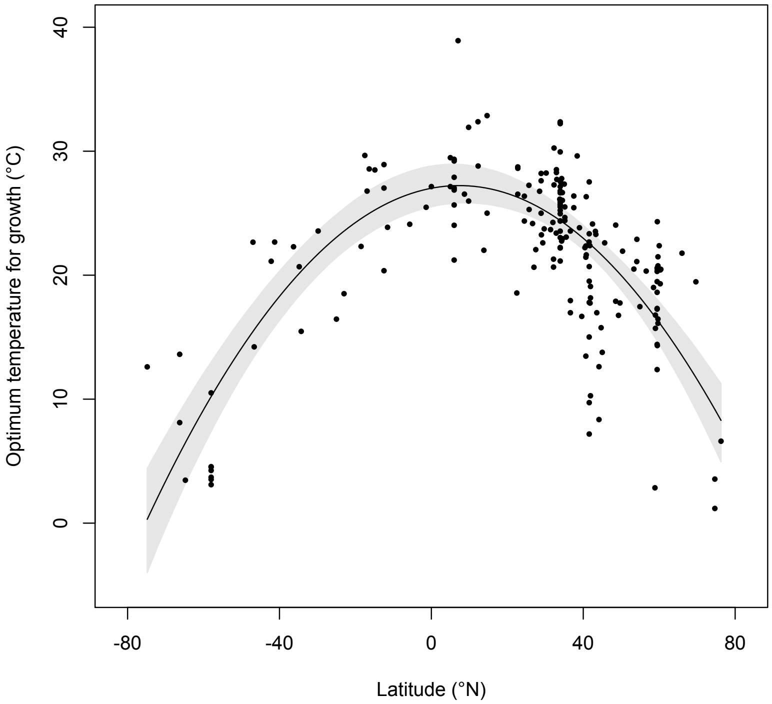


Figure 3.1 Latitudinal gradient in the optimum temperature for growth of marine and estuarine phytoplankton strains (n = 194 strains, $R^2 = 0.55$, $p < 0.0001$). Each point represents the optimum temperature for growth of a single strain, estimated by fitting a thermal tolerance function (Norberg 2004) to the data. The regression line (black) is shown, along with 95% confidence bands (gray). Confidence bands account for asymmetric uncertainty in trait estimates using a bootstrapping algorithm (See methods and Fig. S9 in Thomas et al. 2012).

2. Biogeographical patterns

Our analysis revealed large-scale patterns in thermal traits. First, strains exhibited a clear latitudinal trend in the optimum temperature for growth (Fig. 3.1, coefficient of determination, R^2, = 0.55, $p < 0.0001$), demonstrating the existence of a global pattern in a key microbial trait. Second, optimum temperature was even more strongly related to mean annual temperature at the isolation location (Fig. 3.2 A, $R^2 = 0.69$, $p < 0.0001$), suggesting that temperature is a major selective agent and that adaptation to local environmental conditions occurs in marine microbes despite the potential for long-distance dispersal through ocean currents. In contrast, the width of the thermal niche was unrelated to temperature regimes.

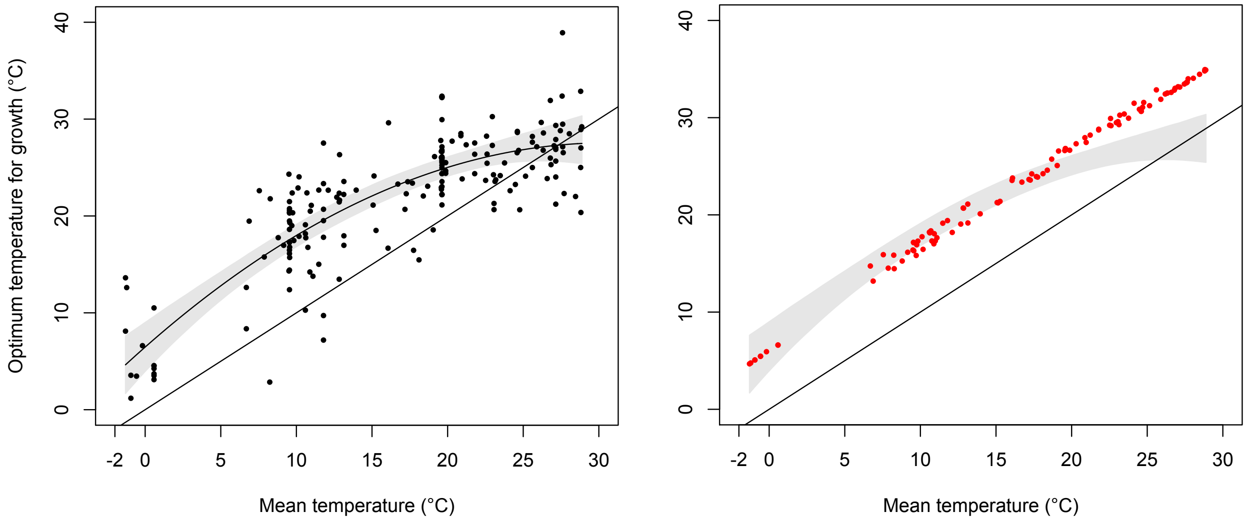


Figure 3.2 Optimum temperatures for growth across a gradient of ocean temperature. A) The optimum temperature of phytoplankton strains is well explained by variation in the mean annual temperature at their isolation locations ($n = 194$, $R^2 = 0.69$, $p < 0.0001$), indicating adaptation to local environmental conditions. The 1:1 line (black, straight), regression line (black, curved) and 95% confidence bands (gray) from bootstrapping are shown (see methods in Thomas et al. 2012). The regression line shown is for the best model (Table S4 in Thomas et al. 2012), which posits a quadratic relationship between mean temperature and optimum temperatures. **B)** The eco-evolutionary model predicts evolutionarily stable optimum temperatures (red points) for each isolation location that are several degrees higher than the mean environmental temperatures (i.e., above the black line) and agree well with the data, except in the warmest waters. The confidence band from A) is shown in gray for comparison.

Third, strains from polar and temperate waters had optimum temperatures that were considerably higher than their mean annual temperatures, whereas tropical strains had optima closer to or lower than the mean temperatures (Fig. 3.2 A). Finally, variation in optimum temperature and niche width was not explained by taxonomic differences above the level of genus, indicating that thermal adaptation is not highly phylogenetically constrained in this group (Tables S1 and S2 in Thomas et al. 2012).

3. Eco-evolutionary model

This strong trait-environment relationship suggests that microbes are adapted to the temperatures that they experience locally. However, this pattern could also occur through a correlated response to selection on other traits. To test whether the observed pattern arose as an adaptive response to variable thermal regimes, we used an eco-evolutionary model (Geritz et al. 1998, Abrams 2001) to predict the optimum temperatures that maximize fitness at each isolation location. The model allows us to study the effects of thermal adaptation alone by forcing all other aspects of strains to be identical. Purely theoretical applications of such eco- evolutionary models have been extensive, but they have rarely been compared to quantitative field data (Stegen et al. 2011).

In the model, strains differ only in their thermal tolerance curves (characterized by their optimum temperature) while competing for a single nutrient. The growth rates of all strains are bounded by an exponential function that increases with temperature, an empirical relationship known as the Eppley curve (Eppley 1972). We require that each individual strain’s thermal tolerance curve touch the Eppley curve at a single point, forcing maximum growth rate to become a function of optimum temperature. Niche widths are held constant across strains, because we found no significant relationship in our data set between niche width and environmental or taxonomic covariates (Tables S1 and S2 in Thomas et al. 2012). Given these constraints, we allow optimum temperatures of a set of strains to evolve in response to deterministic temperature regimes. These regimes were based on model fits to a 30-year sea surface temperature time series at every isolation location (see methods in Thomas et al. 2012, Reynolds et al. 2007). For each environment, we used an evolutionary algorithm based on quantitative genetics to identify evolutionarily stable states (ESSs) (see methods in Thomas et al. 2012, Abrams 2001). At an ESS, the strains that persist (defined by their traits) cannot be invaded by any other strain. These temperature optima serve as a theoretical prediction of the best strategy (or strategies) at each isolation location, which we can then compare to our data as a test of thermal adaptation.

Our eco-evolutionary model predicts that optimum temperatures should increase with mean temperature and exceed it by several degrees (Fig. 3.2 B, also Fig. S3 in Thomas et al. 2012). This is in agreement with the observed pattern (Fig. 3.2 A) and bolsters the case that this relationship arises from adaptation to mean temperature. However, in regions with the highest mean temperatures (the tropics), the model predicts optima that are significantly higher than those observed. Although this discrepancy suggests that tropical strains may be less well-adapted to their environmental temperatures, we estimated that these strains are capable of persistence under the temperature regimes they experience (Figs. 3.2 B and 3.3) (Reynolds et al. 2002). The difference may be a result of interactions between temperature and other factors, constraints on thermal adaptation at high temperatures, or adaptation to laboratory temperatures before measurement. Examining model predictions across a range of assumed niche widths reveals that wider niches lead to larger differences between predicted optima and the mean annual temperatures and to a decrease in the number of coexisting strains (Fig. S3 in Thomas et al.2012). These results illustrate that temperature variation can support species coexistence, although it cannot fully explain the levels of trait diversity observed in the data.

4. Species distribution models

Phytoplankton strains may be adapted to their current conditions, but could be negatively affected by warming oceans. Moving from the eco-evolutionary model to purely physiological mechanistic species distribution models (SDMs), we then examined whether changing environmental temperatures could alter species ranges and global diversity patterns. These models use physiological trait measurements to predict species abundances across environmental gradients (Kearney & Porter 2009) but do not account for species interactions or evolution. We generated growth rate predictions across the

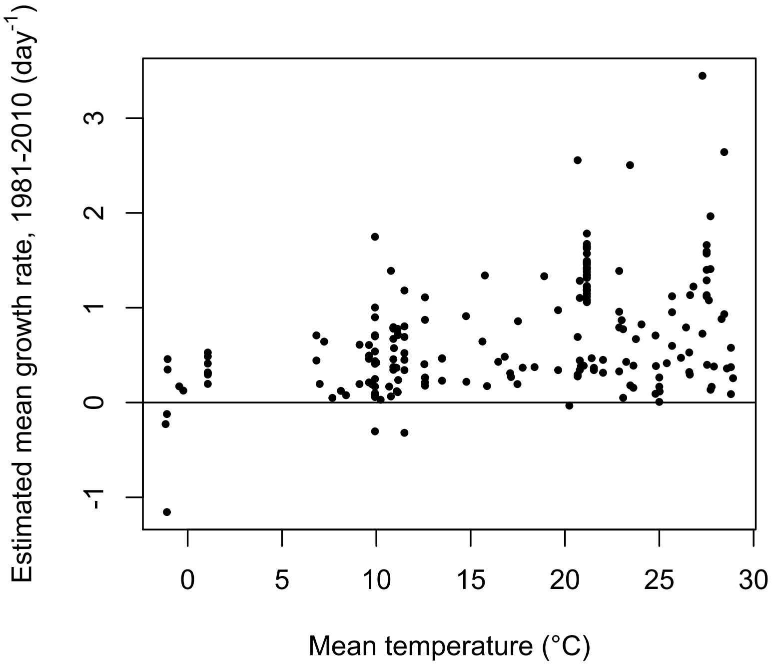


Figure 3.3 Estimated mean daily growth rates of all strains at their isolation locations, between 1980 and 2010. These estimates were based on monthly temperature records (Reynolds et al. 2002) and each strain's thermal tolerance curve, and depend on the assumption that growth is limited solely by temperature. Even warm-water strains have mean growth rates exceeding zero (the horizontal line), indicating that they are capable of persisting in their environment, although their optima are below what our model predicts to be most adaptive.

ocean for each strain represented in our data set, based on their thermal tolerance curves and a 10-year temperature time series (See methods in Thomas et al. 2012). If the 10-year mean growth rate of a strain was positive at a location, the location was deemed to fall within its range. We repeated this using both historical (1991–2000) and future (2091–2100) temperature regimes, the latter having been predicted by a global climate model (See methods in Thomas et al. 2012, Reynolds et al. 2002, IPCC 2007, Nakićenović et al. 2000, Delworth et al. 2006). These estimates indicate that ocean warming is likely to drive poleward shifts in strains' equatorial boundaries, although polar range boundaries remain approximately constant (Fig. S4 in Thomas et al. 2012). Consequently, many strains are predicted to experience a reduction in range size (Figs. S5, S6, and S12 in Thomas et al. 2012), potentially increasing extinction probabilities. Our SDMs assume that growth rates are limited solely by temperature, but other factors, such as nutrient availability, could also be incorporated if relevant trait data were available.

5. Diversity patterns

When the range shifts of all strains are considered in the aggregate, they can be used to predict global patterns of phytoplankton diversity change as a result of ocean warming (Fig. 3.4) (McKenney et al. 2007). In order to do this, we calculated "potential diversity," defined as the number of phytoplankton strains (out of the 194 in our data set) theoretically capable of growing at a location, assuming that temperature is the sole limiting factor (Figs. S7 and S8 in Thomas et al. 2012). A comparison of potential diversity patterns under both historical and future temperature regimes shows that temperature change may drive a large reduction in tropical phytoplankton diversity over the course of

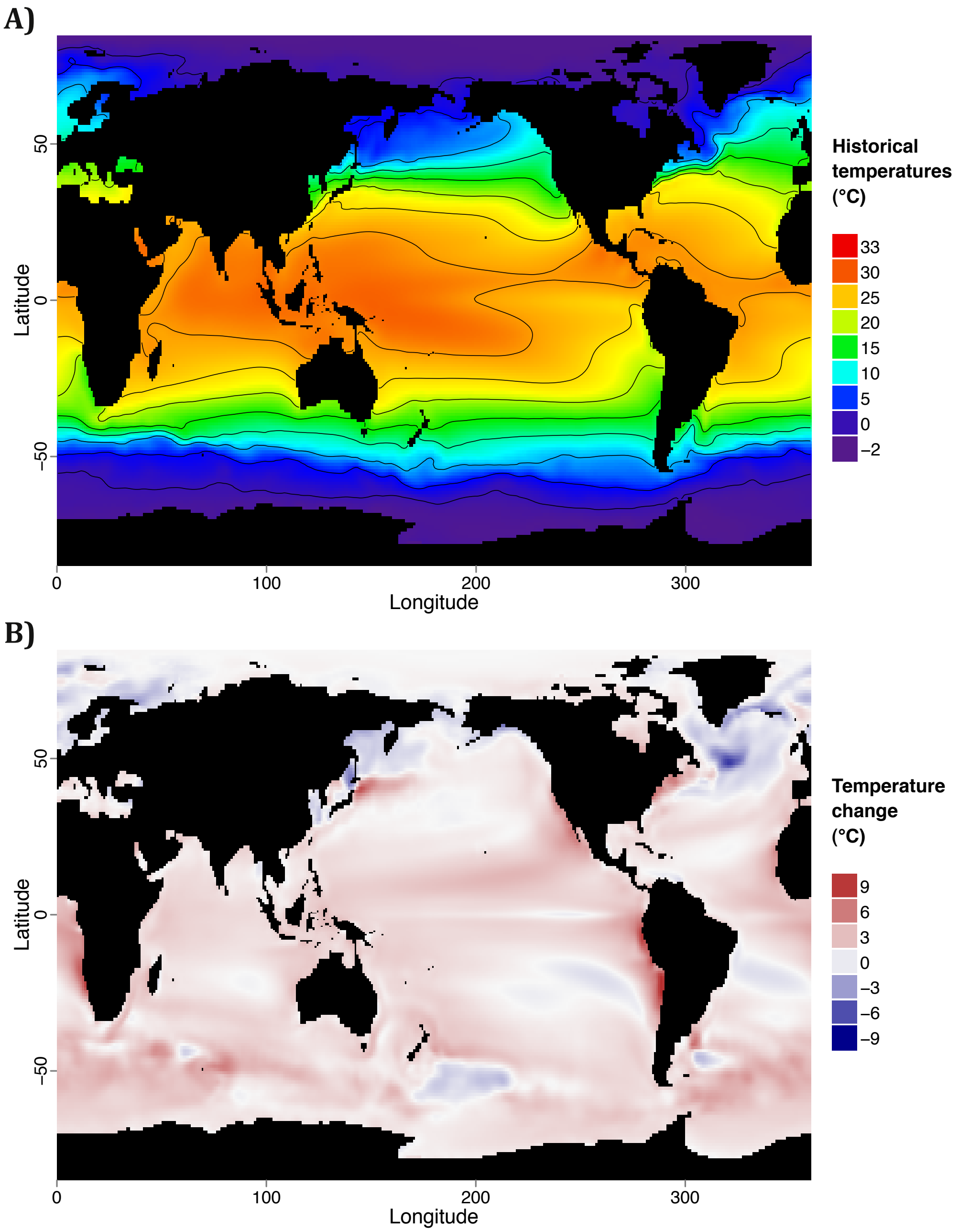
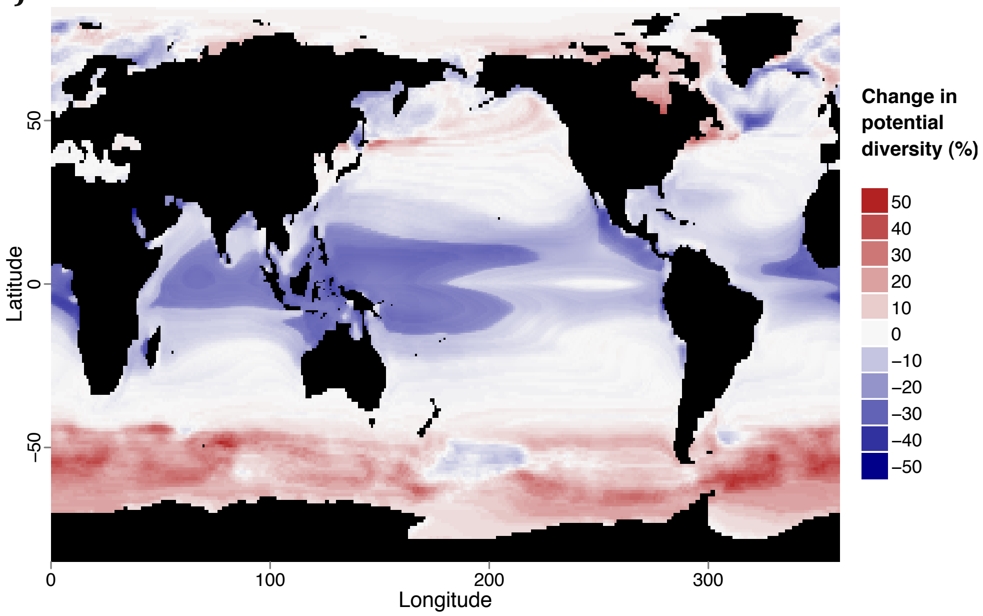


Figure 3.4 Changes in temperature drive changes in the potential diversity of phytoplankton, as predicted by mechanistic species distribution models. A) Mean annual temperature across the oceans over historical (1991–2000) temperature regimes. **B)** Change in mean annual temperature between historical (1991–2000) and predicted future temperature regimes (2091– 2100).

Figure 3.4 (cont'd)

C)



C) Percent change in potential diversity between historical and predicted future temperature regimes. Potential diversity is reduced sharply in the tropical oceans, despite these regions experiencing relatively small increases in temperature.

this century. Approximately one-third of contemporary tropical strains are unlikely to persist there in 2100 (Fig. 3.4 C), despite a change in mean temperature of only ~2°C (Fig. 3.4, A and B). High latitudes may experience small increases in potential diversity, as a result of poleward shifts in strain ranges. Rising temperatures have the strongest effect on tropical strains, because tropical optima are close to current mean temperatures (Fig. 3.2 A) and thermal tolerance curves are negatively skewed. Small increases in temperature can therefore lead to sharp declines in growth rate. A decrease in diversity is likely to have a strong impact on tropical ecosystems, because biodiversity loss is a major cause of ecosystem change (Hooper et al. 2012). One possible consequence is a decrease in tropical primary productivity, which could occur through two distinct mechanisms: the loss of highly productive species or a decrease in complementarity (Tilman et al. 1996, Reich et al. 2012).

6. Conclusions

Our findings lend support to the hypothesis that tropical communities are most vulnerable to increases in temperature (Deutsch et al. 2008). However, the existence of high genetic diversity within species, as has been noted in some cases (Härnström et al. 2011), may prevent the loss of entire species. Adaptation to changing temperatures may mitigate some of the predicted losses in diversity, particularly in rapidly reproducing taxa such as phytoplankton. The evolution of thermal tolerance has been examined in a few taxa, including phytoplankton (Bennett & Lenski 2007, Knies et al. 2006, Huertas et al. 2011), but we currently lack the information necessary to accurately model the consequences of evolutionary change on ecosystem processes (Chown et al. 2010, Angilletta et al. 2003). In the case of phytoplankton, we need estimates of rates of adaptation to high temperature stress in a variety of taxa, as well as an examination of the evolutionary constraints and trade-offs that may be associated with this. Characterizing these constraints will allow us to make improved forecasts of species survival and may prove critical for understanding the fate of tropical communities and oceanic ecosystems.

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CHAPTER 4

ECO-EVOLUTIONARY DYNAMICS OF DIVERSE COMMUNITIES IN PERIODIC ENVIRONMENTS

1. Introduction.

Organisms are commonly confronted by temporal variation in the environments they inhabit. Ecologically, this variation has important consequences for the growth and persistence of particular organisms. It can also support the coexistence of species, influencing community diversity and composition. Evolutionarily, variation affecting the growth (or fitness) of populations and species can impose selective pressures leading to trait evolution and adaptation. Ecological and evolutionary processes can interact in the presence of temporal variation, influencing not only how many species can coexist, but also which species can coexist and with which traits. In this chapter, we explore how complex patterns of coexistence and community structure emerge from simple models of species competition in periodically varying environments. Our investigations combine both ecological and evolutionary approaches, enriching our understanding of this coexistence mechanism.

1.1 Temporal variation & coexistence

Many previous authors have studied the effects of diverse kinds of temporal variation on species coexistence. Hutchinson suggested non-equilibrium mechanisms as a solution to his own ‘paradox of the plankton’ (1961). Temporal variation comes in many forms. It can occur in factors that are biotic (abundances of prey, predators, mutualists) or abiotic (temperature, nutrients, precipitation). It can be stochastic or deterministic, and may be driven by external forces (temperature, climate) or arise endogenously from interactions occurring within communities. Resource fluctuations have been thoroughly shown to support multispecies coexistence (Armstrong & McGehee 1976, Levins 1979, Hsu 1980, Abrams 1984, Grover 1990, 1991, Anderies & Beisner 2000, Litchman & Klausmeier 2001, Xiao & Fussman 2013), including both generalists and specialists (Abrams 2004, Abrams 2006). Several early theoretical papers examined the consequences of fluctuating growth rates and/or carrying capacities in simple two species Lotka-Volterra competition models (Koch 1974, Cushing 1980, Namba 1984), demonstrating coexistence through stable limit cycles. Temporal variation provides the raw material for two different coexistence mechanisms recognized by Chesson: relative non-linearity and the temporal storage effect (Chesson & Warner 1981, Chesson 1994, Chesson 2000).

1.2 Consequences of evolution for ecological coexistence mechanisms in general

The expanding eco-evolutionary synthesis studies the effects of evolutionary processes on the dynamics and stability of ecological systems, and how ecological processes structure selection and evolution. An important line of research within this growing discipline focuses on exploring how trait evolution affects coexistence mechanisms. Theoretical results suggest that evolution can affect both how many species can coexist (typically reducing diversity relative to pure ecological models) and what traits or functions they have. The development of a number of analytical techniques, including adaptive dynamics (Geritz et al. 1998, Abrams 2001, Gertiz et al. 2004, McGill & Brown 2007) has provided new insights into eco-evolutionary models. For example, trait evolution decreases coexistence between generalists and specialists (Egas et al. 2004), and between species competing for limiting resources (Shoresh et al. 2008). Under different competitive scenarios evolution can result in either trait convergence or divergence

(Edwards et al. in review), influencing the interpretation of patterns of over- or under-dispersion of traits in communities or across phylogenies (Mayfield & Levine 2010). When species traits are allowed to evolve a variety of unexpected dynamics can arise, including evolutionary cycles and evolutionary suicide (Dieckmann & Metz 2006, Kisdi et al. 2001, Gyllenberg & Parvinen 2001). When evolution is considered in models, but treated as much slower than ecological processes, it leads to communities with diversity less than or equal to that of the corresponding ecological model. However, evolution can occur rapidly in many systems, influencing coexistence (Lankau 2011). When this occurs, dynamic changes in trait values may result in additional regulating factors and potentially enhance the number of species that can coexist. Additionally, differences in rates of evolutionary response between species may be sufficient to support coexistence. Throughout the remainder of this chapter, however, we will focus on models where evolution is slow relative to ecology.

1.3 And fluctuation-dependent mechanisms in particular

Coexistence mechanisms dependent on temporal variation are not exempt from re-examination in light of evolution, though only a few papers have addressed the topic. Levins (1968) studied the optimal choice or mix of phenotypes in a fluctuating or variable environment, using an optimization approach to study evolution in changing environments. Species with distinct competitive strategies can arise through evolutionary processes and coexist in systems with fluctuating resource levels (Kremer & Klausmeier 2013). However, coexistence is contingent on the relative rates of resource fluctuations and adaptive responses; despite temporal variation, rapid evolution in this system can preclude coexistence. Earlier, Kisdi & Meszéna (1995) showed that trait evolution constrained coexistence in a lottery competition model (similar to that of Chesson & Warner 1981). In a model of annual plants, a temporal storage effect only evolved and persisted under restrictive conditions (Snyder & Adler 2011). In contrast, the storage effect readily evolved for a wide range of assumptions in a modified lottery model (Abrams et al. 2013). These results focused on one or two species competing in an environment oscillating between two discrete environmental states according to varying rules. Additional eco-evolutionary studies, spanning different kinds of temporal variation and temporal coexistence mechanisms, are needed before general patterns can be identified.

1.4 Evolutionarily stable coexistence: more restrictive than ecologically stable coexistence.

If a set of species can coexist with fixed trait values (parameters), they form an ecologically stable community. If it is also true that no species with a different trait value can invade this set of species, then they represent a community that is both ecologically and evolutionarily stable. In this case, each species experiences stabilizing selection and sits at the peak of an adaptive landscape. Such communities are of considerable interest, as they represent the culmination of evolutionary (or community assembly) processes in a system, if it persists long enough that an eco-evolutionary attractor is reached. Evolutionarily stable communities provide predictions not only of community diversity, but also of the distribution of traits represented in the community. These predictions can be made across environmental gradients, and used to study real-world patterns of adaptation (eg, Thomas et al. 2012, Litchman et al. 2009).

Ecological stability is a prerequisite for evolutionarily stability, so principles governing ecological coexistence apply. This includes fundamental ideas such as competitive exclusion (Gause 1934), which restricts the number of species that can coexist to be less than or equal to the number of limiting (or regulating) factors (Tilman 1982, Chase & Leibold 2003, Levin 1970). An associated principle, limiting similarity, encapsulates the idea that species that are too similar to each other will compete strongly, generally leading to competitive exclusion (Hutchinson 1959, MacArthur & Levins 1967, Abrams 1983). Dissimilar species experience weaker interspecific competition (relative to intraspecific competition), favoring coexistence. While it can be shown that there is in fact no theoretical limit to similarity in several models (May & MacArthur 1972, Roughgarden 1979), such cases are degenerate, as the conditions permitting arbitrarily similar species to coexist become prohibitively restrictive and consequently unlikely to occur (Meszéna et al. 2006). Meszéna et al. (2006) focus on limits to how similar species can be, in terms of either their sensitivity to regulating factors or the impact they have on regulating factors, and still coexist robustly in fixed point systems. Their results have also been shown to hold in non-equilibrium, periodically varying systems (Barabás et al. 2012). We expect these principles and patterns of limiting similarity to hold within the evolutionarily stable communities identified in eco-evolutionary models, because such communities are a subset of possible ecologically stable communities.

1.5 Summary

The present work contributes to the currently limited set of studies investigating how evolution moderates coexistence mechanisms that depend on temporal variation. We focus on a model where species' growth rates depend on how closely their trait matches an environmental parameter that varies smoothly through time, following deterministic, periodic fluctuations. For example, the growth rate of ectothermic organisms depends on environmental temperatures, which can fluctuate over time. Different organisms or species typically specialize, achieving their peak growth rates at different temperatures (Thomas et al. 2012). We consider a continuous set of environmental states (in contrast to Abrams et al. 2013), and extend our results to highly diverse communities. These communities display strong patterns of limiting similarity. We also explore the consequences of selecting different periodic forcing functions, which turn out to have substantial effects on the composition, diversity, and persistence of evolutionarily stable communities.

The remainder of this chapter is structured as follows. In section 2, we provide details on our model, techniques for studying periodic systems and conducting evolutionary analyses. The results of our analyses are presented in section 3, and discussed in section 4. Variables used throughout this chapter are defined in Table 4.1.

2. Methods.

2.1 Basic model

We let $T(t)$ describe the fluctuation of some non-interactive, externally forced environmental variable, such as temperature. This variable changes through time according to either a sine wave

$$T(t) = T_{av} + T_{amp} \sin(2\pi t/\tau) \tag{1a}$$

or a triangle wave

$$T(t) = T_{av} + T_{amp} \frac{2}{\pi} \sin^{-1}\left[\sin\left(2\pi\left(\frac{t}{\tau} - \frac{1}{4}\right)\right)\right] \tag{1b}$$

with period τ, peak amplitude T_{amp} and mean T_{av} (which we set to zero without loss of generality). These functions are illustrated in Fig. 4.1, which also shows that for the same mean, amplitude, and period, they imply different distributions of environmental states, with important consequences.

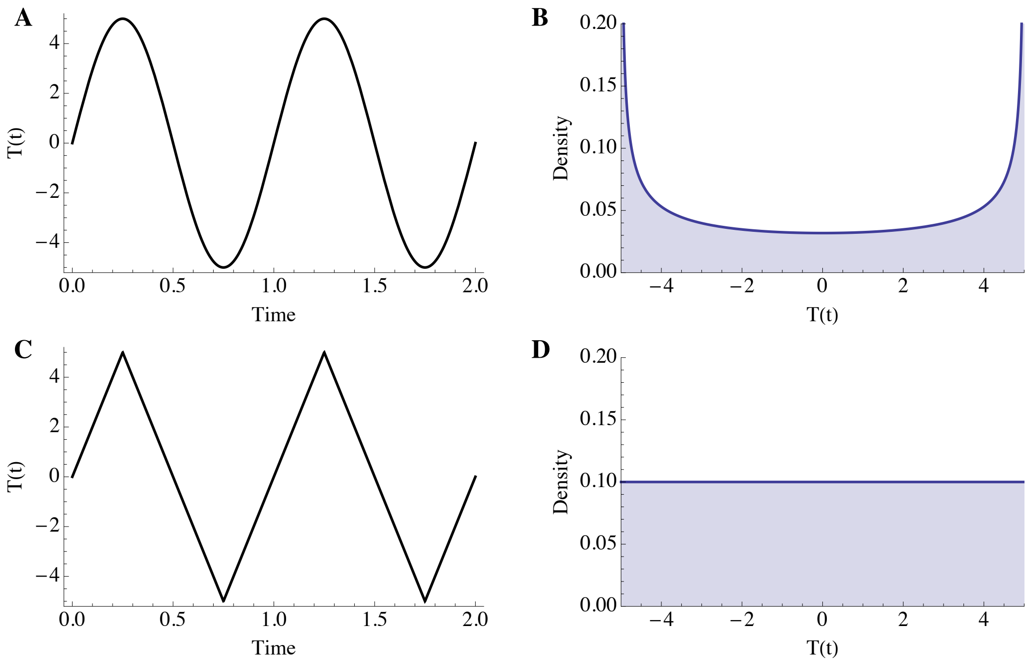

Figure 4.1. Sinusoidal versus triangle wave fluctuations (A and C), and associated density of environmental states (B and D). The sinusoidal fluctuation produces a bimodal distribution **B**), as environmental conditions change most slowly near extreme states (low and high). In contrast, the triangle wave leads to an environmental state that changes at a constant rate at any point in the fluctuation, leading to a uniform density of environmental states **D**).

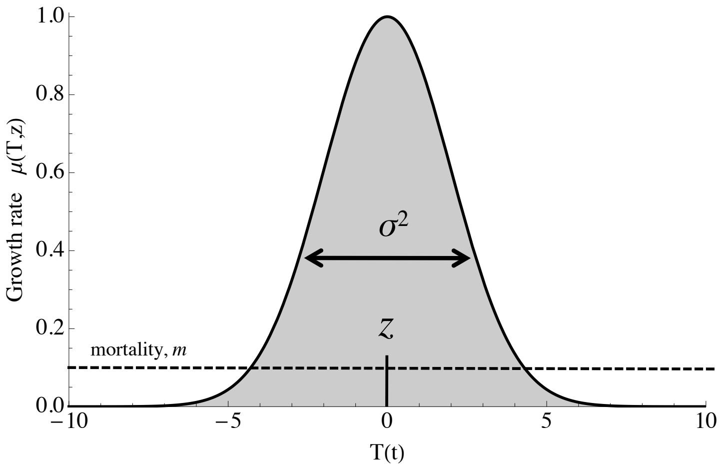

Figure 4.2. Species exhibit environment-dependent growth rates that follow a Gaussian function whose width is controlled by σ^2. They achieve their highest growth rates when the environmental state $T(t)$ matches their optimum z. Density independent mortality m further constrains environmentally determined growth rates.

Variable	**Definition**	**Value**
$T(t)$	Environmental forcing function	-
T_{av}	Average of fluctuation	0
T_{amp}	Amplitude of fluctuation	-
τ	Period of fluctuation	-
μ	Environmentally determined growth rate	-
μ_{max}	Maximum growth rate possible	{0.02, 1}
z	Trait specifying optimum environmental state (corresponding to $\mu = \mu_{max}$)	-
σ^2	Controls width of growth rate function ('niche width')	8
n	Population density	-
m	Density independent mortality rate	0.1
g	Instantaneous per capita growth rate/invasion rate/fitness	-
$R(t)$	Available resource	-
R_{tot}	Total resource supply	100
R^*	Break-even resource level capable of sustaining a species.	-
S	State of system (in SSD approximation)	$\{\emptyset, 1, 2, 3, \ldots, k\}$
$\emptyset$	Denotes the empty state	-
N	Transformed population density (in SSD approximation)	-
$\bar{g}_i$	Average per capita growth rate (over one period)	-
t_c	Critical timings corresponding to potential transitions to the empty state	-

Table 4.1. Showing the variables and corresponding definitions used in this chapter. Parameter values are provided when used consistently for subsequent results.

Next we describe how this environmental fluctuation affects the growth rate μ of species i having some trait z_i characterizing its preferred or optimal environmental state:

$$\mu(T, z_i) = \mu_{max} \exp\left(\frac{-(T - z_i)^2}{\sigma^2}\right) \tag{2}$$

Here μ_{max} provides the maximum growth rate of i achievable only when the environmental state T matches z_i. Finally, σ^2 governs the width of this Gaussian function, essentially controlling the range of T over which species i experiences non-negligible growth rates (Fig. 4.2).

Combining this temporally-variable growth rate with a basic model of resource competition based on linear (or Type I) resource uptake, we arrive at an equation for the per capita growth rate of species *i* as a function of its trait z_i:

$$\frac{1}{n_i}\frac{dn_i}{dt} = \mu\left(T, z_i\right) R\left(t\right) - m \equiv g_i \tag{3}$$

where n_i provides the population density of species *i*, *R(t)* describes the level of available resources, and *m* is a density independent mortality term. The minimum level of resource able to sustain species *i*, referred to as its R^*, is given by $R_i^*(t) = m/\mu_i(t)$, introducing μ_i as shorthand for the time-varying growth rate of a species with trait z_i. Finally, assuming a closed system, available resource levels

$$R\left(t\right) = R_{tot} - \sum_{i=1}^{k} n_i \tag{4}$$

depend on the difference between resource supply R_{tot} and the amount of resource sequestered in biomass across all *k* species present. Together, (1a) or (1b), and (3) and (4) define a complete system of ordinary differential equations (ODEs) governing the population dynamics of one or more species as a function of their environmental tolerances, given some particular choice of $T(t)$ such as (1a) or (1b).

This non-linear, non-autonomous system is not amenable to analytical solution. However, numerical techniques can be used to obtain solutions this ODE system, given the initial population densities and traits of each of the *k* species considered and the environmental forcing function $T(t)$. For large τ, the solutions of this system are typically characterized by intervals of relatively constant dynamics punctuated by abrupt changes (ie, the solutions are stiff), presenting difficulties for standard ODE solvers. These challenges motivate the use of an approximation.

2.2 Successional State Dynamics (SSD) approximation

The model outlined in 2.1 can be simplified using the successional state dynamics (SSD) approach of Klausmeier 2010 (see also Kremer & Klausmeier 2013, Klausmeier & Litchman 2012). Originally developed for systems with piecewise periodic forcing, we justify applying this technique to systems with continuous forcing, such as (1a) or (1b) and large τ in section 5, Supplement A.

One of the key advantages of the SSD approach is that at any point in time t over a single fluctuation our system is characterized by some state S from a finite set of possible states. In the present model, either all species are rare, creating an 'empty state' $\emptyset$, or one species i is dominant, such that $S \in \{\emptyset, 1, 2, 3, \ldots, k\}$ up to k number of species. During the empty state, $R(t) \approx R_{tot}$, but when species i dominates it reduces resource levels to $R(t) \approx R_i^*$. Using the SSD approach, we shift from modeling population density as n to considering N, a transformation of n that equals 0 when a species is dominant and takes on negative values when a species is rare (for details, section 5, Supplement A).

There are two ways that the state S of this system can change, driven by competition and changes in growth rates due to environmental forcing:

$$\begin{cases} S \to i & \text{if } N_i = 0 \text{ and } S \neq i \\ S \to \emptyset & \text{if } R_S^* = R_{tot} \end{cases} \tag{5}$$

In the first, species i rises to dominance, either replacing the empty state or the previous dominant species, as N_i switches from negative to zero. In the second, a dominant species i is replaced by the empty state (rather than a competitor). This happens when its $R_i^* > R_{tot}$ as a result of the effects of environmental forcing on μ_i. When R_i^* first exceeds R_{tot} as R_i^* is increasing (ie, $dR_i^*/dt > 0$), the growth rate of species i must necessarily become negative. If no competing species has increased in abundance enough to become dominant at this point, the dominant species will be replaced by the empty state. For many fluctuations it is possible to solve for $R_i^* = R_{tot}$ explicitly as a function of species trait z and the parameters of $T(t)$, yielding the timings of transitions between dominance and the empty state for each species (See section 6, Supplement B).

We can now define the instantaneous per capita growth rate $g_{i,S}$ (or invasion rate or fitness) of species i, depending on the current state S:

$$g_{i,S} = \begin{cases} \mu\left(T, z_i\right) R_{tot} - m & \text{if } S = \emptyset \\ \mu\left(T, z_i\right) R_j^* - m & \text{if } S = j \\ \quad = m\left(\frac{\mu(T,z_i)}{\mu\left(T,z_j\right)} - 1\right) & \\ 0 & \text{if } S = i \end{cases} \tag{6}$$

Together, the above equations (5 and 6) specify the dynamics of k competing species under each possible state of the system, as well as how and when state changes occur in this system. The resulting model is a hybrid dynamical system, consisting of a discrete state variable and a set of coupled ODEs (6) for k species. Sufficient tools for numerically solving hybrid dynamical systems are found in Mathematica (v. 9), which we use for all of the numerical results presented here. Converting our initial model (generating stiff systems of ODEs) into a hybrid dynamical system using the SSD approximation (and assuming that $\tau \rightarrow \infty$) grants us improved numerical tractability and stability. Finally, it is worth noting that the results of SSD approximations typically correspond closely to those of the original ODE system for even moderately large values of τ (Klausmeier 2010, Kremer & Klausmeier 2013).

2.3 Finding ecological attractors

Given some deterministic, periodic environmental forcing $T(t)$, we can identify the attractors of this model, which will consist of limit cycles. A simple condition for identifying these stable limit cycles is obtained by considering Poincare sections of the cyclical population dynamics of each species. When population dynamics have converged on a limit cycle, they must necessarily pass through the same point of the Poincare section every period. In other words, the density of species *i* at the beginning of one cycle must equal its density by the end of that cycle (ie, the beginning of the next cycle); otherwise the population size is increasing or decreasing and not at an attractor. Notationally, this condition requires that

$$N_i(t+1) = N_i(t) \tag{7}$$

simultaneously holds true for each *i* from *i* = 1, 2, … , *k* coexisting species. The set of initial population densities that satisfy this condition can be determined using numerical root-finding approaches. Alternatively, this condition can be cast in terms of the average growth rates of a species over a single period:

$$\overline{g_i} = \int_0^1 g_{i,S}\, dt = 0 \tag{8}$$

When $\overline{g}_i$ = 0, species *i* exhibits no net increase or decrease in abundance over a period, and thus has reached its limit cycle attractor. When this holds for all species considered, they represent an ecological attractor for the community.

2.4 Identifying singular strategies and evolutionarily stable states

At its ecological attractor, a community consisting of a set of species (characterized by their traits) is stable with respect to the population dynamics of its members. However, such a community may not be stable from an evolutionary perspective. Directional or disruptive selection may often act on species traits, a possibility not typically considered in coexistence models. Extending such models by allowing species' traits to change in response to selection can result in different dynamics and communities (e.g., Egas et al. 2004, Shoresh et al. 2008, Lankau 2011, Kremer & Klausmeier 2013). Community assembly processes can generate very similar patterns; species with different trait values may invade and replace one or more of the original resident species, altering the trait distributions and diversity of the community. Given sufficient time and trait variation, the end result of either of these processes is often a set of species, characterized by their traits, that is uninvasible by any other species. This state is known as an evolutionarily stable state, or ESS.

We can identify ESSs in our system by extending the criteria presented in section 2.3. First, we can define the instantaneous fitness gradient, a quantity encompassing both the direction and strength of selection experienced by a species *i* at a particular point it time, which depends on both its trait z_i and its ecological context *S*:

$$\left.\frac{\partial g_{i,S}}{\partial z}\right|_{z=z_i} = \begin{cases} \frac{2R_{tot}}{\sigma^2}\mu_i\left(T\left(t\right)-z_i\right) & \text{if } S=\emptyset \\ \frac{2R_j^*}{\sigma^2}\mu_i\left(T\left(t\right)-z_i\right) & \text{if } S=j \end{cases} \tag{9}$$

In both of these equations the term $T(t)$ - z_i determines the sign of the fitness gradient, as all other terms are positive. When $T(t)$ is greater (less) than z_i, there is positive (negative) selection on z_i. Species with faster growth rates (larger μ_i) and narrower niches (smaller σ^2) experience stronger selection. Finally, the fitness gradient is scaled by the amount of available resource $R(t)$, either R_{tot} or $R_j^* = m/\mu_j$ depending on the current state.

Equation (9) provides the instantaneous selection felt by a species with trait z_i. However, we are more interested in determining the net selection experienced by *i* over the entire fluctuation period, $\overline{\partial g_i / \partial z}$. This is accomplished by integrating (9) from 0 to 1. When this integral evaluates to zero,

$$\overline{\frac{\partial g_i}{\partial z}} = \int_0^1 \left.\frac{\partial g_{i,S}}{\partial z}\right|_{z=z_i} dt = 0 \tag{10}$$

we know that species *i* has experienced no net selection on its trait z_i. If both (8) and (10) hold for all species given their traits, we have identified a point termed a singular strategy (Geritz et al. 1998). Furthermore, this singular strategy is also considered to be an ESS if

$$\left.\frac{\partial^2 \overline{g_i}}{\partial z^2}\right|_{z=z_i} < 0 \tag{11}$$

for each z_i in $\{z_1, z_2, z_3, \ldots, z_k\}$. This criteria for identifying an ESS community is local by definition (as it is restricted to the vicinity of the traits of represented species), yet communities can sometimes be invaded by mutants or dispersers with traits in non-local regions of trait space. We can additionally require that $\overline{g}_i \leq 0$ for all possible values of z across the entire trait axis. This ensures that the community we have identified is a globally uninvasible ESS, a stricter condition than the local ESS criteria (see McGill & Brown 2007 and Kremer & Klausmeier 2013 for more on local ESSs). A global ESS community can be considered as the endpoint of evolution and diversification along the *z* trait axis or the culmination of community assembly.

2.5 Bifurcation analysis of ESS communities

The diversity and specific trait values of the species comprising an ESS community depend on the parameters of our model (e.g., fluctuation amplitude T_{amp}, growth and mortality rates, μ_{max} and m, and niche width σ^2). We can explore the composition of ESS communities across ranges of parameter space, encompassing variation in one or more of these parameters, using bifurcation theory. In general, if an ESS community (with traits $\{z_1, z_2, z_3, \ldots, z_k\}$) occurs at a fixed point in parameter space, it indicates that a similar ESS community exists at a near-by point in parameter space (with traits $\{z_1 + \delta_1, z_2 + \delta_2, z_3 + \delta_3, \ldots, z_k + \delta_k\}$). In other words, making small changes to our model parameters typically results in a similar ESS community with slightly different trait values. This is a useful property, allowing us to track ESS communities across parameter space without having to work through the diversification of the community through repeated branching or non-local invasion.

Exceptions to this general pattern arise when a bifurcation occurs. Several kinds of bifurcation events are possible (see for example Geritz et al. 1999):

1) An ESS community can lose global, but not local, stability resulting in increased diversity, or (in reverse) a member of the ESS community can develop negative density, losing viability and reducing diversity (Fig. 4.3 A & C).

2) An evolutionary branching point (Geritz et al. 1998) can lead to an increase in diversity of the ESS community, or (in reverse) two previously unique members of an ESS community can collide, reducing diversity (Fig. 4.3 B & D).

Although not yet formalized, this bifurcation approach has been used previously to study the occurrence and stability of evolutionary cases across parameter space, but typically for only 2-3 species (Meszena, Czibula & Geritz 1997, Geritz et al. 1998, Geritz, van der Meijden & Metz 1999, Kisdi & Geritz 1999, Litchman, Klausmeier & Yoshiyama 2009, Kremer &

Klausmeier 2013). Jansen & Mulder (1999) consider higher diversity systems, but suppress details on species' trait values and bifurcation processes.

In the current chapter, we use this approach to study communities of considerably higher diversity (ranging from 1 to 16 distinct species). Well-developed methods from bifurcation theory, termed continuation methods, can be used to expand bifurcation diagrams. An added advantage of the bifurcation approach is that allows detection of ESS cases that might not be reachable through branching processes starting from low diversity (see for example Geritz et al. 1998).

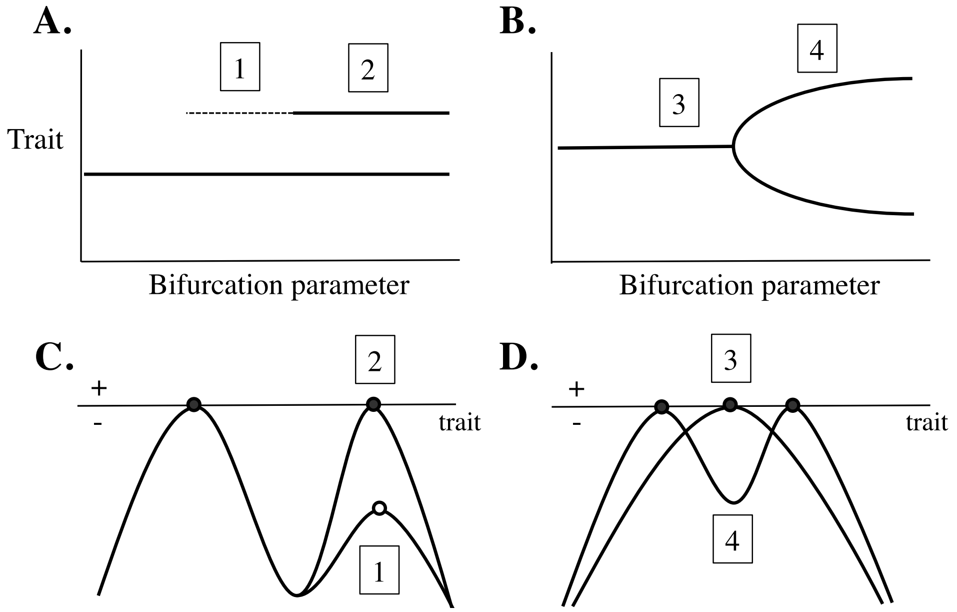

Figure 4.3 ESS communities can undergo at least two kinds of bifurcations as described in the text. A) Loss of global ESS stability occurs as a local maxima of the invasion profile develops. Initially, it has a negative fitness, shown a dashed line in A) and by the open circle in C) perched at the peak of a 'seamount'. However, this maxima increases in height until a region of positive invasion rate occurs (corresponding to a transition between states 1 and 2). **B)** Evolutionary branching occurs when an ESS species loses local stability, resulting in two new ESS species with similar traits (corresponding to a transition between states 3 and 4). Plots of the per capita growth rate of a rare invader as a function of its trait are known as invasion profiles. **C)** and **D)** show the invasion profiles corresponding to states 1 & 2 and 3 & 4 of panels A) and B), respectively.

2.6 Comments on the advantages of symmetry

Both the environment-dependent growth rate and the periodic forcing functions are symmetrical (1a, 1b and 2), leading to the expectation that our ESS communities (and trait distributions) will be symmetrical as well. In particular, we expect (and observe) symmetry around the mean of our periodic fluctuations. We take advantage of this symmetry property to reduce the complexity of our calculations. When we solve for an ESS community, we must identify both a set of traits and initial population densities at the beginning of each period satisfying (8), (10), and $\overline{g}_i \leq 0$ for all possible values of z. However, if we know the trait values of half of the species (eg, all of the species with $z_i < 0$) we can infer that the trait values of the remaining species are $-z_i$. This results in an ESS community with an even number of species. Alternatively, we may have a species with $z_i = T_{av}$, leading to an odd numbered ESS community. In this case, we can still infer the trait values of all of the species above (below) T_{av} by reflecting their values around T_{av} (= 0). When solving for the ESS community at a new value of our bifurcation parameter, instead of solving for $2k$ unknowns (k traits and k initial densities) we can solve for either $(k/2) + k$ or $((k\text{-}1)/2 + k)$ unknowns by invoking the symmetry of this system. An unusual, but observed, exception can arise that prevents taking advantage of symmetry in this manner. Symmetry breaking can lead to the creation of pairs of ESS communities that individually are not symmetric around T_{av}. However, each member of this pair is itself the reflection of the other around T_{av}, maintaining symmetry at a higher level.

3. Results

In the following sections, we outline the kinds of population dynamics occurring in our models, the ESS communities (uncovered by methods described in the previous section) that emerge across a gradient of fluctuation amplitude (Tamp), and resulting patterns of diversity and limiting similarity. Throughout, we draw comparisons between environments forced by triangle and sinusoidal waves, to elucidate how subtle differences between forcing functions can have surprisingly large effects.

3.1 Illustrative population dynamics

Complex temporal patterns of abundance occur for communities ranging from one to many species. A single species may dominate during favorable times but become rare and give way to the empty state when conditions are unfavorable (Fig. 4.4, A). Two competing species may exchange periods of dominance, driven by underlying variation in their growth rates (and R^* values) resulting from environmental forcing (Fig. 4.4, B). Patterns grow more complex for systems of many species, as shown in an example for five species (Fig. 4.5). Some species (with the highest or lowest trait values) experience only one period of dominance each cycle, while others (with intermediate trait values) may dominate multiple times.

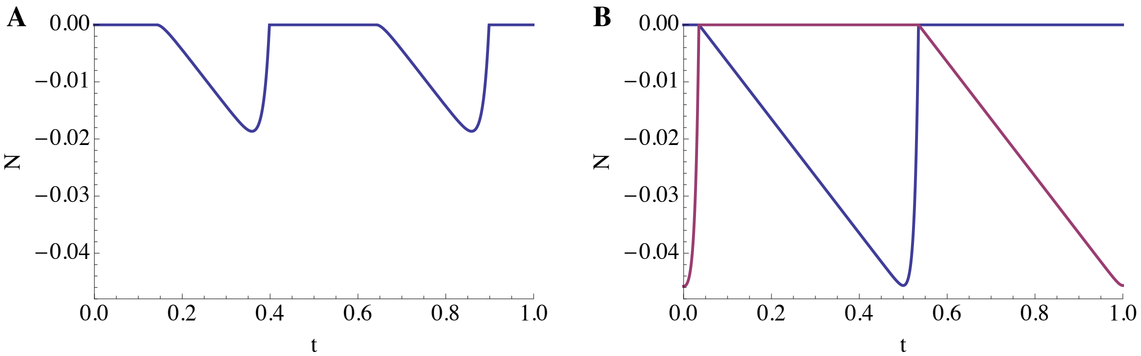

Figure 4.4. Diverse ecological attractors are possible, depending on species traits, environmental fluctuations, and competition between species. A) Even a single species may oscillate between periods of dominance and rarity (z_1 = 10, T_{amp} = 10, μ_{max} = 1). **B)** Competition and environmental fluctuations can drive exchanges in dominance between two species. Parameters as in A), but z_1 = 6.093, z_2= 13.907.

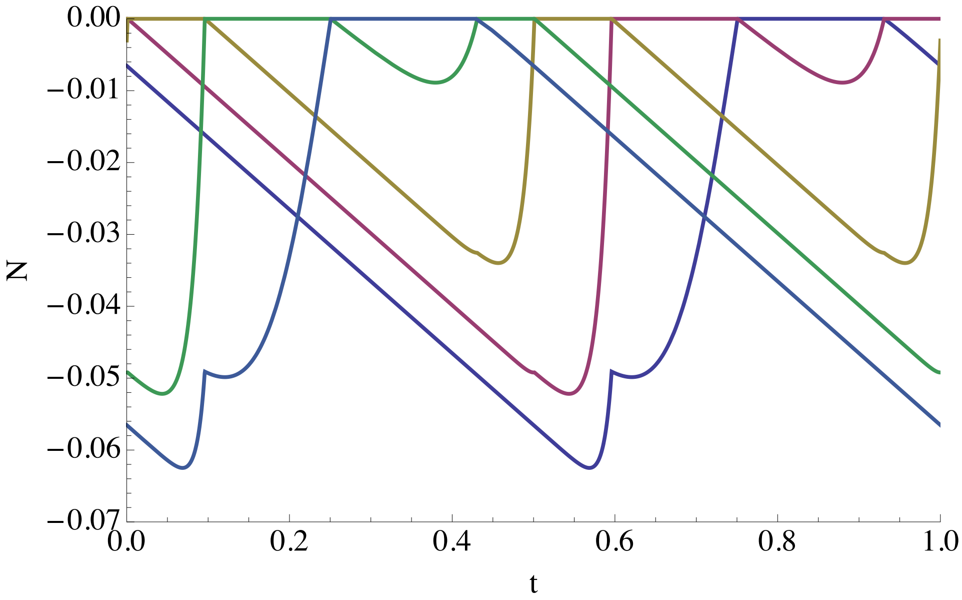

Figure 4.5 With increasing diversity, population dynamics become more complex. Of the five competing species shown here, two dominate once each cycle (both in blue), while the other three each exhibit two distinct periods of dominance (green, yellow, purple). (T_{amp} = 9.585, z = {2.00, 4.83, 10, 15.17, 18.00})

For a given periodic forcing function, we can determine the range of trait values that produce species with positive average growth rates when rare. In other words, we can solve for z such that

$$\int_0^1 g_{i,\emptyset}\, dt > 0 \tag{12}$$

This set of z values defines the range of viable species capable of invading and persisting in an environment. Varying environmental parameters and repeating this calculation defines a viability region as a function of the environment. Within this region, given a particular environment, a subset of individually viable species will also be able to coexist. Of these, there may also exist one or more sets of species that together form an ESS community. In our model, ESS communities must necessarily be contained within the viability region, as a species that cannot persist individually will not be able to persist in competition.

3.2 ESS bifurcation diagrams for sinusoidal & triangle waves

In a constant environment (T_{amp} = 0) it is impossible for multiple species to coexist; a species with trait $z = T_{av}$ will have the highest growth rate (and lowest R^*), allowing it to exclude all other species and making it evolutionarily stable. As T_{amp} increases, niche space due to temporal variation increases, eventually making it possible for multiple species to coexist and for multi-species ESS communities to occur. In the following sections, we explore how diversity changes with T_{amp}, given different forcing functions (1a) and (1b) and maximum growth rates (μ_{max}).

3.2.1 High μ_{max} /m

First we address the situation where maximum growth rate (μ_{max}) is high relative to the constant, density independent mortality rate (m) that all species experience. High values of μ_{max}/m allow species to increase in abundance rapidly when environmental conditions favor their growth, and to achieve higher peak abundances, buffering them against the mortality they experience when conditions are unfavorable. Consequently, we expect high μ_{max} /m to favor diverse ESS communities.

As T_{amp} increases, the range of feasible species and the diversity of ESS does communities increase (Fig. 4.6). Initially, a single species is evolutionarily stable (Fig. 4.6, B), but as T_{amp} increases this species loses stability through evolutionary branching, rapidly leading to the evolutionarily stable coexistence of two species, specializing on low (high) environmental states (Fig. 4.6, C). Further increases in T_{amp} widen the envelope of feasible species and drive additional bifurcations of the ESS community leading to increased diversity (Fig. 4.6). These bifurcations occur predominantly through the loss of global ESS stability, as species specializing on extreme low (high) states gain the ability to invade the system. Past $T_{amp} \approx 17$, multiple ESS communities are possible under identical fluctuations (Fig. 4.6, D). These alternate evolutionarily stable communities consist of either an even or odd number of species (depending on the presence or absence of a central species with $z = T_{av}$). The details of the diversification or community assembly process, and the comparative convergence stability (or domains of attraction) of the alternate ESSs, determine which community is more likely to occur in a particular environment.

Sinusoidal and triangle wave forcing functions produce very similar ESS bifurcation diagrams across wide ranges of T_{amp} (Fig. 4.7). As T_{amp} increases, the diversity of ESS communities climbs higher and higher for both fluctuation types, through repeated losses of global stability (Fig. 4.7). Alternate ESS communities are possible for both fluctuations and prevalent across most values of T_{amp}. Slight differences do occur in the exact values of T_{amp} corresponding to bifurcation events.

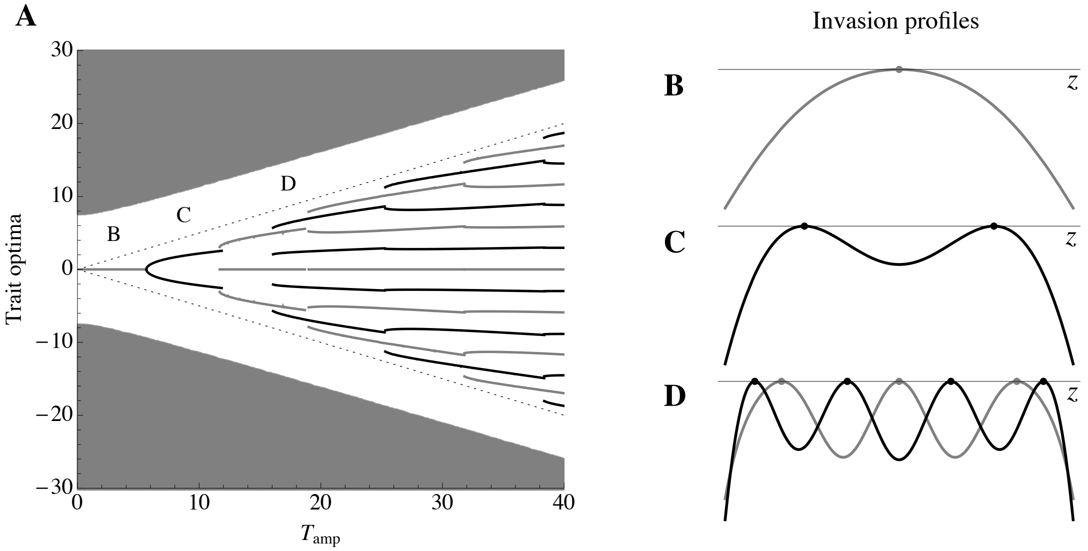

Figure 4.6 A) The diversity of ESS states increases with the amplitude of fluctuations (T_{amp}) given a sinusoidal forcing function. The set traits permitting positive average growth fall within the white region of the plot. Dashed lines show how the minimum and maximum environmental states change with T_{amp}. Solid lines indicate the traits of species composing ESS communities, with gray (black) indicating odd (even) communities. Invasion profiles shown for **B)** a one species ESS, T_{amp} = 5, **C)** a two species ESS, T_{amp} = 10, and **D)** alternate three- and four-species ESSs, T_{amp} = 18.

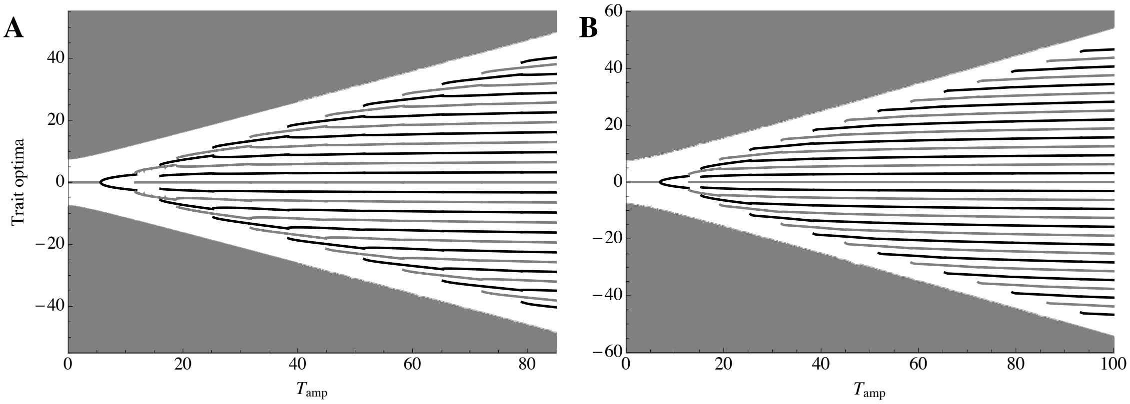

Figure 4.7 ESS bifurcation diagrams for A) sinusoidal and B) triangle wave forcing functions. Plot features and parameters are the same as in Fig. 4.6. These ESS bifurcations were tracked to community diversities of 14 and 16 species, in A and B, and continue to propagate in a similar manner for higher and higher T_{amp} values.

3.2.2 Low μ_{max}/m

In general, as the amplitude of fluctuations increases, the proportion of each period during which $T(t)$ falls between two values (say, T_L and T_U) grows smaller. Any given species with trait z has a finite range of $T(t)$ values favoring its growth. Together, these observations suggest that as T_{amp} increases, the duration of each species' temporal niche must necessarily decrease. When μ_{max}/m is high, as in the previous section, the effect of this phenomenon is imperceptible. However, when μ_{max}/m is low, species are less able to take advantage of the brief periods that favor them. Additionally, the gains they do make during favorable intervals are offset by the longer period of mortality they experience. Ultimately, this has the effect of limiting the ranges of species traits and T_{amp} values allowing solitary species to persist, as well as constraining the diversity and structure of ESS communities. The nature of these limits will depend both on the balance between niche width, maximum growth rate and mortality, and also on the kind of fluctuation we impose. ESS bifurcation diagrams for μ_{max} = 0.02 allow us to explore these effects (Fig. 4.8).

The diversity of ESS communities again increases with increasing T_{amp} following bifurcation patterns very similar to those observed in Fig. 4.7, for both sinusoidal and triangle wave fluctuations (e.g., Fig. 4.9 A). As T_{amp} increases further, the envelope of viability (white region defining the set of traits with positive average growth rates) collapses for both fluctuations, but in very different ways (Fig. 4.8). Under sinusoidal forcing, odd-numbered ESS communities disappear around $T_{amp} \approx 60$. By $T_{amp} \approx 64$, species with intermediate trait values cannot persist even without competition (Fig. 4.9 B). The diversity of ESS communities subsequently declines as species with intermediate z's become unviable. The resulting ESS communities are characterized by species specializing on increasingly extreme trait values.

In contrast to this gradual decline in diversity, when environmental fluctuations are driven by the triangle wave ESS communities collapse abruptly and at a much lower T_{amp} (Fig. 4.8, B). These differences are driven by the different environmental densities implied by sinusoidal and triangle waves. Over the course of one period, the derivative of the triangle wave remains constant in magnitude, while the magnitude of the derivative of the sinusoidal wave peaks at T_{av} and declines at either extreme. This results a uniform distribution of environmental states given a triangle wave, and a bimodal distribution given a sinusoidal wave, despite equivalent T_{av} and T_{amp} (Fig. 4.1). The bimodality arising from the sinusoidal wave allows species with extreme trait values to remain viable much longer than those with intermediate traits. Under the uniform distribution created by the triangle wave, no such refuge exists, and species lose viability almost simultaneously, whatever their trait value.

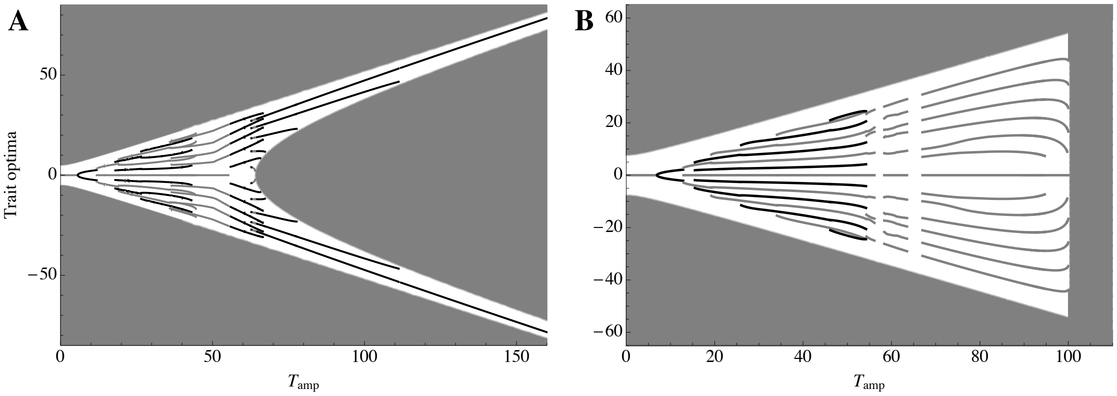

Figure 4.8 At low μ = 0.02, ESS community diversity first increases, then decreases with T_{amp}. The collapse of diversity occurs gradually in the **A)** sinusoidal case, but very abruptly in the case of the **B)** triangle wave. As before, the envelope of viability is shown in white, solid lines show the traits of ESS community members, and even (odd) numbered communities are shown in gray (black).

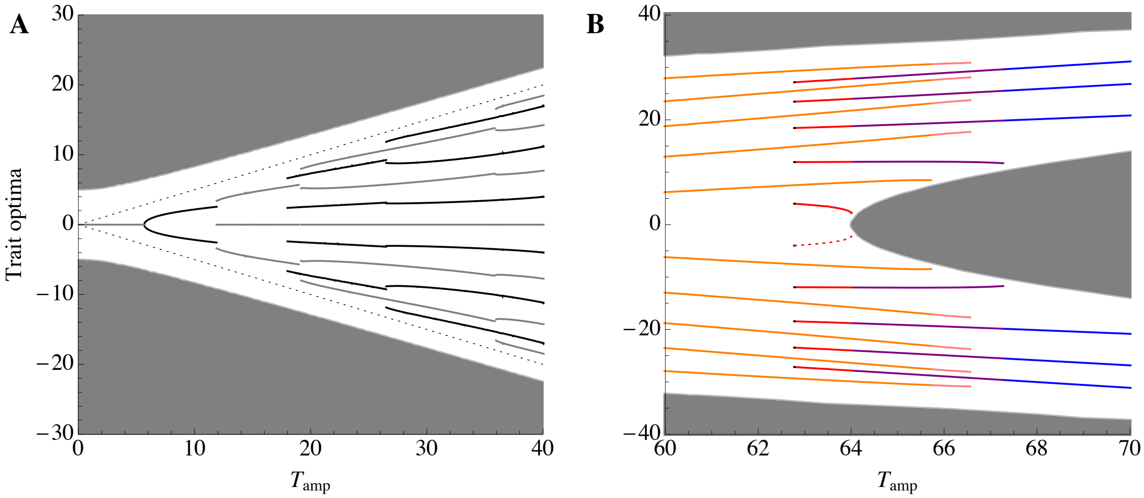

Figure 4.9 Detailed views of the ESS bifurcation diagram for the sinusoidal forcing function with μ_{max} = 0.02. A) Initial patterns of diversification are largely unchanged from μ_{max} = 1 (see Fig. 4.6 A). **B)** At higher T_{amp}, only even numbered ESS communities remain, including alternate ESS cases shown in different colors. Species with intermediate trait values begin to individually lose viability by $T_{amp} \approx 64$, leading to the collapse of ESS tracks as they intercept the envelope of viability. Interestingly, a pair of asymmetric ESS communities occurs (shown in red) around $T_{amp} \approx 63$, where either the central dashed or corresponding solid tracks are present, but not both (see section 2.6).

3.3 Accumulation of diversity and limiting similarity

A wealth of classic research and theoretical results focus on the concepts of competitive exclusion and limiting similarity, the idea that there are limits to how similar two species can be and yet coexist. Because evolutionarily stable communities must also be ecologically stable (ie, species must coexist), we expect (and observe) patterns of limiting similarity between the ESS species in our results. Ultimately, the number of species that can coexist ecologically and robustly in a given environment depends both on limits to how similar species can be and the size or dimensionality of the environment. In this section, we explore patterns of diversity and limiting similarity emerging from ESS communities as they develop across a range of T_{amp}.

For sinusoidal fluctuations, at high μ_{max}, diversity increases roughly linearly with T_{amp}. The number of species present in an ESS community is then roughly proportional to the size of the temporal niche (driven by T_{amp}) divided by the characteristic spacing between the most similar species (which converges on ~6 in diverse communities and should be sensitive to σ^2) (Fig. 4.10, A & C). We can approximate the actual level of diversity uncovered through the preceding ESS bifurcation analyses by quantifying the size of the viability region as a function of T_{amp} (ie, the range of traits allowing positive mean growth), as shown by the dashed line in Fig. 4.10 (A and B). For a lower value of μ_{max}, as before we observe initial increases in diversity. The diversity of the ESS communities peaks, then declines, as species with intermediate traits are lost. Whether increasing or decreasing, diversity levels are still roughly proportional to the width of the viability region (Fig. 4.10 B).

Similar results hold for the triangle wave fluctuations (Fig. 4.11). Diversity increases monotonically across a large range of T_{amp} given high μ_{max}, but peaks and declines abruptly with low μ_{max}. These trends are again quite neatly proportional to the width of the viability region. A characteristic separation develops between species adjacent to each other in trait space, saturating at a comparable level. These relationships do exhibit more scatter near the peak and collapse of diversity.

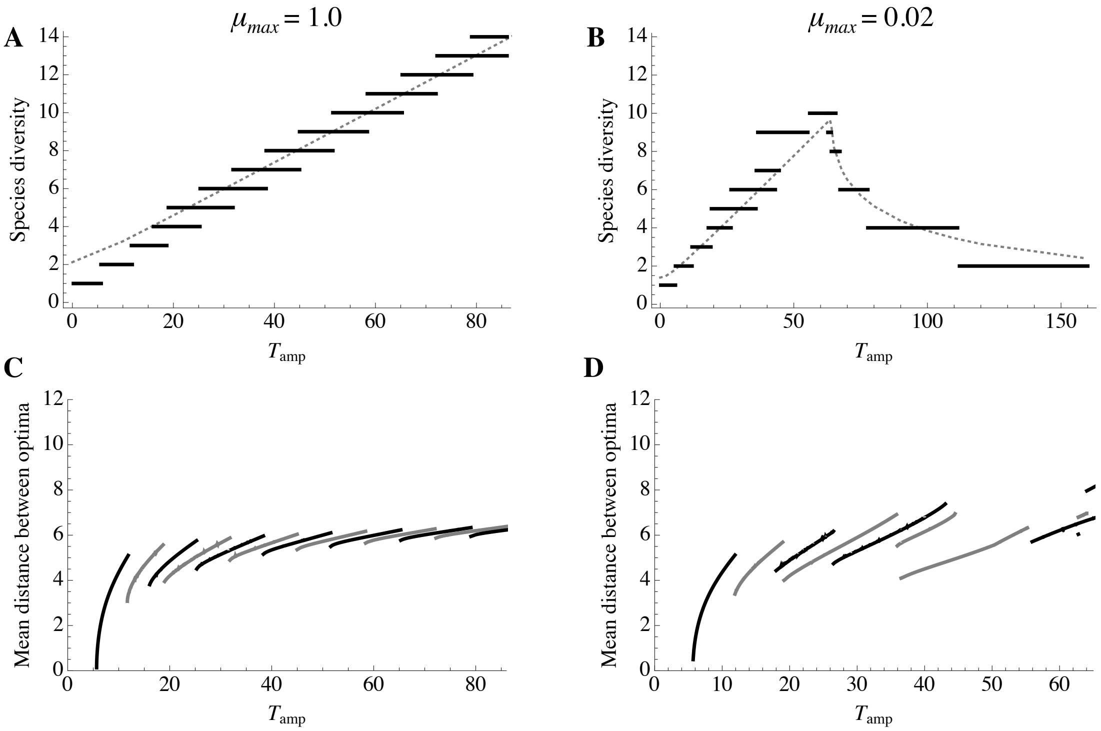

Figure 4.10 Derived patterns from ESS bifurcation diagrams given sinusoidal fluctuations. A) and **B)** provide diversity trends for different μ_{max}, with ESS community diversity indicated by black bars and the size of the viability region (scaled by 1/3.5) shown as the dashed gray line. **C)** and **D)** plot the mean distance between the traits of adjacent species in the ESS communities as a function of T_{amp}, with gray (black) lines representing odd (even) numbered communities, for different μ_{max}.

3.4 General patterns & theory

Some general patterns emerge from the construction of these bifurcation diagrams, considering the roles of μ_{max} (relative to m) and T_{amp} (relative to σ^2). In particular, we draw now on our results showing that the width of the viability region provides a readily computable and reasonably accurate estimate of the diversity of ESS communities (see previous section). Conceptually, these ideas are laid out in Fig. 4.12. This figure recognizes two significant axes governing model results. The first encompasses variation in T_{amp}, our

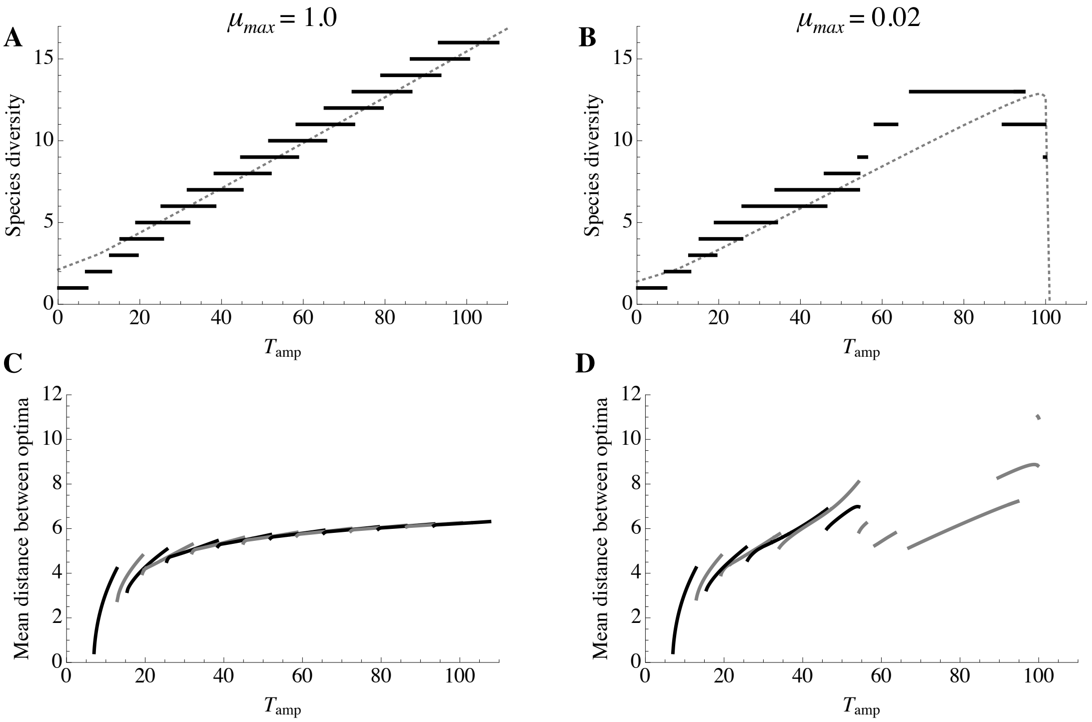

Figure 4.11 Same as Fig. 4.10 but for triangle wave fluctuations. Diversity trends are shown in **A)** and **B)** for different μ_{max}, while **C)** and **D)** again contain the trait difference between adjacent ESS species.

bifurcation parameter throughout the preceding work (which could be re-scaled by σ^2). The second, μ_{max} (relative to m), influences the point where diversity collapses in combination with T_{amp}, as we have shown. Each of our bifurcation diagrams (Fig. 4.7 and 4.8) represent detailed slices through this parameter space, at $\mu_{max} = 0.02$ and $\mu_{max} = 1$, across a range of T_{amp} values.

We have constructed analogs of this conceptual figure using the width of the viability region as a proxy for the diversity of ESS communities. This approach allowed us to explore a wider range of T_{amp} and μ_{max} values than is feasible using the full bifurcation analysis approach, given its complexity. Results are shown for both the sinusoidal and triangle wave forcing functions in Fig. 4.13 A and B. In general, diversity increases with T_{amp}, to some maximum level set by the balance of μ_{max} / m. At this point, diversity declines

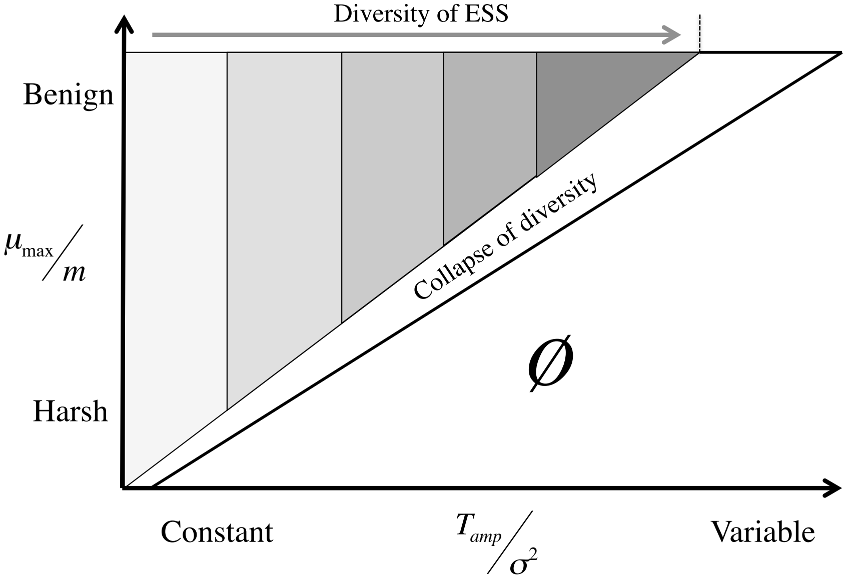

Figure 4.12. This figure provides a conceptual overview of the most important axes of parameter variation for our system. On the x-axis we have a comparison between the amplitude of fluctuations, T_{amp}, and the width of species' environmental tolerances (σ^2). On the y-axis we have a comparison of species' maximum growth rate and mortality rate (μ_{max}/m). In general, we expect (for most smooth, continuous fluctuations) that as T_{amp}/σ^2 increases, the diversity of an ESS community will increase approximately linearly. At some point, the increase in diversity will cease, as the environment begins to change so rapidly and over such an extreme range of values relative to sigma, that species cannot persist. The point at which diversity begins to collapse should be sensitive to the balance between maximum growth rate and mortality.

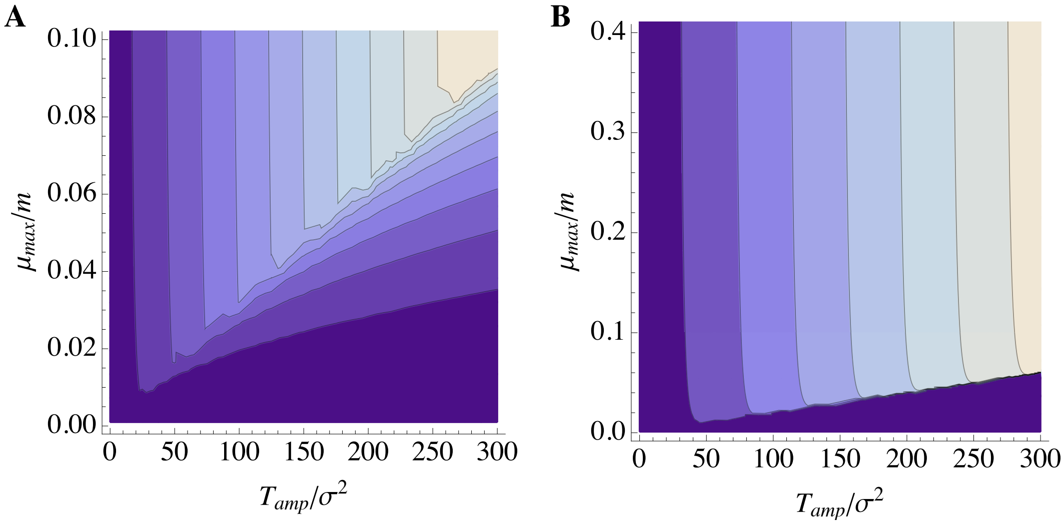

Figure 4.13. The size of the viability region (a proxy for ESS community diversity) increases with T_{amp}, (as shading goes from dark to light) but is limited by the balance between maximum growth rate and mortality (μ_{max}). **A)** Sinusoidal and **B)** triangle wave fluctuations yield different patterns; in particular, the abrupt collapse of diversity with triangle wave fluctuations is clearly discernable.

until no species remain. The form of this decline (gradual or abrupt) is influenced by differences in the distribution of environmental states imposed by different forcing functions.

4. Discussion & Conclusions

4.1 General patterns of diversity/coexistence

We have shown that temporal variation in species growth rates can produce diverse communities of coexisting species, each specializing on different environmental states occurring at different times over a period (Fig. 4.7 and 4.8). Furthermore, evolutionarily stable coexistence is possible.

As the amplitude of environmental fluctuations increases, more temporal niche space becomes available, allowing additional species to coexist and adding to the diversity of the community. However, increasing the range of temporal niches (environmental states) necessarily decreases the quality of these niches. As fluctuation amplitude grows too large, each environmental state persists for increasingly brief periods of time, limiting the growth and performance of species. Eventually, this leads to a decline in the diversity of evolutionarily stable communities, at a point that depends on the balance between maximum growth rate and mortality rate (Fig. 4.8 and 4.13).

While the bifurcation patterns generated by this system are complex, several consistent patterns emerge that transcend the arcane details of these bifurcation diagrams. In particular, the ESS communities exhibit consistent patterns of limiting similarity (characterized by the distance between adjacent species in trait space) from low to high diversity communities, and for multiple forcing functions (Fig. 4.10 and 4.11). This result is consistent with our expectation that evolutionarily stable communities must obey the same principles governing ecologically stable communities.

We are also able to approximate the diversity present in ESS communities for a given fluctuation amplitude, which we show is proportional to the range of environmental states over which any species with any trait can grow (the width of the viability region) (Fig. 4.10 and 4.11). The exact value of this proportionality should be intimately related to the niche width of species σ^2, which itself governs the degree of similarity possible between species in ESS communities. These results suggest that depending on the focus a particular study, estimates of community diversity could be made without invoking the complexities and analytical challenges of exactly determining ESS communities in specific environments.

4.2 Prevalence of alternative ESS communities

One of the intriguing theoretical results from this study suggests that the possibility of alternate ESS communities occurs over broad ranges of parameter space (Fig. 4.6-4.8). These alternate community states are analogous to the much-discussed phenomenon of alternate stable states explored theoretically and empirically over many decades (Beisner et al. 2003). While alternate ESS communities typically differ little in their diversity levels in our results, their constituent species display different trait values. These alternate possibilities also imply that the outcome of community assembly or evolutionary diversification in a given environment will depend on initial conditions and transient dynamics. Which ESS community arises will also depend on the convergence stability of each community, an important property considered as part of adaptive dynamics analyses (Geritz et al. 1998). Convergence stability becomes difficult to assess for highly diverse communities and non-equilibrium models, and is not addressed by our current results.

One informal numerical strategy that we employed to aid in initially identifying and tracking ESS communities involves simulating the eco-evolutionary dynamics of a set of k species, given some initial abundances and trait values. When trait values are allowed to change in response to (10), the net fitness gradient they experience over a period, their traits ideally converge gradually on an ESS community. When multiple ESS communities are possible, the particular ESS identified by this approach depends on the initial conditions we selected. It was often the case that one of a set of ESS communities was far more likely to occur across a range of initial conditions, suggesting that it had a much larger basin of attraction than the alternatives (CTK, personal observation).

4.3 Choice of forcing function drives diversity patterns

An important part of our analyses was exploring the consequences of different kinds of forcing functions. The vast majority of previous studies invoking periodic environmental forcing employ a sinusoidal function. Such functions are mathematically convenient as they are continuous, smooth and naturally periodic. Many environmental variables from temperate locations also exhibit fluctuations that are reasonably described by sine waves (such as temperature, and solar radiation). However, as shown by our results, the choice of forcing function can have dramatic effects on patterns of coexistence and ESS community structure. Sinusoidal fluctuations support (low diversity) communities across much wider ranges of fluctuation amplitude than triangle waves (Fig. 4.8). This phenomenon is due to the bimodal distribution of environmental states produced by the sine wave, which bolsters the viability of species with extreme trait values. Declines in diversity with increasing amplitude occur much more abruptly when environmental forcing follows a triangle wave (Fig. 4.8, 4.10 B and 4.11 B). The uniform distribution of environmental states favors (or disfavors) all species equally; when these states become rare enough that one species loses viability, all other species face the same situation.

When trying to predict the consequences of environmental change, such as an increase in temperature variation driven by climate change, on community structure, using an inappropriate forcing function that inaccurately captures the real distribution of environmental states could lead to dramatic errors. The default assumption of many existing studies (sinusoidal forcing) carries underappreciated and important consequences. Considering the distributions of environmental states implied by different forcing functions (see Fig. 4.1) offers an opportunity to link studies of deterministic fluctuations to those exploring temporal variation that is stochastic (which usually sample environmental states from probability distributions). Stochastic time series drawn from a distribution can quite often be matched by the appropriate choice of periodic function, matching the mean, range, and distribution of environmental states. The key remaining difference is that deterministic forcing functions specify a particular sequence of environmental states (autocorrelation structure), which may differ from stochastic variation.

4.4 Limitations of current results – theoretically

Our results answer several interesting questions and advance the work of Abrams et al. (2013) on the evolution of a temporal storage effect; we consider a continuous range of environments and highly diverse communities. However, there are several significant limitations to our work. Employing the SSD approximation (for computational reasons) required us to assume that the period of fluctuations is large relative to the rates of processes such as growth, death, and competitive exclusion. This assumption is reasonable for many, but certainly not all systems. The form of evolutionary analysis that we used requires a separation of evolutionary and ecological processes. However, sufficiently rapid evolution can alter coexistence predictions. When species competing for a fluctuating resource can adapt quickly to changing environmental conditions, temporal niche partitioning collapses (Kremer & Klausmeier 2013). We expect that rapid evolution would have a similar affect on coexistence in the current model, something that can be addressed in future work. Other analyses and intriguing extensions of the current model are possible. Many species are capable of dormancy, forming resting stages allowing them to dramatically reduce their mortality rates during bad times. Combining a structured population model with the model we present would allow us to study the effects of dormancy. Additional analyses even of the current results are possible, including a rigorous investigation of the convergence stability of ESS communities (including alternate ESS communities).

4.5 Limitations of current results – empirically

The current model is loosely motivated by our earlier work investigating the thermal adaptation of marine phytoplankton to variable ocean temperatures (Thomas et al. 2012). Phytoplankton growth rates exhibit unimodal responses to temperature, and different species achieve their maximum growth rates at different temperatures. These aspects of the real system are consistent with our work here (where our environmental variable becomes temperature). However, there are several important differences between these systems. First, in our present model we assume growth rates decline symmetrically away from a species' optimum environmental state, whereas real thermal tolerance curves are typically left skewed. This asymmetry would propagate, leading to asymmetric viability regions and ESS bifurcations. The width of empirical thermal tolerance curves are also substantially wider than those generated by assuming a σ^2 of 8, meaning that empirical systems likely exist at the lower values of T_{amp}/σ^2 (Thomas et al. 2012, Boyd et al. 2013, Thomas et al. in prep). In this region, temperature fluctuations on the order of annual ocean temperature variation support only a few species at best. However, this kind of model is appropriate for many ectothermic organisms facing temperature fluctuations, and may be suitable for other kinds of environmental fluctuations and organisms. Empirically, temperature variation supports the coexistence of competing microbes (Descamps-Julien & Gonzalez 2005, Jiang & Morin 2007). The diversity of marine foraminifera peaks at intermediate latitudes where temporal variation is highest, consistent with the habitats our model would predict to produce maximal diversity given the coexistence mechanism we study (Rutherford et al. 1999).

4.6 Multiple evolving traits

In the real world, the fitness of organisms is a product of many factors and likely dozens or hundreds of traits. Our results speak to the possible outcomes of selection on a single trait when that trait represents the most important determinant of fitness. Theoretical frameworks exist for studying the stability and simultaneous evolution and of two or more traits, a process typically governed not just by direct selection on each trait independently, but also contingent on the covariance between traits and tradeoffs in their ability to evolve (Leimar 2009). A natural next step for this work, again referring to the dynamics of thermal adaptation of phytoplankton, would be to consider the simultaneous evolution of both the optimum environmental state and the range of environmental states supporting growth (σ^2). Such a model would allow species to adjust both the environmental state that they specialize on and the degree to which they specialize at all. Ackermann & Doebli (2004) addressed a similar question, studying competition between species for a continuous range of resources; species evolved broad niches unless there was a cost to being a generalist. Empirically, different species and functional groups of phytoplankton exhibit variation in both their optima and niche width, suggesting that both are subject to selection in the wild (Thomas, Kremer, & Litchman, in prep).

While considering multiple evolving traits would lead to different predictions in terms of the traits and exact level of diversity of ESS communities, we expect that again several fundamental relationships will hold. Species diversity will remain less than or equal to what it could be without evolution (see exploration of generalist-specialist coexistence in Egas et al. 2004), and species that are too similar will not coexist or be present in ESS communities. Adding more trait dimensions allows species to differ in more ways, but sufficient similarity in even one dimension is enough to reduce the robustness and stability of coexistence (Meszéna et al. 2006).

4.7 Concluding remarks

Our results contribute to the limited number of studies exploring evolution and coexistence in temporally varying environments. We show that species specializing on different environmental states can coexist in a continuous, periodically varying environment, producing highly diverse and evolutionarily stable communities. We find that alternate ESS communities are not only possible, but also common across a range of conditions, challenging our ability to uniquely predict trait distributions in different habitats. The capacity of temporal variation to support diversity is not without limits, however. The diversity of ESS communities is tied closely to the amplitude of environmental fluctuations and inescapable patterns of limiting similarity between coexisting species. We also demonstrate that the selection of a continuous, periodic function driving environmental variation has important and underappreciated consequences for diversity patterns across a range of fluctuation amplitudes. Moving forward, more studies investigating eco-evolutionary dynamics in temporally varying habitats are needed, examining different kinds of fluctuations, forging links between deterministic and stochastic variation, and exploring models with asymmetry or multiple evolving traits. Such work will shed light on the form and function of communities structured by competition and selection in an ever-changing world.

5. Supplement A: Successional State Dynamics for continuously forced systems

The Successional State Dynamics (SSD) approach was first developed by Klausmeier (2010) and has subsequently been applied to a number of ecological models subject to piecewise periodic forcing (Klausmeier & Litchman 2012, Kremer & Klausmeier 2013). In the current work, we apply the SSD approach for the first time to a continuously forced periodic model. Here we provide additional details on this method and comment briefly on its application to continuous models.

At the heart of the SSD approach is the realization that as period length τ increases, given a periodically changing environment and fixed biological rates, several dynamical properties of the system become easily predictable. In particular, the system tends to exist at one of a finite number of discrete states at any fixed point in time. This is described in the main text, and time series for the finite τ model given increasingly long periods are show in Fig. 4.A.1 below. Any given species tends to exist in one of two conditions; either it is rare ($n_i \approx 0$) and increasing or decreasing in abundance ($\overline{g}_i \neq 0$), or it is dominant ($n_i \approx R_{tot}$) and at its equilibrium density ($\overline{g}_i = 0$). If we additionally let $\tau \to \infty$, several simplifications arise. We can shift from modeling the dynamics of population density n to tracking $N = \log(n)/\tau$ (see appendix of Klausmeier 2010). In the limit $\tau \to \infty$, N becomes 0 when a species is dominant (as $\log(n) \to \log(R_{tot})$) and negative when it is rare (as $\log(n) \to -\infty$). We can also rescale our time variable by period length τ, modifying the forcing functions (1a) and (1b) such that $\tau = 1$. Collectively, this implies that we can model the population dynamics of species i as

$$\frac{dN_i}{dt} = \begin{cases} 0 & \text{when dominant} \\ \overline{g_i} & \text{when rare} \end{cases} \tag{A.1}$$

Transitions between states of dominance occur as described in the main text, and between states where a species is dominant and the empty state as detailed in section 6, Supplement B. Ultimately, for sufficiently long periods, a plot of $\log(n) - \log(R_{tot})$ from the finite period model begins to agree extremely well with the corresponding dynamics for N_i returned by the model obtained from the SSD approximation with similar parameters (Fig. 4.A.2).

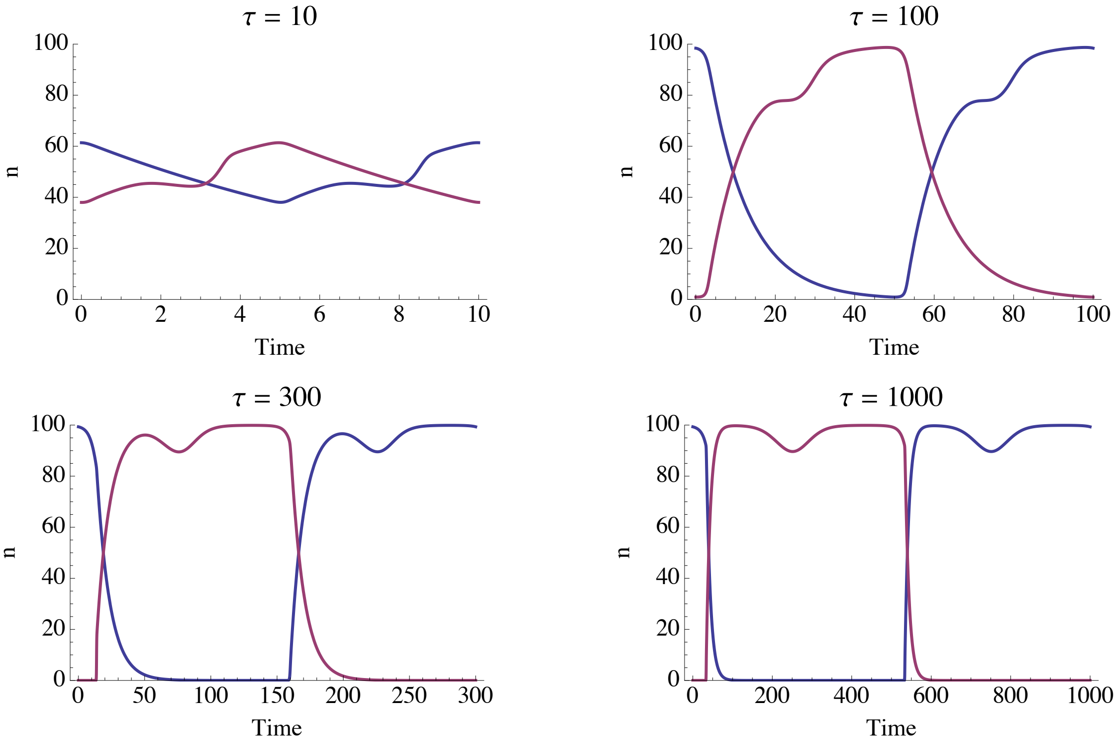

Figure 4.A.1. As period length τ increases, the time series of population density for two competing species are increasingly characterized by periods of dominance by one species (whose abundance is relatively constant) and sharp transitions between dominance. Traits z_1 = 6.093 and z_2 = 13.91, μ= 1, T_{amp} = 10.

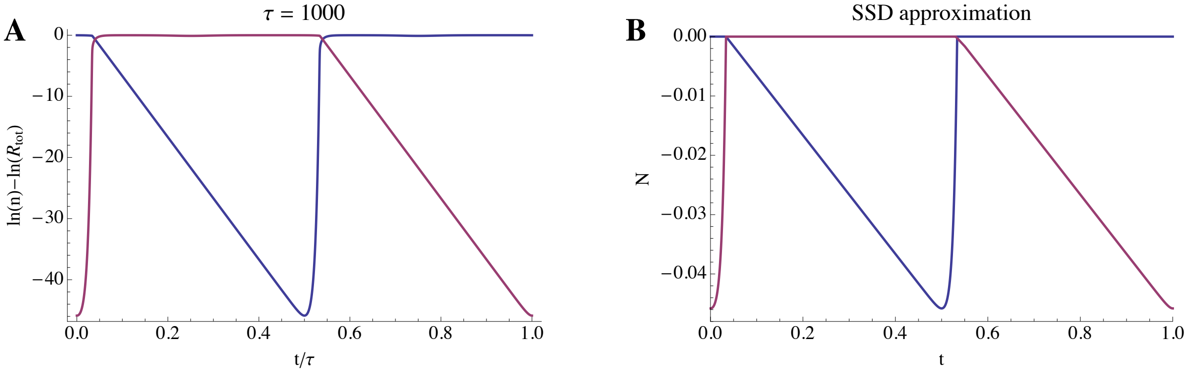

Figure 4.A.2. A) The transformed dynamics of the continuous periodic model for finite period length τ = 1000 correspond closely to **B)** the values obtained from the SSD approximation. Traits z_1 = 6.093 and z_2 = 13.91, μ= 1, T_{amp} = 10.

6. Supplement B: Environmental timings for sinusoidal and triangle waves.

6.1 Sinusoidal wave

For $T(t) = T_{av} + T_{amp}\, 2\, \pi \sin(t)$, we have up to 4 possible critical timings, where $R^* = R_{tot}$. These consist of

$$t_c = \begin{cases} \frac{1}{2} + \frac{1}{2\pi} \sin^{-1}\left[\frac{T_{av} - z + \sigma\sqrt{\log \frac{R_{tot}\mu_{max}}{m}}}{T_{amp}}\right] \\ \frac{1}{2} + \frac{1}{2\pi} \sin^{-1}\left[\frac{T_{av} - z - \sigma\sqrt{\log \frac{R_{tot}\mu_{max}}{m}}}{T_{amp}}\right] \\ \frac{-1}{2\pi} \sin^{-1}\left[\frac{T_{av} - z + \sigma\sqrt{\log \frac{R_{tot}\mu_{max}}{m}}}{T_{amp}}\right] \\ \frac{1}{2\pi} \sin^{-1}\left[\frac{-T_{av} + z + \sigma\sqrt{\log \frac{R_{tot}\mu_{max}}{m}}}{T_{amp}}\right] \end{cases} \tag{B.1}$$

Of these, at most two will correspond to transitions where R^* is increasing above R_{tot}. To determine which case we are in, we must consider $dR^*/dt > 0$, as follows:

$$\frac{dR^*}{dt} = \frac{4m\pi T_{amp}}{\sigma^2 \mu(T,z)} \cos(2\pi t)(T - z) \tag{B.2}$$

The sign of (B.2) depends on the product $\cos(2\pi t)(T - z)$ as all other terms are positive. So, we can evaluate

$$\cos(2\pi t)(T(t) - z)\Big|_{t=t_c} \tag{B.3}$$

for each permissible t_c. When (B.3) > 0, then the corresponding t_c provides the timing of a state change from dominance of the current species with trait z to the empty state. This would, of course, only occur if the current species were dominant prior the transition (which, due to competition, is not a guarantee).

6.2 Triangle wave

Given that $T(t)$ is a triangle wave, four possible critical values t_c exist where $R^*(t) = R_{tot}$, for all combinations of ± in the following expression:

$$t_c = \frac{z + T_{amp} \pm T_{av} \pm \sigma \sqrt{\log \frac{R_{tot}\mu_{max}}{m}}}{4T_{amp}} \tag{B.4}$$

Of these, we are only interested in cases where $0 \leq t_c \leq 1$ and where $dR^*/dt > 0$, as these correspond to situations where R^* is increasing above R_{tot}. We can solve for (and simplify) dR^*/dt, obtaining:

$$\frac{dR^*}{dt} = \frac{8mT_{amp}}{\sigma^2 \mu\left(T, z\right)}\left(T - z\right) \tag{B.5}$$

The sign of (B.5) depends only on the term $(T - z)$ as all other terms are positive. So, we can evaluate

$$\left.\left(T\left(t\right) - z\right)\right|_{t=t_c} \tag{B.6}$$

for each permissible t_c. When (B.6) > 0, then the corresponding t_c provides the timing of a state change from dominance of the current species with trait z to the empty state.

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