COMMUNITY COMPOSITION AND COEXISTENCE: THE EFFECTS OF TEMPORAL VARIATION AND ENVIRONMENTAL FORCING ON COMMUNITY TRAIT DISTRIBUTIONS AND DIVERSITY

By

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ABSTRACT

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Community ecology is complicated and difficult, but global climate change and massive biodiversity loss makes it imperative that we strive toward a coherent understanding of the processes that guide community assembly and structure. In this dissertation I look at how communities are assembled and diversity is maintained in the phytoplankton through both data-driven and theoretical methods, using a trait-based approach to understand the mechanistic basis of community structure and diversity. The first chapter asks what environmental factors drive the distribution of a crucial trait, cell size across a broad spatial scale. The theory chapters are concerned with the role of environmental variation in maintaining diversity. In all, I highlight the importance of temporal variation in shaping the function of communities.

I dedicate this dissertation
To my academic brothers Colin and Mridul
To my best friend Lisa
To my love Joe

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INTRODUCTION

Biodiversity loss is one of the most pressing ecological problems of our time. We are currently living in what researchers have called the sixth mass extinction, with species losses up to 100 times higher than expected background rates (Ceballos *et al.*, 2015). Ecological communities face ever-worsening habitat loss, changing climate, and invasion by introduced species. As scientists and conservationists race to preserve what diversity remains, we are hindered by a lack of a cohesive theory of how communities are shaped and diversity is maintained. To adequately respond to the drastic changes occurring across biological communities, we must work toward an understanding of communities and what processes control community assembly and diversity.

One way to create a predictive framework for community ecology is to examine species in terms of their traits, and consequently to understand communities in terms of trait distributions (McGill *et al.*, 2006). Trait-based ecology is not new (Grime, 1974; Austin, 1982) but its current renaissance has been buoyed by more advanced statistical capabilities and growing databases of traits and species distributions. It has the double advantage of allowing comparison between communities and incorporating a framework for evolutionary analysis. Comparison across communities is facilitated by the use of traits rather than species identities to understand the community composition. Two communities dissimilar in species may in fact be similar in function (Fukami *et al.*, 2005). Evolutionary analysis is also facilitated because the same process of selection that leads to a change in the trait distribution within a community through species turnover can lead to change in the trait distribution within individual species (Ackerly, 2003). It is increasingly appreciated that the processes of ecology and evolution can happen on similar timescales (Thompson, 1998; Hairston *et al*., 2005). To understand ecological dynamics, especially long-term ecological outcomes, we must consider evolutionary processes.

Phytoplankton are an ideal system in which to study the regulation of community traits and diversity (Litchman & Klausmeier, 2008). They are diverse and ancient, and represent a wide swath of the tree of life. They form the basis of most aquatic food webs and so changes in the phytoplankton community can have profound effects through higher trophic levels. Freshwater phytoplankton communities are also conveniently quantized into lakes. For the pelagic communities within these lakes, their environmental conditions can be defined relatively easily with little spatial structure apart from depth gradients in light and nutrients, and even that is lacking in the mixed layer. The maintenance of diversity within the phytoplankton has fascinated ecologists for years (Hutchinson, 1961). For theoretical purposes they lend themselves nicely to differential equations because of their fast turnover and high densities. They have been the system of choice for many theoretical studies of coexistence (Tilman, 1977; Grover, 1995; Abrams & Walters, 1996; Litchman & Klausmeier, 2001; Klausmeier *et al*., 2007).

In this dissertation I look at how communities are assembled and diversity is maintained in the phytoplankton through both data-driven and theoretical methods. The first chapter asks what environmental factors drive the distribution of a crucial trait, cell size across a broad spatial scale. The theory chapters are concerned with the role of environmental variation in maintaining diversity. Because these are eco-evolutionary models, they track the distribution of traits within the community through time.

Chapter Summaries

In chapter 1 of this dissertation (Controls of continental-scale patterns of phytoplankton cell size distributions), I look at how the distribution of cell size traits in the phytoplankton communities of freshwater lakes in the US changes across environmental gradients. Cell size is an important phytoplankton trait that affects resource cycling and trophic processes. I test a set of empirical and theoretical hypotheses about how mean cell size and variation in cell size in communities change with environmental and geographical factors including temperature, nutrients, latitude and altitude. Investigating how trait distributions change over environmental gradients has been mainly the province of terrestrial ecologists (Wright *et al.*, 2004; Westoby & Wright, 2006; Swenson & Weiser, 2010), but see Thomas et al (2012). Using large datasets, I can see whether hypothesized trait-environmental interactions are borne out and what are the most important factors shaping community assembly and gain a better understanding of to what extent environmental factors can explain the variation in ecological communities (Moller & Jennions, 2002).

In chapters 2 and 3, I use eco-evolutionary modeling to understand the role of temporal variation in maintaining species diversity. Temporal variation is ubiquitous in ecological systems, and it has long been seen as one of the major drivers of diversity especially in the phytoplankton. Hutchinson (1961) pointed to environmental variation and seasonal succession as one of the solutions to his paradox of the plankton.

Much of coexistence theory is based on models that assume static species traits, but in systems like phytoplankton where growth rates are high and populations are large, evolutionary forces must also be accounted for. Coexistence that is stable for non-evolving populations might break down if those populations are allowed to evolve to their trait optima. An evolutionarily unstable coexistence mechanism could probably not account for long-term coexistence. For these chapters, I use adaptive dynamics techniques (Geritz *et al.*, 1998) that allow the investigation of both ecological and evolutionary processes.

In chapter 2 (Evolutionary stability of coexistence due to the storage effect in a two-season model) I look at the evolutionary stability of one particular coexistence mechanism, the storage effect. This mechanism works through species differentiating in their environmental response traits. Because they experience different "good" and "bad" times, coexisting species have different temporal niches. This study looks at the effect of temperature fluctuations on phytoplankton communities that are competing for a single resource. By varying the frequency of these temperature fluctuations and the duration of each season, the model explores the range of conditions under which species specializing on different seasons can coexist.

In chapter 3 (Synergistic or independent interaction of relative non-linearity and the storage effect: How environmental variation affects the potential for diversity) I extend my study of theoretical coexistence mechanisms to include the interaction between two different mechanisms. Both mechanisms, the storage effect and relative nonlinearity, depend on variation in the environment to allow coexistence. The interaction of coexistence mechanisms been rarely studied, even though it is often assumed that to account for the diversity observed in the natural world many mechanisms must work at once. In this chapter I look at how the magnitude and type of variation in the environment affects the diversity that can be maintained and whether the two coexistence mechanisms interact synergistically to produce diversity that would not be expected by examining either mechanism working on its own.

Main Results and Significance

In chapter 1, I show that the mean cell size in phytoplankton communities is most strongly affected by altitude and latitude, but that pH and total phosphorus also have an effect. The main factors affecting the variance in cell size (functional diversity) are again altitude and latitude, but cell size variance also depends on variation in temperature and species richness. The total amount of variance explained is moderate (r^2 between 0.16 and 0.27) but well within the range of similar studies in plants (Moles *et al.*, 2014). One important result was that analyses that looked at the time-integrated trait distribution and environment of a lake had higher r^2 than analyses that considered each sampling date. This implies that the selective factors that shape phytoplankton communities act over longer timescales and that single measurements of a lake and its community will not give an accurate picture.

In chapter 2, I find that the potential for coexistence of two species competing in a two-season environment depends heavily on the frequency of fluctuations in the environment relative to the lifespan of the competitors. When the competitors can complete several life cycles per season, coexistence is easier to achieve than when the seasons change more quickly. This finding means that I can expect the storage effect to contribute to species diversity only when the environment has long period fluctuations or when species lifespans are relatively short compared to the period of fluctuations.

In chapter 3, I find that the storage effect and relative non-linearity interact to produce more diversity than would be expected from either one alone when the variation in the environment is continuous as opposed to a model of discrete seasons. The different outcomes in these scenarios seems to be due to the fact that continuous change in the environment leads to a continuous temperature niche (as opposed to two discrete niches) which increases the overall dimensionality of trait space. This may mean that coexistence mechanisms that rely on continuous niche space (like a resource spectrum) are more likely to interact with each other and produce more diversity than mechanism that rely on discrete niches (such as substitutable resources).

Overall, this dissertation highlights the importance of temporal variation in maintaining the diversity of phytoplankton communities, both in theory and in nature. The statistical results show the extent to which we can understand the factors controlling community structure across continental scales and the modeling results give insight into the maintenance of diversity across systems.

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CHAPTER 1

CONTROLS OF CONTINENTAL-SCALE PATTERNS OF PHYTOPLANKTON CELL SIZE DISTRIBUTIONS

Abstract

Cell size is an important trait in phytoplankton communities because it affects processes ranging from predation to nutrient uptake. Both the mean and variance of cell size in a community are hypothesized to be affected by multiple drivers. In this study I combine a database of phytoplankton cell sizes with a continental-scale database of United States lakes to investigate the role of temperature, nutrients, mixed layer depth, latitude, altitude, pH, and environmental variation on the mean and variance of the distribution of cell sizes in the phytoplankton communities. I analyze the data at two temporal scales: instantaneous (within one sampling date) and yearly (averaged within a lake across multiple sampling dates). I compare standard bivariate regressions to structural equation models to disentangle direct and indirect effects as well as correlated drivers. I find that although many factors hypothesized to govern cell size and variance in cell size are significant across continental scales, the overall effect sizes are small. Altitude had the strongest overall effect on both mean cell size and cell size variance and latitude also had a strong effect on cell-size variance. Interestingly, yearly analyses are more predictive than those that consider only single sampling events.

Introduction

The search for general rules in community ecology is a fraught and sometimes disheartening topic (Lawton 1999; Simberloff 2004). How can ecologists hope to explain the vast and idiosyncratic differences between communities over space and time? One of the ways that we can simplify the complexity and come to some mechanistic conclusions is to examine the trait distributions within communities and over environmental gradients (McGill et al. 2006). The interaction between the traits of a species and environmental conditions determine where and when it will thrive (Webb et al. 2010). By examining the distribution of traits within communities over a gradient in a particular environmental factor, we can come to understand the contribution of that factor to shaping those communities. In the past decade, studies have examined the distribution of traits over environmental gradients to understand everything from adaptive radiations (Ingram and Shurin 2009) to species ranges (Sonnier et al. 2010) to predicting responses to climate change (Thomas et al. 2012). Examining the way that trait distributions change over environmental gradients is an important tool for understanding what factors shape complex communities.

Phytoplankton communities form the base of many aquatic food webs, fixing the carbon that makes possible all other life in most aquatic ecosystems. One of the most important phytoplankton traits is size. Cell size in phytoplankton is often referred to as a “master trait” (Brown et al. 2004; Litchman and Klausmeier 2008) because it influences many aspects of performance, including nutrient uptake (Bratbak and Thingstad 1985; Thingstad et al. 2005; Yoshiyama and Klausmeier 2008), sinking rate (Reynolds 1984), grazing susceptibility (Sunda and Hardison 2010), and growth rate (Banse 1976; Chisholm 1992). The size structure of the community greatly influences the flow of nutrients through the trophic levels and nutrient cycling within the community (Legendre and Rassoulzadegan 1997; Finkel et al. 2009). Consequently, understanding what factors determine cell size in phytoplankton communities can give a great deal of insight into the overall performance of lake ecosystems as well as phytoplankton communities.

In addition, the variation in cell size within a community is a good proxy for the level of functional diversity in that community. For example, since different zooplankton grazers have different size preferences, variation in cell size with the phytoplankton community would imply variation in the grazer community it can support. Functional diversity is relevant to invasibility by introduced species (Fridley et al. 2007), ecosystem services provided by a community (Gamfeldt and Hillebrand 2008), and biodiversity conservation. Finally, the maintenance of diversity is a fundamental question in ecology and understanding what drivers lead to more or less functional diversity is crucial to understanding how diversity is maintained.

Many factors have been proposed to explain cell size and variation in cell size in phytoplankton communities. In this paper I test them with a large and comprehensive dataset of freshwater phytoplankton communities collected by the EPA (Stomp et al. 2011) in conjunction with a database of cell sizes for individual species (Kremer et al. 2014). By combining these two datasets, I can get an estimate of mean cell size and cell size variance for each lake community sample, resulting in a comprehensive picture of what drives cell size in phytoplankton across a continental-scale range.

Overview of Hypothesized Drivers of Cell Size Patterns

In the following paragraphs I review some proposed drivers and the justifications for their effects on average cell size in a community (mean size), variance in cell size within a community (cell size variance) or both (summary in Table 1.1). Because the EPA National Eutrophication Survey did not collect information on zooplankton, I cannot directly explore the role of grazers on cell size distribution and, consequently, focus on the abiotic drivers.

Temperature – Mean Size

As temperature increases the size of organisms are often observed to decrease, a ubiquitous pattern commonly referred to as the Temperature-Size Rule. Within species it is thought to arise because increases in temperature lead to larger increases in reproductive rate than growth rate with adults maturing at smaller sizes (Atkinson 1994; Atkinson and Sibly 1997). For phytoplankton, the discrepancy between increases in growth and reproductive rate means that cells divide at a smaller size at higher temperatures. A decrease in size at division leads to a decrease in size within species, but not necessarily replacement of larger species with smaller ones. Species replacement toward smaller celled species is regularly observed in oceans over an increasing temperature gradient (Morán et al. 2010; Mousing et al. 2014; López-Urrutia and Morán 2015). The decrease in size with temperature is sometimes attributed to differences in nutrient supply and sinking rate with increased stratification (Marañón et al. 2012), but in microcosom experiments Peter and colleagues (2012) showed that temperature *per se* had a strong species composition effect on the size structure. They propose an interaction between temperature and nutrients, with an increase in the requirements for nutrients at higher temperatures, leading smaller cells to be more competitive. Dataset compilations in the world oceans have also shown direct temperature effects on species replacement (Mousing et al. 2014; López-Urrutia and Morán 2015).

Nutrients – Mean Size and Size Variance

Smaller cells are assumed to be better nutrient competitors due to an increased rate of nutrient uptake (Smith and Kalff 1982), increased maximal growth rate (Banse 1976; Sommer 1983) and decreased cross-membrane transfer limitation due to increased surface area to volume ratio for spherical cells (Grover 1989). The effect of size on nutrient uptake capacity leads to selection for a decrease in cell size with a decrease in nutrient availability (Parsons and Takahashi 1973; Grover 1989; Chisholm 1992; Yoshiyama and Klausmeier 2008). The pattern of decreasing size with decreasing nutrients is so strong that the dominance of small cells when major nutrients appear to be abundant leads to suspicion of limitation by some other trace nutrient (Chisholm 1992). The decrease in cell size with decrease in nutrients has been seen in global marine datasets (Marañón et al. 2012; Marañón et al. 2015) and in experiments (Peter and Sommer 2015). In combination with smaller cell sizes being better nutrient competitors, increasing nutrient concentrations should support the addition of increasing size classes because larger species, that are poorer competitors but better defended against grazers can invade when the nutrients are increased (Chisholm 1992; Armstrong 1994; Grover 1994; Irwin 2006). The addition of larger size classes should lead to an increase in mean size and cell size variance at higher nutrient concentrations.

Mixed Layer Depth – Mean Size

When a lake stratifies it, cells that sink out of the mixed layer often sink out of the photic zone where they can no longer reproduce. A shallower mixed layer leads to higher sedimentation rates (Diehl 2002; Diehl et al. 2002), which can lead to a decrease in the prevalence of sinking taxa when the mixed layer is shallow (Ptacnik et al. 2003). Because cell size positively affects sinking rates (Reynolds 1984), I expect a positive correlation between cell size and the depth of the mixed layer. In addition, when a mixed layer forms it prevents nutrients from the hypolimnion from reaching the mixed layer. Since the bulk of the light availability is at shallow depths, the rapid cell growth there quickly depletes the nutrient supply, and a shallower mixed layer leads to a more nutrient limited surface layer (Taylor and Joint 1990). Since smaller cells are better nutrient competitors, this is a second mechanism by which a shallower mixed layer should lead to smaller cells.

Latitude – Size Variance

The latitudinal diversity gradient (Pianka 1966) is the well documented, yet poorly understood pattern of higher diversity toward the equator than at the poles. The pattern is present in a wide and comprehensive array of taxa (as reviewed by Hillebrand (2004)), including freshwater phytoplankton (Stomp et al. 2011). Many explanations have been proposed including the increased length of time for speciation, increased carrying capacity of species, and increased rate of diversification, summarized by Mittelbach et al (2007). One explanation that is particularly relevant for this study is the increase in interspecific interactions at lower latitudes (Schemske et al. 2009). It is hypothesized that interspecific interactions open up new and different niches (due to coevolution) than those that are set by abiotic factors alone. More species occupying different niches is reflected in an increase in functional diversity. Phytoplankton might experience a change in diversity over latitude due to more constant and possibly benign lake conditions with no winter freeze. The relaxation of requirements to survive the winter could allow for more complex interspecific interactions and therefore more functional diversity.

Altitude—Mean Size and Size Variance

Altitude itself may not have direct effects on cell size, but increases in elevation lead to an increase in ultra-violet light (UV) exposure. Cells are sensitive to the degrading effect of UV and the greater the surface area to volume ratio, the more UV can penetrate the cell and damage the DNA (Karentz et al. 1991). The fitness effects of UV damage makes smaller cells more sensitive to UV than larger cells (Karentz et al. 1991; Litchman et al. 2002), leading to a positive effect of altitude on cell size.

The altitudinal diversity gradient is also a well-studied pattern in ecology. Usually it is seen as a unimodal relationship (Rahbek 2004) or a decrease in diversity with altitude (Nogués-Bravo et al. 2008). One explanation for loss of diversity with altitude is that a decrease in the area of similar climate with an increase in altitude leads to a smaller pool of possible species (Rahbek 1995). There are fewer lakes at the top of a mountain than its base, and thus it supports fewer species by the diversity-area relationship (Lomolino 2001). The same pattern has been found in aquatic plants (Jones et al. 2003) and I predict that I will see the same effect of decreasing functional diversity with altitude in a negative relationship between cell size variance and altitude.

pH—Mean Size and Size Variance

Studies of acidification have shown that experimental acidification induces an increase in mean cell size in phytoplankton (Schindler 1990; Havens and Heath 1991). One possible mechanism is that acidification alters the grazer community by decreasing the prevalence of larger grazers and relaxing grazing pressure on larger cells (Havens 1992). The lack of grazers will lead to a relative increase in size and therefore a negative relationship between pH and mean size in my study. In addition, many studies of anthropogenically and experimentally acidified lakes show a marked decrease in species diversity as the pH decreases (Findlay and Kasian 1990; Schindler 1990). Again, I would expect to see a decrease in species diversity accompanied by a decrease in variance in cell size.

Environmental Variability – Size Variance

The idea that environmental variability can support functional diversity in the phytoplankton community goes back to Hutchinson's "paradox of the plankton" (1961). The theoretical justification for the influence of environmental fluctuations on species diversity has a long history (Armstrong and McGehee 1976; Grover 1991a; Chesson 1994; Litchman and Klausmeier 2001). Variability in environmental factors can open up more niches for coexistence, with species specializing on environmental conditions that occur at different times (the storage effect) (Chesson 1994). In addition, species can coexist on variable resources if they experience a tradeoff between performance at high and low resource availability (relative non-linearity) (Chesson 1994). Experimental tests have also borne out the idea that increased environmental variability (especially in nutrient availability) leads to increased diversity (Sommer 1984; Grover 1991b). Thus, I expect to see the increase in functional diversity associated with an increase in cell size variance in important environmental factors (temperature, nutrients, pH).

Research Questions & Approach

This paper answers two types of questions: 1) Do the lake phytoplankton data support my hypotheses about the effects of individual drivers on the community mean cell size and variance? 2) Taken together, how well do these drivers predict the cell size distribution of a community? These questions reflect distinct scientific purposes. The first question is concerned with hypothesis testing: how do environmental factors affect the cell size of a community, and do the conclusions drawn from laboratory studies apply over a large scale? Hypotheses about the effects of individual factors on cell size can be assessed by examining the significance of relationships between the drivers and cell size mean and variance, and is most concerned with the responses to a single driver at a time. The second question is one of predictability: how well can I predict the size structure of the communities? This question can by assessed by examining effect size and r^2 and though multiple regression.

Testing whether the above predictions are borne out on a continental scale seems straightforward: simple bivariate linear models would show whether I see the expected correlation between environmental factor and response. However, many of the drivers are correlated, such as temperature and nutrients, leading to the problem of potentially spurious relationships between mean cell size or cell size variance and the predicted driver. Two recent papers that illustrate the problem of correlated drivers analyze the same data but come to differing conclusions about the effect of temperature on cell size. López-Urrutia and Morán (2015) conclude that temperature drives the relative percentage of pico- and nano-plankton in the ocean, while Marañón and colleagues (2015) suggest that their results were due to the correlation between temperature and nutrients, and nutrient levels are actually driving the relationship. Clearly, the problem of correlated drivers can obscure what is affecting cell size. In both of these papers the authors subset the data into groups of similar nutrient concentration to get around the correlated drivers, but multiple regression provides another solution. An additional complication with my current study is that drivers are not just correlated but possibly causally related. For example, latitude is expected to affect temperature, but not the other way around, leading to a specific direction of causality not captured by multiple regression. Structural equation modeling (SEM) (Kline 2011; Grace et al. 2014) can help address these issues. SEM analyses allow for hierarchical and causal relationships as well as correlations as way to sort out complex causal networks. Looking at another complex question, diversity-productivity relationships, Grace et al (2014) found that explicitly stating the causal network lead to more robust conclusions than bivariate analysis alone.

Characterizing the Cell Size Distribution

Any distribution can be characterized fully by an infinite series of descriptive statistics known as a moment expansion. The first two terms in the series are the familiar and often used mean and variance. For a normal distribution, these two terms are sufficient to perfectly describe the whole distribution. For any other distributions, they provide two key pieces of information: where the distribution is centered and how far it spreads. For the questions posed in this study, changes in the mean size give a good approximation of changes in the location of the size distribution, or the overall cell size of the community, and changes in the variance in size give a good approximation of changes in the width of the size distribution, or the size diversity within the community. Calculating these values is not completely straightforward since I do not have data on each individual cell. My data gives species counts and sizes in each community and so I weight cell size mean and variance by abundance. Another recent study (Peter and Sommer 2013) uses the same abundance weighting to look at the interactive effects of warming and nutrient limitation on cell size.

Phytoplankton communities and their trait distributions are not constant in time and most lakes in the EPA survey were sampled multiple times throughout the growing season. These multiple measurements give us the opportunity to consider multiple timescales in my analysis. Because phytoplankton communities turn over quickly (Sommer et al. 1986), an instantaneous snapshot of the community (a single sampling) might reflect the current selection pressures faced by the community, although there might be a lag between the community and environmental conditions leading to transitory communities (Klausmeier & Litchman 2012, Chapter 2 of this thesis). Instantaneous measures of community trait distributions will be most useful when environmental changes on the same time scale or more slowly than the population dynamics. I would particularly expect instantaneous measures to reflect variation that is driven by the community itself. For example, since phytoplankton consumption often drives the nutrient concentration, I would expect phytoplankton dynamics and nutrient dynamics to be on similar timescales. If, on the other hand, population dynamics are slower than environmental change, I would expect to see the signal of environmental forcing in the yearly trait distributions. To understand the yearly dynamics I can aggregate the communities over all sampling dates within a year. Yearly dynamics are especially relevant when I ask about the effect of environmental variability on cell size variance.

Methods

Data

In the 1970s the Environmental Protection Agency (EPA) conducted an extensive survey of lakes in the contiguous United States. The full description of the data collection methods can be found in Taylor et al (1979) and I provide a brief summary here. The EPA surveyed 540 lakes across the US, chosen by relevance to water quality and recreation concerns as well as to represent a large cross section of the eutrophication gradient. Generally, lakes were sampled three times within a year (spring, summer, fall) but sometimes they were sampled one to four times. Four-meter integrated water samples were taken from the surface over the deepest point and subsampled for chemical analysis and algal identification and enumeration. Algal samples were identified to the species or genus level. All other measurements were taken according to EPA protocol. To provide a complete picture of the factors affecting cell size, I included the following covariates from the dataset: temperature at the surface; total phosphorus, total nitrogen, Secchi depth, pH, and chlorophyll a from the integrated sample; surface area, lake depth, latitude, and longitude. I determined depth of the mixed layer (MLD) by fitting a logistic function to the temperature profile and estimating a threshold value, for those profiles that were not best fit by a logistic function I assumed that the lake was mixed to the bottom. I determined altitude using Google Maps with latitude and longitude as provided in the dataset.

The phytoplankton community data was matched against the AlgaeBase database (Guiry and Guiry 2013) to provide the most consistent taxonomy, and then matched against Kremer *et al*.'s (2014) cell size database to provide cell sizes for each species. This database compiles many measurements for each species and I used the median measurement as the cell size estimate. I were able to find cell sizes for roughly 80% of the species and 95% of the cells. For colonial species the EPA dataset reported number of colonies, and so I used colony size as the unit measure, also from the Kremer et al database. Unit size is the relevant measure for many processes of interest including nutrient uptake, sinking, and grazing resistance. I calculated richness as the number of species counted per lake on a single sampling date.

Mean and Variance in Community Cell Size

To calculate community mean and variance in cell size, I weighted all calculations by the number of algal units (cells and colonies) represented by each species. I calculated all metrics on the $\log_{10}$ size. I calculated the mean cell size by multiplying the size ($\log_{10}$ size) of each species in a community by the percentage of the community it represents (by count) and then summing this value across all species in a given sample. I calculated the cell size variance by taking the variance of all the logged sizes in the community. The variance of the logged size had an extremely skewed distribution, and so I logged it in my analyses. For the instantaneous analyses I treated each sampling date as a separate data point. For the yearly measures, I summed the counts for each species across the sampling dates to gain a whole year count. This yearly summed community was then used to calculate the average size or variance in size as above. For the environmental variability analyses, I used only the lakes where there were at least three sampling dates (all but six of 540 lakes).

Statistical Analysis

Questions about individual factor influence and overall predictability require different analytical methods. To address the first question, about whether the hypothesized drivers affected the cell size mean and variance, I used standard least squares regressions. Then, I checked whether these results were caused by correlated drivers using Structural Equation Modeling. The SEM analysis also quantified the overall predictability of cell size. All of my statistical analyses and data manipulation were done in the R statistical environment (R Core Team 2014). I tested my a priori expectations using linear regression. There were no visually obvious curvilinear relationships, so it was not necessary to introduce non-linear methods.

SEM Methods

The first step in any SEM analysis is to define an initial model that contains all of the factors and connections deemed potentially important. I arranged the predictor variables in four hierarchical levels that represented a flow of causality: 1) geographical, 2) physical, 3) chemical/resource, and 4) biological. Predictors could be correlated with others on their own level, but I assumed to have a causal relationship to those on higher levels so the flow of causality was always in the direction from geographical to biological. The geographical variables (latitude, longitude, and altitude) could not be caused by any of the other variables in the model, and were initially set as causal to all other variables and correlated among themselves. The physical variables were depth, surface area, and temperature for the cell size variance models, with MLD added for the size models. The chemical/resource variables were TN, TP, pH, and Secchi depth. Finally, the biological variables were richness, Chla, Chla^2 (added because of a hypothesized hump shaped relationship between diversity and productivity (Abrams 1995; Waide et al. 1999; Mittelbach et al. 2001)) for cell size variance models. I omitted Chla^2 in the size models for lack of any hypotheses about a hump-shaped relationship between size and productivity. These biological variables were not causal to any others, but could be correlated amongst themselves. Additionally, in the yearly cell size variance models I had the environmental variability measures to include. These were variance in temperature, included as a physical factor, and variance in TN and TP included as chemical/resource factors. The schematic of the initial models for all four SEM models are given in Figure 1.1.

I began with causal links that included all of my hypothesized cell size mean and variance drivers as well as any reasonable causal links among the drivers. For example, latitude was hypothesized to have a causal effect on temperature and temperature was hypothesized to have a causal link on MLD. Then I added all correlations within a hierarchical level (see Appendix for a full list of causal hypotheses in the SEM models). Next, I ran the initial model and assessed the fit. The typical measure of fit, $\boldsymbol{X}^2$, measures the significance of the difference between the model and the data, and ideally one would have a non-significant difference. Because I had such large sample sizes it is nearly impossible to get a non-significant result regardless of the true fit of the model (Schumacker and Lomax 2004). I used the Root Mean Square Error of Approximation (RMSEA) instead. An acceptable model was one whose lower RMSEA 95% CI was < 0.05 and upper RSMEA 95% CI < 0.10 (Browne et al. 1993). RMSEA shows that the model is both good enough to describe the data and that the error is low. If the RMSEA was not in the correct range, I examined the coefficient residuals for any values that were far from zero. Coefficients residuals indicate the correlations between all possible drivers, even those not included in the model. A high residual value (> 0.10) indicated that there was a relationship between those two predictors that was not being accounted for by the model, so I added the missing link. Once the model was sufficient to explain the data, I began the trimming process to obtain the most parsimonious model. I excluded non-significant links in a stepwise fashion. I eliminated the least significant links first and then reassessed the model fit (sometimes the residuals would indicate that a previously missing link should be added after another link was eliminated) and repeated the process until all links were significant or further removal of links did not improve the AIC score of the model. This trimming process improved the model fit, but did not change which predictors were significant compared to the initial model estimation (also included in the Appendix). All of my analyses were done with the R package Lavaan (Rosseel 2012) for the SEM and bbmle (Bolker 2016) for the AIC comparisons.

I ran all of my SEM analyses on standardized variables and report all of my results in standardized coefficients to facilitate comparison of the relative contribution of drivers to explaining cell size mean and variance. A standardized coefficient gives the change in standard deviation units of the dependent variable caused by a change of one standard deviation in the independent variable, controlling for all the other independent variables. As a hypothetical example: if the path between temperature and mean cell size has a coefficient of 0.2 and the path between TP and mean cell size has a coefficient of 0.1, the effect on cell size of temperature is twice as strong as the effect of TP. The coefficients cannot be compared in the same way across models. For example, if the path between temperature and cell size variance has a coefficient of 0.4 I cannot say that temperature has twice the effect on cell size variance as it has on mean cell size.

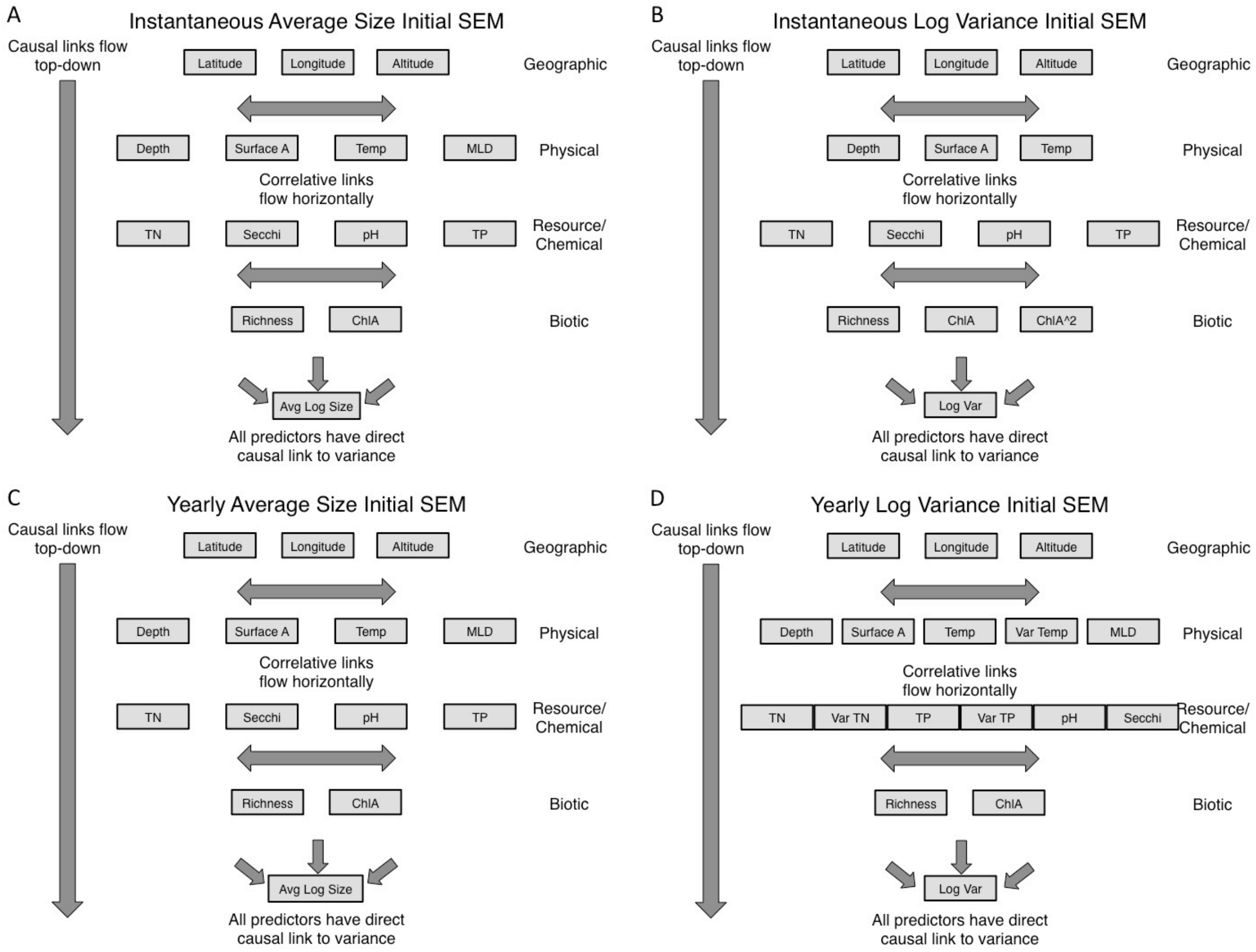

Figure 1.1 Conceptual diagram showing the initially hypothesized structural equation models for instantaneous models of A) mean cell size B) variance in cell size and the yearly models of C) mean cell size and D) variance in cell size. The predictors are arranged hierarchically. Actual hypothesized links are omitted in the figure for visual clarity, but can be found in text form in the Appendix. The arrows indicate the flow of causality, with double-headed arrows indicating the position of correlative links and single headed arrows indicating the position of causal links.

Results

Question 1: Individual Drivers of Cell Size Distributions

In this section I will investigate whether my hypotheses about mean cell size and cell-size variance for different environmental drivers found support in my dataset. I will first present the simple linear model results, then the support or complications from the SEM model. All results are given in Table 1.2.

Drivers of Mean Size

Temperature

I predicted that temperature should negatively correlate with cell size. My analysis showed the temperature size relationship to be significant and more than twice as strong, by r^2, for yearly temperature than the instantaneous analyses (instantaneous: $r^2 = 0.04$ and $p << 0.001$; yearly: $r^2 = 0.1$, $p << 0.001$, Figure 1.2). The SEM results (Figure 1.5, 1.6) showed that temperature was not a statistically significant factor for the instantaneous analyses, but that it had a significant negative indirect effect when I considered the yearly data. Contrary to my hypothesis, temperature didn't work through nutrients or mixed layer as suspected, but through pH. The MLD effect was ultimately trimmed from all models, so the hypothesis that temperature could affect cell size through stratification is not supported.

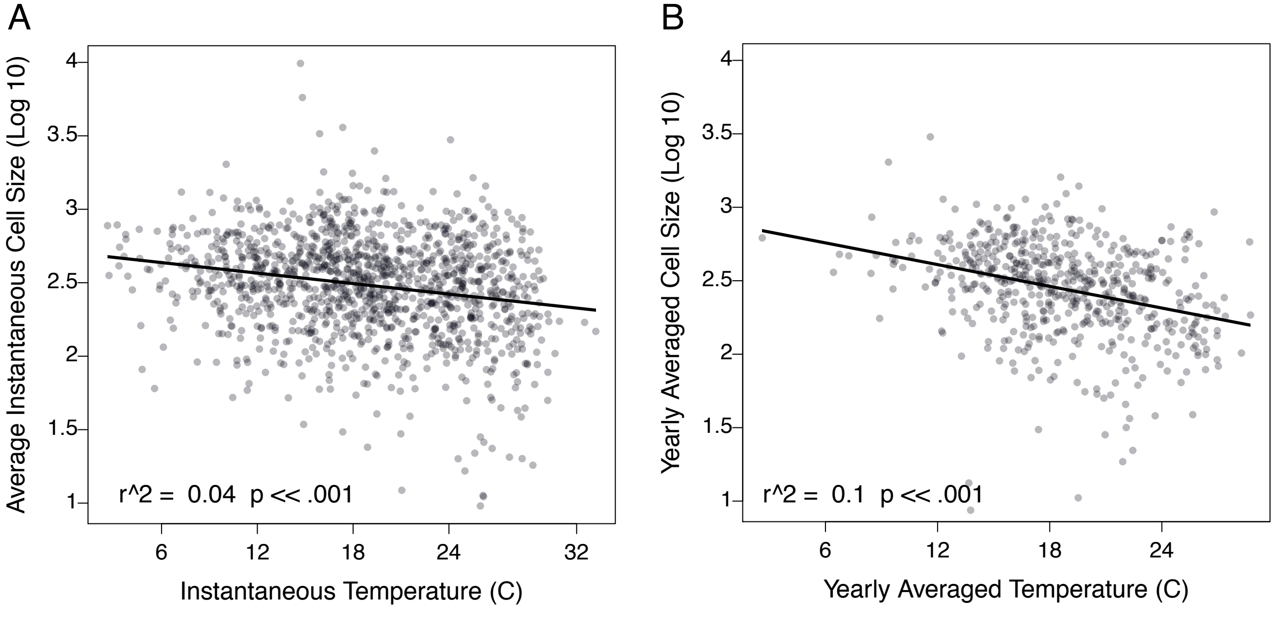

Figure 1.2 The effect of temperature on average cell size A) Instantaneous temperature and cell size. B) Yearly temperature and cell size.

Nutrients

I predicted that small cells would dominate at low nutrients due to increased nutrient uptake efficiency at high surface area to volume ratios, leading to positive correlations between cell size and total phosphorus (TP) and total nitrogen (TN) concentrations. TN was never significant in the bivariate analyses and always dropped out of the SEM analysis during tree trimming. The results of the bivariate analysis were somewhat contradictory. TP had the expected positive effect in the instantaneous analyses, but it was small and barely significant ($r^2 = 0.002$, $p = 0.047$, Figure 1.3A) and had no significant effect in the yearly analysis (Figure 1.3B). However the SEM analysis showed more consistent results, with a positive effect for TP in both the instantaneous and yearly analysis (Figures 1.5 and 1.6).

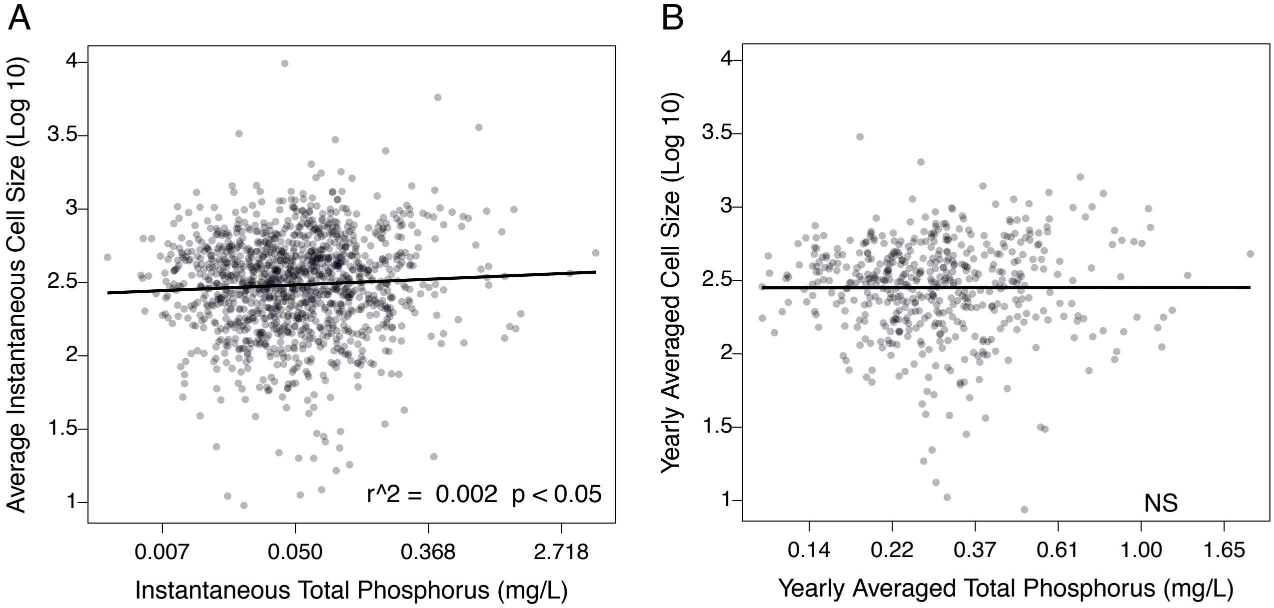

Figure 1.3 The effect of Phosphorus on average cell size A) Instantaneous TP versus average cell size. B) Yearly TP and cell size.

Mixed Layer Depth

I predicted that MLD would be positively correlated with mean size because a deeper mixed layer decreases the chance of sinking out of the photic zone for large cells. I did not find support for an effect of MLD in either the instantaneous analysis or the yearly analysis. The instantaneous SEM model likewise did not show a direct effect, but had an unanticipated positive indirect effect through pH (Figure 1.5), while the yearly SEM showed no effect.

Altitude

I predicted that altitude would be positively related to cell size because bigger cells are better defended against UV exposure. The bivariate analyses showed a positive effect of altitude on cell size for both the instantaneous and the yearly communities (instantaneous: $r^2 = 0.053$, $p << 0.001$, yearly: $r^2 = 0.046$, $p << 0.001$) (Figure 1.4). The SEM models agreed. Both the yearly and the instantaneous SEM analyses identified altitude as a direct positive effect as well as having multiple indirect pathways of mixed sign (Figures 1.5, 1.6). Indirect positive effects for the instantaneous model showed altitude working through MLD and pH as well as through surface area and TP. A negative indirect effect worked through depth and TP. In the yearly model, altitude had a negative indirect effect through both TP and pH, but also worked through temperature and depth for a positive indirect effect.

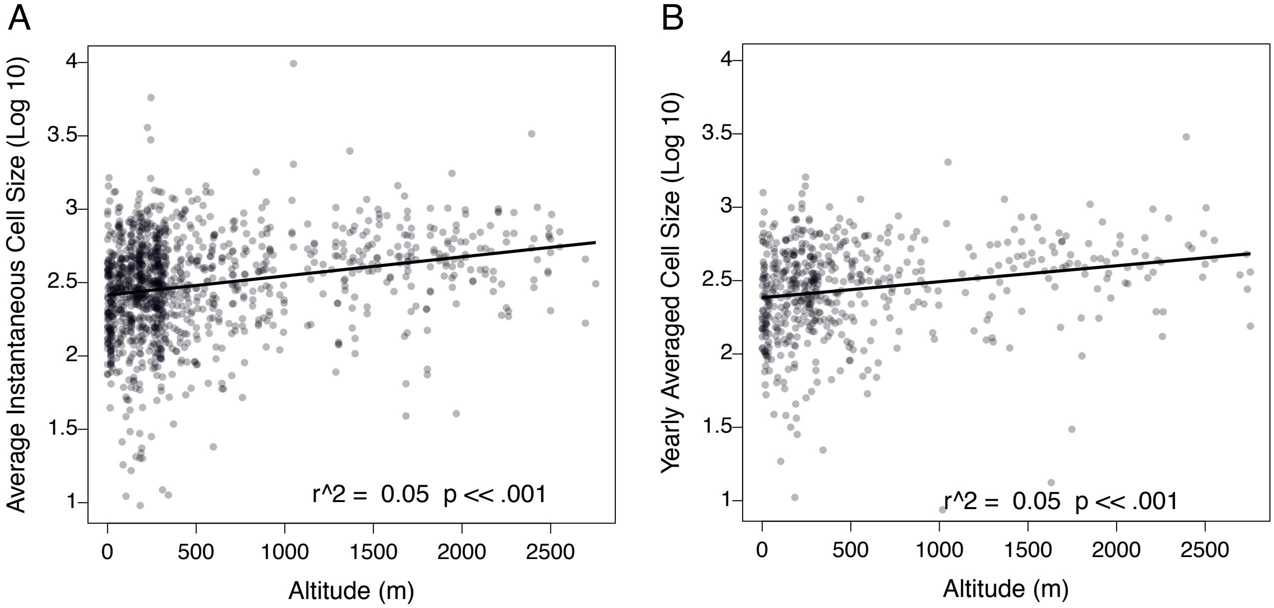

Figure 1.4 Cell size increases with altitude A) Instantaneous cell size. B) Yearly cell size.

pH

I predicted that pH would have a negative correlation with cell size, due to an indirect effect through grazers (unmeasured in this dataset, so any relationship would be seen as direct in my model). While the bivariate analyses showed no significant effects of pH on cell size, the SEM models showed pH as a consistently negative direct driver (Figure 1.5, 1.6).

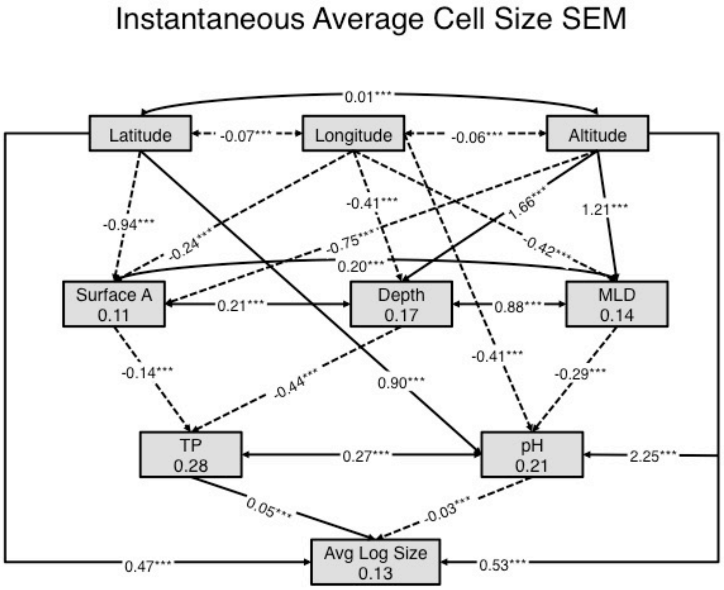
Instantaneous Average Cell Size SEM

Figure 1.5 The final SEM for the instantaneous average size Double pointed arrows imply a correlation while single pointed arrows show a causal relationship. Solid lines represent positive correlations or regressions. Dotted lines are negative relationships. The standardized coefficient (relative strength) of each relationship is given on the connecting line, along with the statistical significance (all $p < 0.001$). The r^2 for each dependent variable in the model is given underneath the variable name.

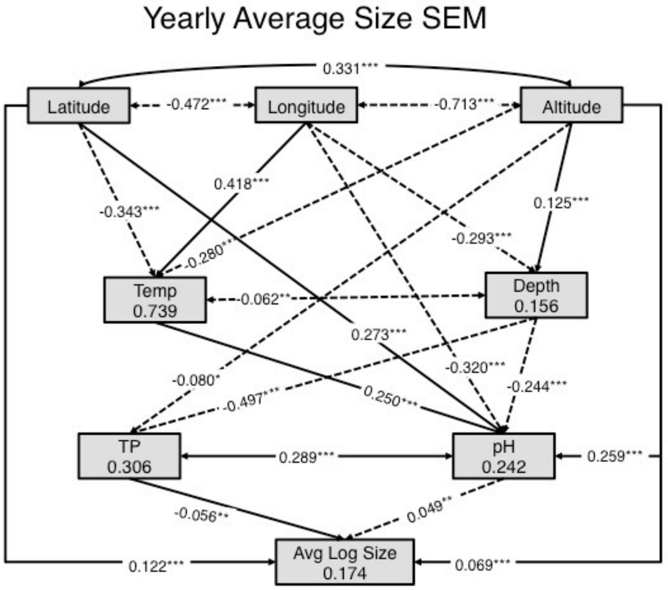

Figure 1.6 The final SEM for the yearly average size Double pointed arrows imply a correlation while single pointed arrows show a causal relationship. Solid lines represent positive correlations or regressions. Dotted lines are negative relationships. The standardized coefficient (relative strength) of each relationship is given on the connecting line, along with the statistical significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). The r^2 for each dependent variable in the model is given underneath the variable name.

Drivers of Cell Size Variance

Nutrients

I predicted that the addition of nutrients would increase the cell size variance by allowing the coexistence of larger size classes. The bivariate analyses showed overall positive effects of both TP and TN on cell-size variance for the instantaneous as well as the yearly analyses. The instantaneous analysis of TP ($r^2 = 0.02$, $p << 0.001$, Figure 1.7A) showed a weak signal, while the yearly model was better but still weak ($r^2 = 0.05$, $p << 0.001$, Figure 1.7B). The bivariate pattern was almost identical for the TN analyses (instantaneous: $r^2 = 0.02$, $p << 0.001$, Figure 1.7C; yearly: $r^2 = 0.05$, $p << 0.001$, Figure 1.7D). The SEM analyses supported a positive direct effect of TP on the instantaneous community variance (Figure 1.13), but not on the yearly community variance (Figure 1.14). The direct effect of nitrogen was significant but negative for the instantaneous SEM model, both directly and indirectly through richness (Figure 1.13).

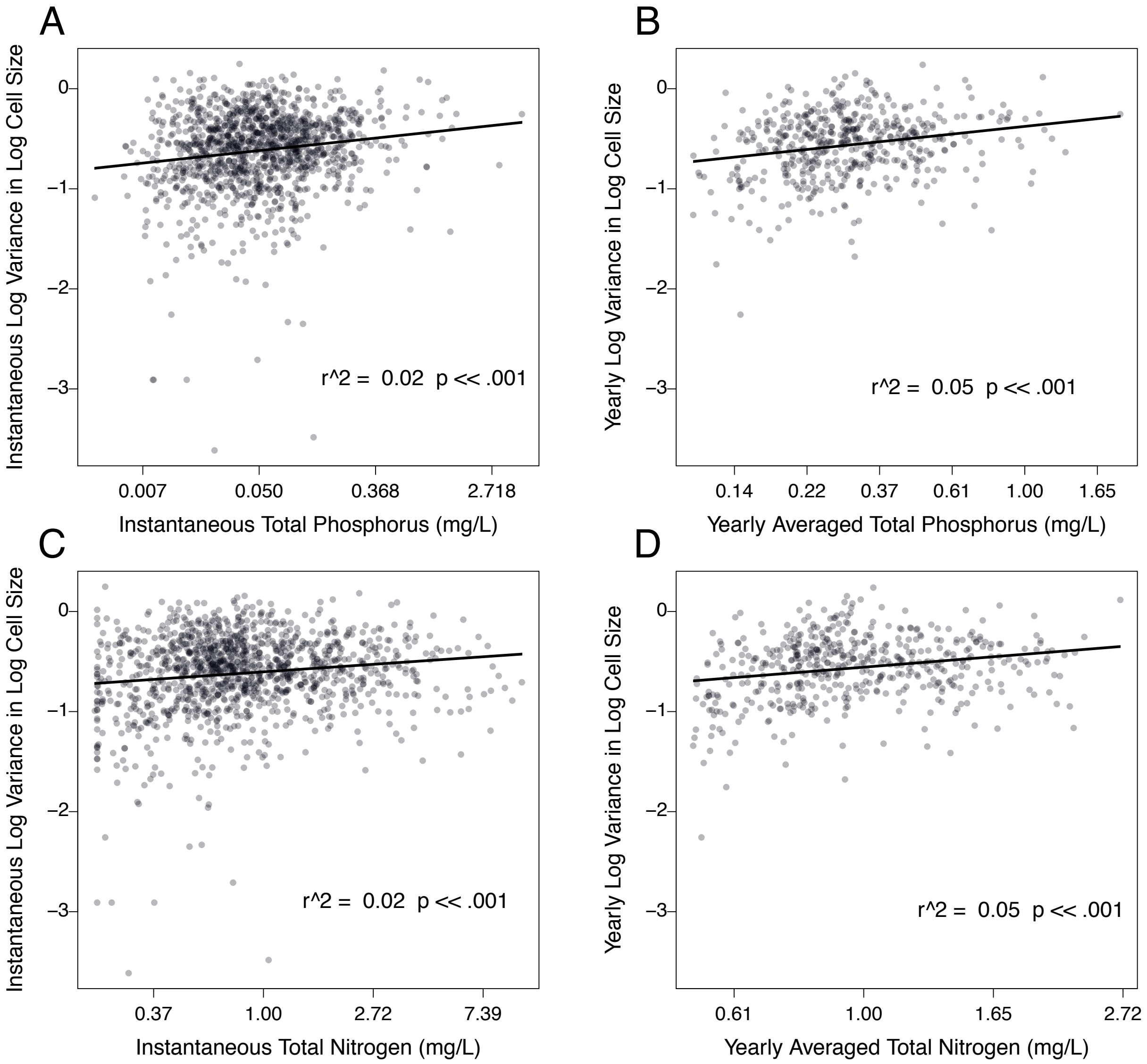

Figure 1.7 Nutrients have a positive effect on variance in cell size A) Instantaneous phosphorus and cell size variance. B) Yearly phosphorus and cell size variance. C) Instantaneous nitrogen and cell size variance. D) Yearly nitrogen and cell size variance.

Diversity

I predicted a strong positive correlation between taxonomic and functional diversity and therefore a positive correlation between species richness and cell-size variance. I found the expected positive correlation between variance and richness in my bivariate analyses in both the instantaneous ($r^2 = 0.10$, $p << 0.001$), and the yearly ($r^2 = 0.15$, $p << 0.001$) analyses. Furthermore, richness was a significant, direct, and positive driver of cell-size variance in both of my SEM analyses (Figures 1.13-1.14).

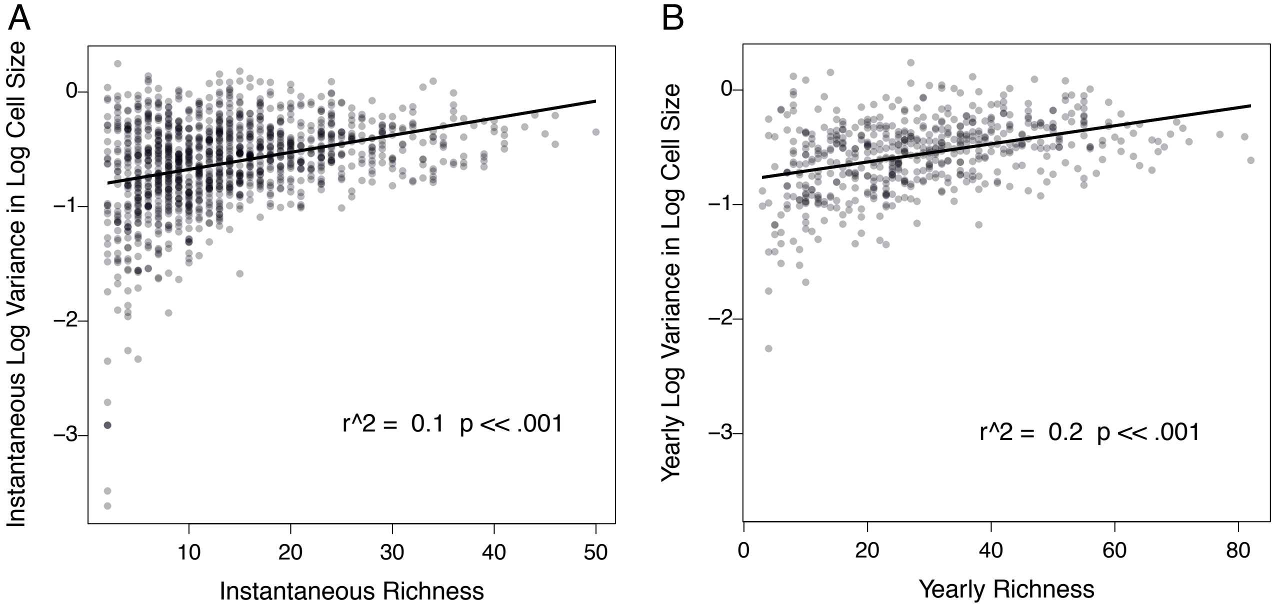

Figure 1.8 Richness has a positive effect on variance in cell size A) Instantaneous richness and cell size variance. B) Yearly richness and cell size variance.

Latitude

Due to the latitudinal diversity gradient (LDG), I expected to see a negative relationship between latitude and cell-size variance. The bivariate instantaneous ($r^2 = 0.075$, $p << 0.001$, Figure 1.9B) and yearly ($r^2 = 0.10$, $p << 0.001$, Figure 1.9B) analyses supported a negative effect of latitude on variance. Interestingly, although I assume that the LDG must work indirectly through things like temperature, the SEM analyses found direct negative effects of latitude on variance in cell size (as well as multiple indirect effects with mixed signs, Figures 1.13-1.14). The observed direct effect indicates that there is some other driver intermediate between latitude and cell-size variance not included in my model.

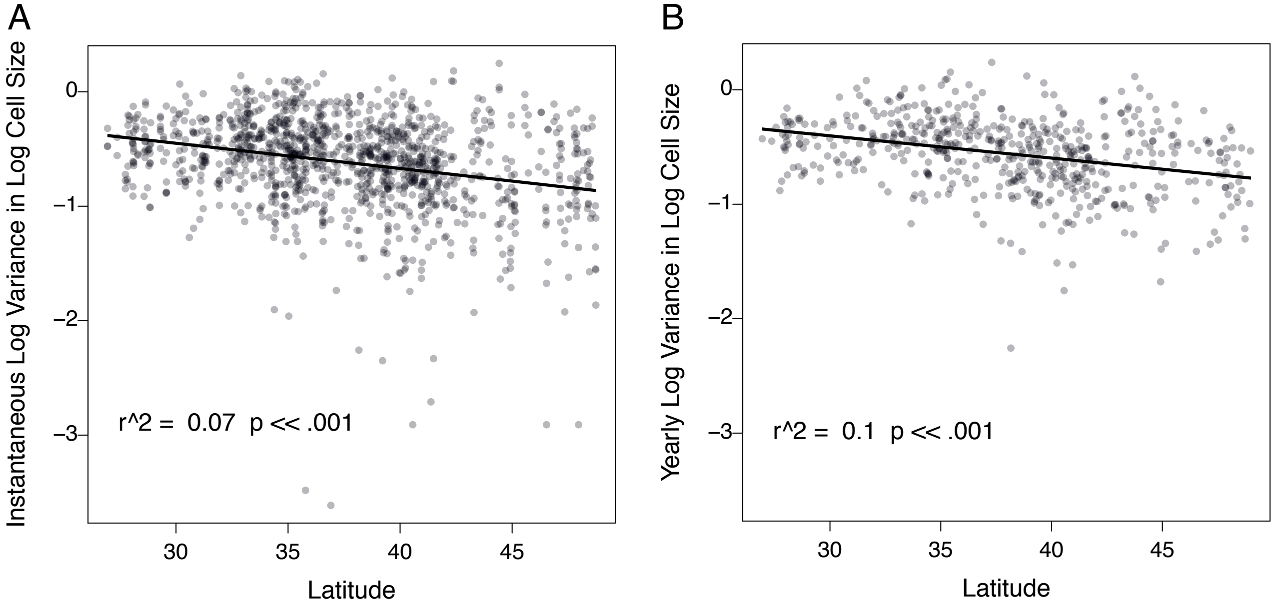

Figure 1.9 Latitude has a negative effect on variance in cell size A) Instantaneous cell size variance and latitude. B) Yearly cell size variance and latitude.

Altitude

I hypothesized and found a negative relationship between variance and altitude in the bivariate analyses (instantaneous: $r^2 = 0.10$, $p << 0.001$, Figure 1.10A; yearly: $r^2 = 0.17$, $p << 0.001$, Figure 1.10B). Both of the SEM analyses showed direct negative effects of altitude on variance in cell size, but also negative indirect effects through multiple pathways (Figures 1.13 and 1.14). These negative indirect effects are mediated by depth, surface area, temperature, and species diversity, while altitude has an indirect positive effect through TN.

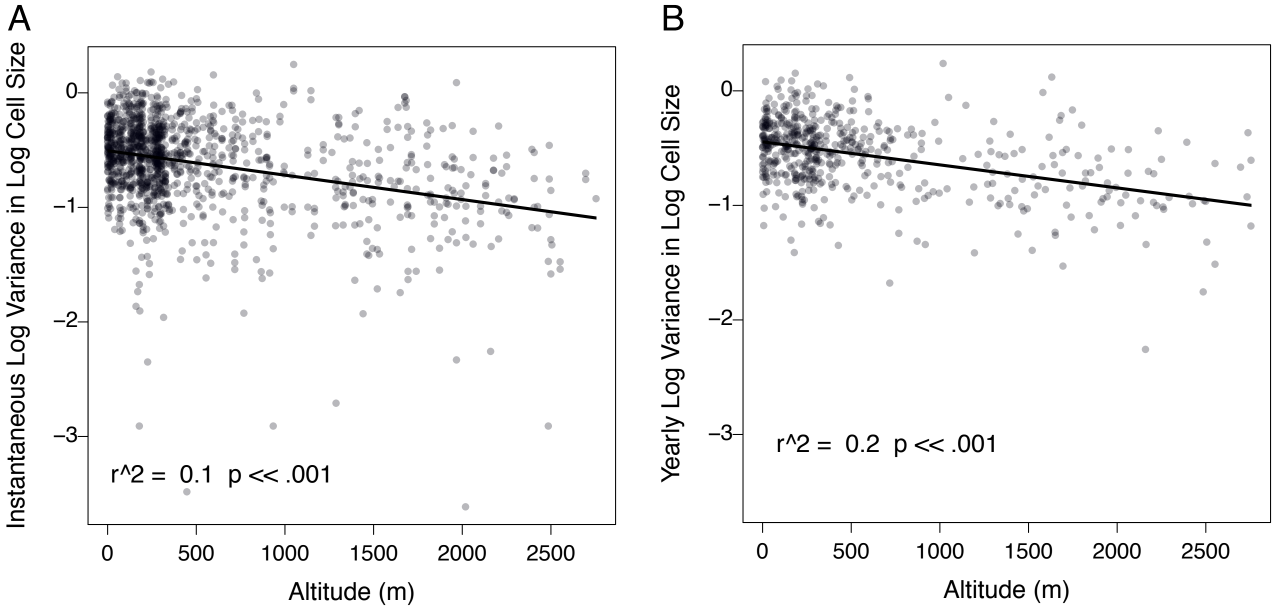

Figure 1.10 Altitude has a negative effect on variance in cell size A) Instantaneous cell size variance and altitude. B) Yearly cell size variance and altitude.

pH

I predicted that there would be a positive association between pH and cell-size variance based on acidification studies. My bivariate analyses showed the opposite, a negative association for both the instantaneous and yearly analyses (instantaneous: $r^2 = 0.01$, $p < 0.001$, Figure 1.11A; yearly: $r^2 = 0.01$, $p < 0.02$, Figure 1.11B). However, my SEM analyses never found any direct or indirect effect of pH on cell size variance.

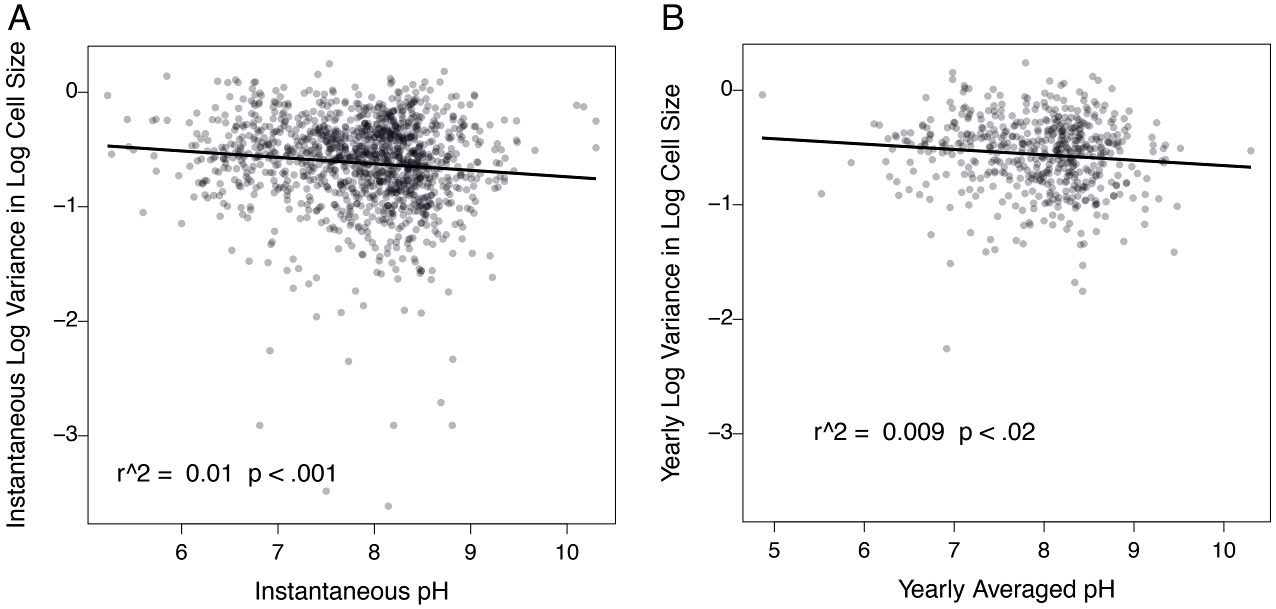

Figure 1.11 The negative effect of pH on variance in cell size A) Instantaneous pH and cell size variance. B) Yearly pH and cell size variance.

Environmental Variation

I predicted that increased variability in the environment would lead to greater variance in cell size, due to a wider niche space for species to coexist. The effect of variability in the environment through time could only be tested on the yearly dataset since multiple recordings of the same lake were required to measure variance in the environment. My bivariate analyses generally supported this hypothesis. Variance in temperature ($r^2 = 0.010$, $p < 0.02$, Figure 1.12A), phosphorus ($r^2 = 0.036$, $p << 0.001$, Figure 1.12B), nitrogen ($r^2 = 0.026$, $p < 0.0002$, Figure 1.12C), and pH ($r^2 = 0.008$, $p < 0.03$, Figure 1.12D) all had the expected, although weak, positive effect on cell size variance. Variation in Secchi depth, on the other hand had a negative effect on cell size variance ($r^2 = 0.056$, $p << 0.001$ Figure 1.12E). Only variation in temperature, however, was significant in the SEM analysis (Figure 1.14).

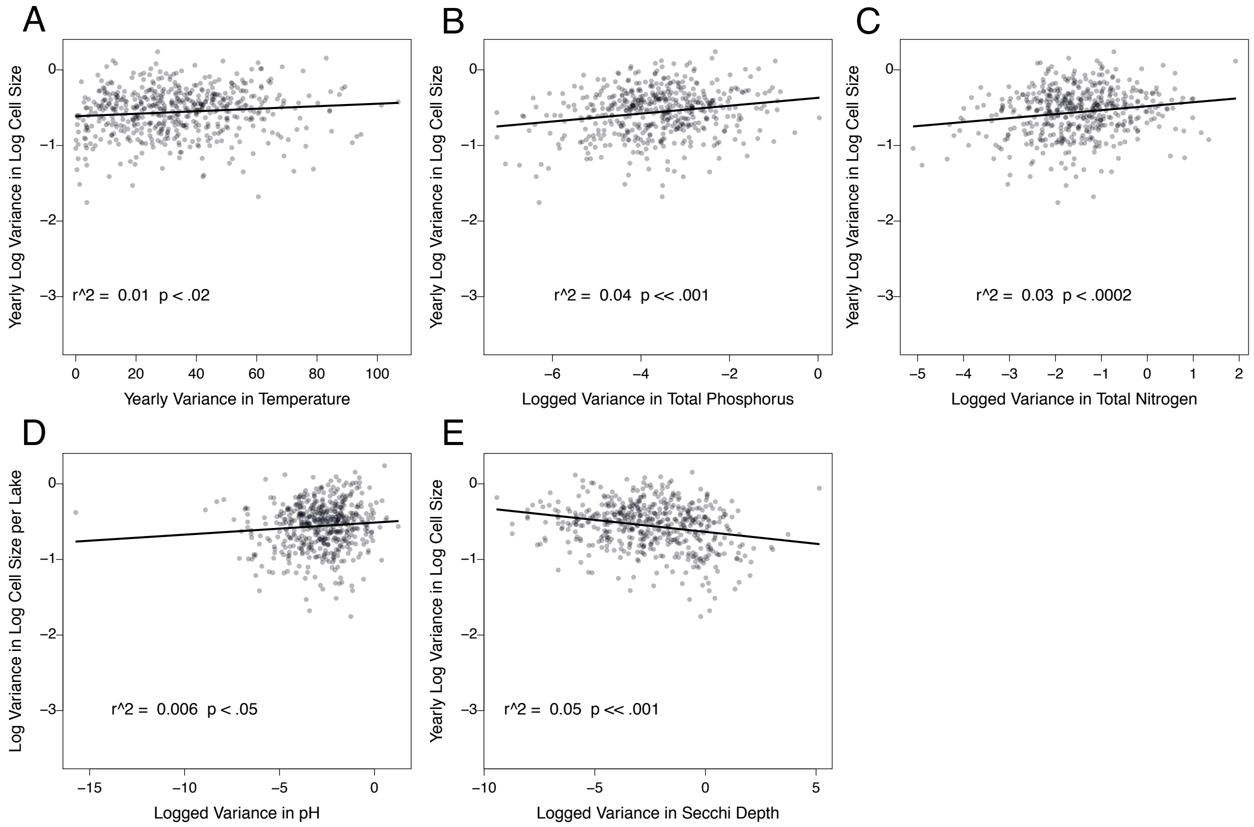

Figure 1.12 Environmental variation has a mostly positive effect on variance in cell size A) Variance in temperature increases cell size variance. B) Variance in phosphorus increases cell size variance. C) Variance in nitrogen increases cell size variance. D) Variance in pH increases cell size variance. A) Variance in Secchi depth decreases cell size variance.

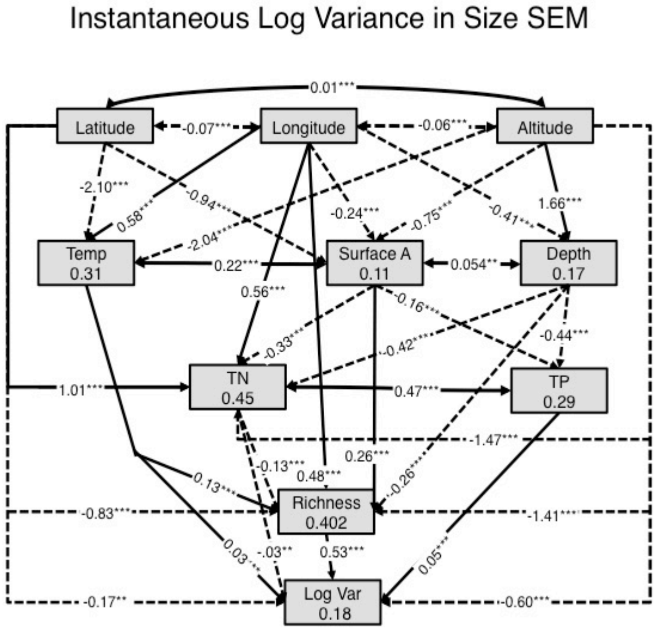

Figure 1.13 The final SEM for the instantaneous variance in cell size Double pointed arrows imply a correlation while single pointed arrows show a causal relationship. Solid lines represent positive correlations or regressions. Dotted lines are negative relationships. The standardized coefficient of each relationship is given on the connecting line, along with the statistical significance (** $p < 0.01$, *** $p < 0.001$). The r^2 for each dependent variable in the model is given underneath the variable name.

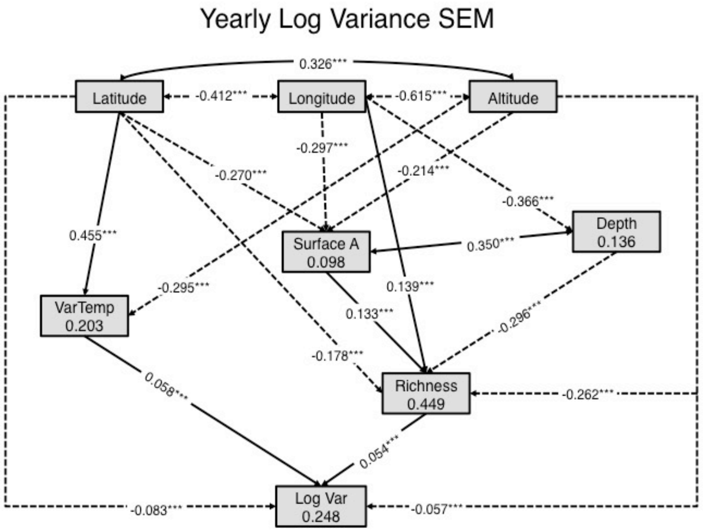

Figure 1.14 <u>The final SEM for the yearly variance in cell size</u> Double pointed arrows imply a correlation while single pointed arrows show a causal relationship. Solid lines represent positive correlations or regressions. Dotted lines are negative relationships. The standardized coefficient of each relationship is given on the connecting line, along with the statistical significance (all $p < 0.001$). The r^2 for each dependent variable in the model is given underneath the variable name.

Question 2: Overall Predictability of Cell Size Distributions

The SEM analysis was designed to check the validity of my bivariate analyses by allowing for correlated drivers. It also answers the question of how much of the total variation I are able to explain. The final SEM results are given in Figures 1.5, 1.6, 1.13, and 1.14.

On the question of overall predictability, I was only able to explain a moderate amount of the total variation. The r^2 of the instantaneous average size model was 0.131 (RMSEA 95% CI = (0, 0.039), $X^2 = 0.09$, df = 12, Figure 1.5). The instantaneous variance was similarly explicable, with $r^2 = 0.18$ (RMSEA 95%CI = (0, 0.038), $X^2 = 0.154$, df = 11, Figure 1.6). The yearly models accounted for more of the variation. The yearly average size model had an r^2 of 0.174 (RMSEA 95%CI = (0.03, 0.084), $X^2 = 0.115$, df = 9, Figure 1.13) and the yearly variance model had an r^2 of 0.248 (RMSEA 95%CI = (0, 0.068), $X^2 = 0.004$, df = 9, Figure 1.14).

Discussion

I showed that many of my predictions held: increased temperature does lead to a decrease in cell size, an increase in nutrients (specifically phosphorus) leads to an increase in cell size as well as an increase in variance, and cell size increased with altitude and decreased with pH. Predictive power was weak: r^2 ranged between 0 and 0.25. The predicted relationships between MLD and size and pH and variance were not found, but the latitudinal and altitudinal diversity gradients were.

The strength of the altitude signal on cell size was surprising; although my analysis allowed for an indirect effect through temperature, this path was not supported. I speculate that direct effect of altitude on size is actually an indirect effect through increased UV exposure, but it could also have to do with a difference in seasonality. A shorter growing season such as might be expected at higher altitudes may provide fewer temporal niches thus decrease diversity. Theoretical studies have shown that the possibility for species coexistence between a predation resistant and nutrient competitive species decreases as the length of the growing season decreases (Klausmeier and Litchman 2012). It could also be due to dispersal limitation on mountaintops or a change in food web structure. Further research is needed to disentangle these effects.

An interesting result was that when there was a significant effect in both the instantaneous and yearly communities, the yearly result was usually stronger (higher r^2). The strength of the yearly analyses could indicate that the yearly measurements were on the whole more accurate than the ones that reflected only an instantaneous measure of the community because they smooth over variability due to sampling error or other sources of community variation not related to my focal drivers. The improvement in model fit was especially apparent in the SEM analysis, even true in cases like latitude and altitude, which don't change through time. The improved fit through more frequent sampling offers a caution to researchers who might sample a lake only once; a single sampling might not accurately reflect the dynamics of the lake. A more time-integrated approach is called for.

In general, the effect sizes in my analysis were small. The highest r^2 for any model was 0.248, for the yearly variance, involving temperature variance, richness, surface area, depth, latitude, longitude, and altitude. The type of data that I have may pose an especially harsh test of the strength of these mechanisms on a continental scale because I use cell sizes collected from a database, instead of the actual *in situ* sizes. The lack of intraspecific data means that I am only able to detect size differences due to species difference, nothing due to local adaptation. Another possible reason for my lack of explanatory power is the lack of information on grazers in the dataset; some of my factors, pH for example, are theorized to work through changes in the grazer community. The addition of grazer data would probably account for some of the variance. This sort of small effect of environmental factors on species traits is common in other systems. Wright et al (2004) found that most of the variation in leaf traits was within communities, and adding climate variables (like rainfall and temperature) only added at most 0.05 to the r^2 of their models of leaf mass per area and photosynthetic assimilation rates. Swenson and Weiser (2010) looked at the relationship between forest tree traits and precipitation and found r^2 values between 0.07 and 0.16 for the mean and at most 0.07 for the variance. In a recent meta-analysis of studies looking at terrestrial plant traits over environmental gradients, Moles et al (2014) showed that the effect of temperature on widely measured traits like wood density and specific leaf area is similar in effect size to those I measured, ranging from 0.006 to 0.25 with the majority of significant effects < 0.01. My study is well within that range.

Conclusion

Understanding broad geographical patterns in species traits is a basic goal of trait-based ecology (McGill et al. 2006). Researchers make predictions about how traits should affect species performance at small scales and in laboratory settings, but we know that over larger scales the patterns could change. It is crucial that we challenge small-scale conclusions with large-scale data. To try to understand whether patterns of trait distribution hold over large scales, there have been a large number of studies looking at the distributions of ecologically relevant traits over environmental gradients. Many of these studies concern plant traits: wood density versus temperature (Swenson and Weiser 2010), leaf economics versus temperature and latitude (Reich and Oleksyn 2004; Wright et al. 2004), seed mass versus temperature and rainfall (Murray et al. 2004), and height versus temperature (Swenson and Weiser 2010). There have been fewer such studies in algae, but see Thomas et al (2012) for temperature optima in marine phytoplankton, Kruk et al (2010) for morphological traits in freshwater phytoplankton, and Liu et al (2013) for attachment traits in benthic diatoms. In this paper I took this same trait-based approach to understand the factors affecting cell size over continental scale gradients.

Altitude was the strongest predictor of average cell size, while altitude and latitude were the strongest predictors of cell-size variance. The amount of variation accounted for by all of these factors, however, remains low. Low predictability might be a result cell size's role as a master trait. Because cell size is a higher-order trait controlled by many things and responsible for many things, explaining 25% of the variance is a significant achievement. Cell size is complex and subject to myriad influences that we can only hope to explain bit by bit.

Table 1.1: Hypothesized relationship between drivers and size and variance

Driver	Predicted Size Effect	Rationale for Mean Size	Predicted Variance Effect	Rationale for Size Variance
Temperature	↘	Increase in minimum quota, making nutrient competition more important. Water column stabilization increases sinking.		
Nutrients	↗	Surface area to volume ratio influences nutrient affinity. Smaller cells have higher ratio and are better nutrient competitors	↗	Trade off between competitive ability and grazer resistance leads to addition of larger (more resistant) cells with higher nutrients
Mixed Layer Depth	↗	Stable water column leads to nutrient limitation, smaller cells better nutrient competitors. Shallower mixed layer increases sinking.		
Latitude			↘	More species interactions at lower latitudes and less strong abiotic filtering lead to coevolution and more different niches.
Altitude	↗	Larger cells more are UV tolerant, and UV increases with altitude. Small cells more sensitive to UV degradation,	↘	Larger species pool at lower altitude due to species area relationship: mountaintops have less area than mountain bottoms.
pH	↘	Lower pH decreases grazers, releasing grazer pressure and increasing cell size when grazers are size selective	↘	Decrease in species diversity due to change in grazer community. Fewer grazers implies fewer niches at least for grazing resistant species.
Environmental Variance			↗	Increased niche space. Successional dynamics through the year

Table 1.2: All results from all analyses, presented by driver

Mean Cell Size					
Factor	**Predicted Relationship**	**Bivariate Regression**		**SEM**	
		Analysis	**Result**	**Analysis**	**Result**
Temperature	—	Instantaneous	- ($r^2 = 0.04$, $p << 0.001$)	Instantaneous	Not Significant
		Yearly	- ($r^2 = 0.10$, $p << 0.001$)	Yearly	Indirect Negative
Nutrient	+	Phosphorus		Phosphorus	
		Instantaneous	+ ($r^2 = 0.002$, $p < 0.05$)	Instantaneous	+ Direct
		Yearly	Not Significant	Yearly	+ Direct
		Nitrogen		Nitrogen	
		Instantaneous	Not Significant	Instantaneous	Not Significant
		Yearly	Not Significant	Yearly	Not Significant
MLD	+	Instantaneous	Not Significant	Instantaneous	+ Indirect
		Yearly	Not Significant	Yearly	Not Significant
Altitude	+	Instantaneous	+ ($r^2 = 0.053$, $p << 0.001$)	Instantaneous	+ Direct, Mixed Indirect
		Yearly	+ ($r^2 = 0.046$, $p << 0.001$)	Yearly	+ Direct, Mixed Indirect
pH	—	Instantaneous	Not Significant	Instantaneous	- Direct
		Yearly	Not Significant	Yearly	- Direct
Variance in Size					
Factor	**Predicted Relationship**	**Bivariate Regression**		**SEM**	
		Analysis	**Result**	**Analysis**	**Result**
Nutrient	+	Phosphorus		Phosphorus	
		Instantaneous	+ ($r^2 = 0.02$, $p << 0.001$)	Instantaneous	+ Direct
		Yearly	+ ($r^2 = 0.05$, $p << 0.001$)	Yearly	Not Significant
		Nitrogen		Nitrogen	
		Instantaneous	+ ($r^2 = 0.02$, $p << 0.001$)	Instantaneous	- Direct
		Yearly	+ ($r^2 = 0.05$, $p << 0.001$)	Yearly	Not Significant
Richness	+	Richness		Richness	
		Instantaneous	+ ($r^2 = 0.10$, $p << 0.001$)	Instantaneous	+ Direct
		Yearly	+ ($r^2 = 0.15$, $p << 0.001$)	Yearly	+ Direct
Latitude	—	Instantaneous	- ($r^2 = 0.07$, $p << 0.001$)	Instantaneous	- Direct, Mixed Indirect
		Yearly	- ($r^2 = 0.10$, $p << 0.001$)	Yearly	- Direct, Mixed Indirect
Altitude	—	Instantaneous	- ($r^2 = 0.10$, $p << 0.001$)	Instantaneous	- Direct and Indirect
		Yearly	- ($r^2 = 0.17$, $p << 0.001$)	Yearly	- Direct and Indirect
pH	+	Instantaneous	- ($r^2 = 0.01$, $p < 0.0003$)	Instantaneous	Not Significant
		Yearly	- ($r^2 = 0.01$, $p < 0.02$)	Yearly	Not Significant
Variance in the Environment	+	Variance in Temperature	+ ($r^2 = 0.010$, $p < 0.02$)	Variance in Temperature	+ Direct
		Variance in Phosphorus	+ ($r^2 = 0.036$, $p << 0.001$)	Variance in Phosphorus	Not Significant
		Variance in Nitrogen	+ ($r^2 = 0.026$, $p < 0.0002$)	Variance in Nitrogen	Not Significant
		Variance in pH	+ ($r^2 = 0.006$, $p < 0.05$)	Variance in pH	Not Significant
		Variance Secchi Depth	- ($r^2 = 0.052$, $p << 0.001$)	Variance in Secchi Depth	Not Significant

APPENDIX

APPENDIX—INITIAL SEM MODELS

Initial Model Instantaneous Mean Size

Direct Effects

AverageBVcell ~ StdTemp + StdSurfA + StdTP + StdTN + StdSecchi + StdChlA + StdpH + StdLon + StdLat + StdAlt + StdMLD + StdRich + StdDepth

Biological Properties

StdChlA ~ StdLon + StdLat + StdAlt + StdTP +StdTN + StdTemp + StdMLD + StdpH + StdSecchi

StdRich ~ StdLon + StdLat + StdAlt + StdTP + StdSurfA +StdTN + StdTemp + StdpH + StdMLD + StdDepth + StdSecchi

Chemical/Resource Properties

StdTP ~ StdLon + StdLat + StdAlt + StdMLD + StdDepth + StdSurfA

StdTN ~ StdLon + StdLat + StdAlt + StdMLD + StdDepth + StdSurfA

StdpH ~ StdLon + StdLat + StdAlt + StdMLD + StdDepth

StdSecchi ~ StdLon + StdLat + StdAlt + StdTemp + StdMLD + StdSurfA + StdDepth

Physical Properities

StdTemp ~ StdLon + StdLat + StdAlt

StdSurfA ~ StdLon + StdLat + StdAlt

StdMLD ~ StdLon + StdLat + StdAlt

StdDepth ~ StdLon + StdLat + StdAlt

Covariances

StdTemp ~~ StdSurfA

StdTemp ~~ StdMLD

StdTemp ~~ StdDepth

StdDepth ~~ StdMLD

StdDepth ~~ StdSurfA

StdSurfA ~~ StdMLD

StdTP ~~ StdTN

StdTP ~~ StdpH

StdpH ~~ StdTN

StdSecchi ~~ StdChlA

StdSecchi ~~ StdRich

StdDiv ~~ StdChlA

StdLon ~~ StdLat

StdLon ~~ StdAlt

StdLat ~~ StdAlt

Table A1: Model results: instantaneous mean size			
Number of Observations		1239	
Degrees of Freedom		6	
P-value		0	
Regressions:			
		Estimate	P(>|z|)
AverageBVcell	~		
	StdTemp	-0.004	0.578
	StdSurfA	-0.024	0.168
	StdTP	0.041	0.006
	StdTN	-0.011	0.349
	StdSecchi	-0.018	0.118
	StdChlA	0.035	0.019
	StdpH	-0.033	0
	StdLon	0.008	0.66
	StdLat	0.386	0
	StdAlt	0.364	0
	StdMLD	-0.023	0.089
	StdRich	-0.063	0
	StdDepth	0.024	0.101
StdSecchi	~		
	StdLon	-0.048	0.283
	StdLat	0.948	0
	StdAlt	0.338	0.181
	StdTP	-0.591	0
	StdTN	-0.144	0
	StdTemp	0.121	0
	StdMLD	0.037	0.255
	StdpH	-0.006	0.768
	StdSurfA	-0.254	0
	StdDepth	0.152	0

Table A1 (con’t)			
StdChlA	~		
	StdLon	0.17	0
	StdLat	0.244	0.026
	StdAlt	-0.305	0.141
	StdTP	0.265	0
	StdTN	0.114	0
	StdTemp	0.062	0
	StdMLD	-0.069	0
	StdpH	0.165	0
StdRich	~		
	StdLon	0.467	0
	StdLat	-0.48	0.002
	StdAlt	-1.018	0.001
	StdTP	0.161	0
	StdSurfA	0.151	0.001
	StdTN	-0.042	0.199
	StdTemp	0.112	0
	StdpH	0.094	0
	StdMLD	-0.009	0.804
	StdDepth	-0.159	0
StdTP	~		
	StdLon	-0.062	0.148
	StdLat	0.154	0.274
	StdAlt	-0.627	0.018
	StdMLD	0.044	0.198
	StdDepth	-0.472	0
	StdSurfA	-0.152	0.001
StdTN	~		
	StdLon	0.515	0
	StdLat	1.206	0
	StdAlt	-1.86	0
	StdMLD	-0.079	0.053
	StdDepth	-0.364	0
	StdSurfA	-0.298	0
StdpH	~		
	StdLon	-0.437	0
	StdLat	0.965	0
	StdAlt	2.024	0
	StdMLD	-0.27	0
	StdDepth	-0.023	0.657

Table A1 (cont'd)			
StdTemp	~		
	StdLon	0.576	0
	StdLat	-2.097	0
	StdAlt	-2.042	0
StdSurfA	~		
	StdLon	-0.245	0
	StdLat	-0.941	0
	StdAlt	-0.751	0
StdMLD	~		
	StdLon	-0.415	0
	StdLat	0.012	0.947
	StdAlt	1.206	0
StdDepth	~		
	StdLon	-0.411	0
	StdLat	-0.028	0.867
	StdAlt	1.668	0
Covariances:			
		Estimate	P(>|z|)
StdTemp	~~		
	StdSurfA	0.044	0.044
	StdMLD	-0.232	0
	StdDepth	-0.05	0.218
StdMLD	~~		
	StdDepth	0.875	0
StdSurfA	~~		
	StdDepth	0.213	0
	StdMLD	0.198	0
StdTP	~~		
	StdTN	0.466	0
	StdpH	0.272	0
StdTN	~~		
	StdpH	0.499	0
StdSecchi	~~		
	StdChlA	-0.008	0.551
	StdRich	0.003	0.88
StdChlA	~~		
	StdRich	0.229	0
StdLon	~~		
	StdLat	-0.066	0
	StdAlt	-0.06	0

Table A1 (cont'd)			
StdLat	~~		
	StdAlt	0.01	0

Initial Model Instantaneous Variance

Direct Effects

LogVar ~ StdTemp + StdSurfA + StdDepth + StdTP + StdTN + StdNtoP + StdSecchi + StdChlA + StdChlASq + StdLon + StdLat + StdAlt + StdRich

Biological Properties

StdChlA ~ StdLon + StdLat + StdAlt + StdTP +StdTN + StdSecchi+ StdTemp

StdChlASq ~StdLon + StdLat + StdAlt + StdTP +StdTN + StdSecchi+ StdTemp

Chemical/Resource Properties

StdTP ~ StdLon + StdLat + StdAlt + StdDepth

StdTN ~ StdLon + StdLat + StdAlt + StdDepth

StdNtoP ~ StdLon + StdLat + StdAlt + StdDepth

StdSecchi ~ StdLon + StdLat + StdAlt + StdTemp

Physical Properities

StdTemp ~ StdLon + StdLat + StdAlt

StdSurfA ~ StdLon + StdLat + StdAlt

StdDepth ~ StdLon + StdLat + StdAlt

Covariances

StdTemp ~~ StdSurfA

StdTemp ~~ StdDepth

StdTemp ~~ StdTP

StdTemp ~~ StdTN

StdTemp ~~ StdNtoP

StdSurfA ~~ StdDepth

StdSurfA ~~ StdTP

StdSurfA ~~ StdTN

StdSurfA ~~ StdNtoP

StdSurfA ~~ StdSecchi

StdSurfA ~~ StdChlA

StdDepth ~~ StdSecchi

StdDepth ~~ StdChlA

StdTP ~~ StdTN

StdTP ~~ StdNtoP

StdTN ~~ StdNtoP

StdNtoP ~~ StdSecchi

StdSecchi ~~ StdChlA

StdLon ~~ StdLat

StdLon ~~ StdAlt

StdLat ~~ StdAlt

StdChlA ~~ StdChlASq

Table A2: Model results: instantaneous cell size variance			
Number of Observations	1239		
Degrees of Freedom	8		
P-value	0.005		
		Estimate	P(>|z|)
LogVar	~		
	StdTemp	0.028	0
	StdSurfA	0.023	0.261
	StdDepth	-0.019	0.119
	StdTP	0.069	0
	StdTN	-0.029	0.031
	StdSecchi	0.031	0.02
	StdChlA	0	0.985
	StdChlASq	-0.017	0.078
	StdLon	0.015	0.495
	StdLat	-0.179	0.007
	StdAlt	-0.565	0
	StdpH	0.004	0.676
	StdRich	0.049	0
StdTemp	~		
	StdLon	0.576	0

Table A2 (cont'd)			
	StdLat	-2.097	0
	StdAlt	-2.042	0
StdSurfA	~		
	StdLon	-0.245	0
	StdLat	-0.941	0
	StdAlt	-0.751	0
StdDepth	~		
	StdLon	-0.411	0
	StdLat	-0.028	0.867
	StdAlt	1.668	0
StdTP	~		
	StdLon	-0.074	0.084
	StdLat	0.108	0.437
	StdAlt	-0.688	0.009
	StdDepth	-0.426	0
	StdSurfA	-0.202	0
StdTN	~		
	StdLon	0.515	0
	StdLat	1.168	0
	StdAlt	-1.889	0
	StdDepth	-0.421	0
	StdSurfA	-0.336	0
StdpH	~		
	StdLon	-0.473	0
	StdLat	1.173	0
	StdAlt	2.267	0
	StdDepth	-0.238	0
	StdTemp	0.103	0
StdSecchi	~		
	StdLon	-0.061	0.222
	StdLat	0.778	0
	StdAlt	1.076	0
	StdTemp	0.114	0
	StdDepth	0.479	0
StdChlA	~		
	StdLon	0.16	0
	StdLat	0.27	0.013
	StdAlt	-0.247	0.231
	StdTP	0.234	0
	StdTN	0.103	0

Table A2 (cont’d)			
	StdTemp	0.066	0
	StdpH	0.172	0
	StdDepth	-0.125	0
StdChlASq	~		
	StdLon	-0.049	0.437
	StdLat	0.107	0.565
	StdAlt	-0.229	0.513
	StdTP	0.066	0.107
	StdTN	0.117	0.002
	StdTemp	0.003	0.897
	StdpH	0.15	0
	StdSurfA	-0.21	0
StdRich	~		
	StdLon	0.461	0
	StdLat	-0.476	0.003
	StdAlt	-0.993	0.001
	StdTP	0.153	0
	StdTN	-0.047	0.15
	StdTemp	0.111	0
	StdpH	0.095	0
	StdDepth	-0.206	0
	StdSecchi	0.011	0.724
	StdSurfA	0.156	0.001
Covariances:			
		Estimate	P(>lzl)
StdTemp	~~		
	StdSurfA	0.044	0.044
	StdDepth	-0.05	0.218
StdSurfA	~~		
	StdDepth	0.213	0
StdTP	~~		
	StdSecchi	-0.489	0
StdTN	~~		
	StdSecchi	-0.42	0
StdpH	~~		
	StdSecchi	-0.239	0
StdTN	~~		
	StdpH	0.506	0
StdTP	~~		

Table A2 (cont’d)			
	StdpH	0.267	0
	StdTN	0.464	0
StdLon	~~		
	StdLat	-0.066	0
	StdAlt	-0.06	0
StdLat	~~		
	StdAlt	0.01	0
StdChlA	~~		
	StdChlASq	-0.022	0.253
StdChlASq	~~		
	StdRich	0.021	0.437
StdChlA	~~		
	StdRich	0.225	0

Initial Model Yearly Average Size

Direct effects

AvgSize ~ StdAvgChlA + StdAvgTP + StdAvgTN + StdAvgpH + LogSecchi + StdTempAvg + StdSurfA + StdDepth + StdLon + StdLat + StdAlt

Biological Properties

StdAvgChlA ~ StdAvgTP + StdAvgTN + LogSecchi + StdTempAvg + StdDepth + StdAvgpH + StdSurfA + StdAlt

Chemical/Resource Properties

LogSecchi ~ StdTempAvg + StdSurfA + StdDepth + StdAvgTP + StdAvgTN + StdLat

StdAvgTP ~ StdTempAvg + StdSurfA + StdDepth + StdLat

StdAvgTN ~ StdTempAvg + StdSurfA + StdDepth + StdLon + StdLat + StdAlt

StdAvgpH ~ StdTempAvg + StdSurfA + StdDepth + StdLon + StdLat + StdAlt

Physical Properities

StdTempAvg ~ StdLon + StdLat + StdAlt

StdSurfA ~ StdLon + StdLat + StdAlt

StdDepth ~ StdLon + StdLat + StdAlt

Covariances

StdAvgTP ~~ StdAvgTN

StdAvgTP ~~ StdAvgpH

StdAvgpH ~~ StdAvgTN

StdDepth ~~ StdSurfA

StdTempAvg ~~ StdSurfA

StdTempAvg ~~ StdDepth

Table A3: Model results: yearly mean size			
Number of Observations		438	
Degrees of Freedom		10	
P-value		0	
		Estimate	P(>|z|)
AvgSize	~		
	StdAvgChlA	0.053	0.013
	StdAvgTP	0.048	0.054
	StdAvgTN	-0.038	0.191
	StdAvgpH	-0.058	0.002
	LogSecchi	-0.005	0.931
	StdTempAvg	0.002	0.939
	StdSurfA	-0.017	0.268
	StdDepth	-0.028	0.13
	StdLon	-0.002	0.934
	StdLat	0.096	0
	StdAlt	0.042	0.039
	StdRich	-0.115	0
StdAvgChlA	~		
	StdAvgTP	0.237	0
	StdAvgTN	0.285	0
	LogSecchi	-0.065	0.61
	StdTempAvg	0.067	0.112
	StdDepth	-0.173	0
	StdAvgpH	0.237	0
	StdSurfA	-0.028	0.419
	StdAlt	-0.085	0.047
StdRich	~		
	StdAvgTP	0.061	0.353
	StdAvgTN	-0.002	0.982
	LogSecchi	-0.17	0.276
	StdTempAvg	0.207	0
	StdDepth	-0.202	0
	StdAvgpH	0.053	0.225
	StdSurfA	0.114	0.007
	StdAlt	-0.312	0

Table A3 (cont'd)			
LogSecchi	~		
	StdTempAvg	0.016	0.334
	StdSurfA	-0.057	0
	StdDepth	0.074	0
	StdAvgTP	-0.178	0
	StdAvgTN	-0.081	0
	StdLat	0.067	0
StdAvgTP	~		
	StdTempAvg	0.106	0.059
	StdSurfA	-0.097	0.026
	StdDepth	-0.47	0
	StdLat	0.065	0.213
StdAvgTN	~		
	StdTempAvg	0.162	0.006
	StdSurfA	-0.165	0
	StdDepth	-0.369	0
	StdLon	0.278	0
	StdLat	0.257	0
	StdAlt	-0.073	0.038
StdAvgpH	~		
	StdTempAvg	0.3	0
	StdSurfA	-0.054	0.263
	StdDepth	-0.237	0
	StdLon	-0.319	0
	StdLat	0.308	0
	StdAlt	0.288	0
StdTempAvg	~		
	StdLon	0.378	0
	StdLat	-0.364	0
	StdAlt	-0.287	0
StdSurfA	~		
	StdLon	-0.328	0
	StdLat	-0.295	0
	StdAlt	-0.15	0.014
StdDepth	~		
	StdLon	-0.279	0
	StdLat	-0.037	0.473
	StdAlt	0.192	0.001
Covariances:			

Table A3 (cont’d)			
StdAvgTP	~~		
	StdAvgTN	0.391	0
	StdAvgpH	0.285	0
StdAvgTN	~~		
	StdAvgpH	0.327	0
StdSurfA	~~		
	StdDepth	0.379	0
StdTempAvg	~~		
	StdSurfA	0.044	0.065
	StdDepth	-0.059	0.01
StdLon	~~		
	StdLat	-0.489	0
	StdAlt	-0.678	0
StdLat	~~		
	StdAlt	0.35	0

Initial Model Yearly Cell Size Variance

Direct Effects

LogVar ~ StdAvgChlA + StdVarTP + StdAvgTP + StdVarTN + StdAvgTN + StdAvgpH + LogSecchi + StdTempAvg + StdVarTemp + StdSurfA + StdDepth + StdLat + StdAlt + StdRich

Biological Properties

StdAvgChlA ~ StdAvgTP + StdAvgTN + LogSecchi + StdTempAvg + StdDepth + StdAvgpH + StdSurfA + StdAlt+ StdVarTP+ StdVarTN + StdVarTemp

StdRich ~ StdAvgTP + StdAvgTN + StdAvgpH + StdVarTN + StdVarTP + StdTempAvg + StdVarTemp + StdDepth + StdLon + StdLat + StdAlt

Chemical Properties

LogSecchi ~ StdTempAvg + StdSurfA + StdDepth + StdAvgTP + StdAvgTN + StdLat

StdAvgTP ~ StdTempAvg + StdSurfA + StdDepth + StdLat + StdVarTemp

StdAvgTN ~ StdTempAvg + StdSurfA + StdDepth + StdLon + StdLat + StdAlt

StdAvgpH ~ StdTempAvg + StdSurfA + StdDepth + StdLon + StdLat + StdAlt

StdVarTN ~ StdLon + StdDepth + StdLat + StdSurfA

StdVarTP ~ StdDepth + StdVarTemp + StdSurfA

Physical properities

StdVarTemp ~ StdLat + StdAlt + StdSurfA

StdTempAvg ~ StdLon + StdLat + StdAlt

StdSurfA ~ StdLon + StdLat + StdAlt

StdDepth ~ StdLon + StdLat + StdAlt

Covariances

StdAvgChlA ~~ StdRich

StdAvgTP ~~ StdAvgTN

StdAvgTP ~~ StdVarTP

StdAvgTN ~~ StdVarTP

StdVarTN ~~ StdAvgTP

StdVarTN ~~ StdAvgTN

StdVarTN ~~ StdVarTP

StdAvgTP ~~ StdAvgpH

StdVarTP ~~ StdAvgpH

StdVarTN ~~ StdAvgpH

StdAvgpH ~~ StdAvgTN

StdDepth ~~ StdSurfA

StdTempAvg ~~ StdVarTemp

StdTempAvg ~~ StdSurfA

StdTempAvg ~~ StdDepth

Table A4: Model results: yearly cell size variance			
Number of Observations		431	
Degrees of Freedom		24	
P-value		0.003	
Regressions:			
		Estimate	P(>|z|)
LogVar	~		
	StdAvgChlA	-0.018	0.45
	StdVarTP	0.035	0.134
	StdAvgTP	-0.003	0.926
	StdVarTN	0.007	0.705
	StdAvgTN	-0.036	0.233

Table A4 (cont’d)			
	StdAvgpH	0.021	0.2
	LogSecchi	0.01	0.863
	StdTempAvg	0.02	0.41
	StdVarTemp	0.05	0
	StdSurfA	0.008	0.611
	StdDepth	-0.017	0.343
	StdLat	-0.078	0
	StdAlt	-0.081	0
	StdRich	0.061	0.001
StdAvgChlA	~		
	StdAvgTP	0.324	0
	StdAvgTN	0.241	0
	LogSecchi	-0.188	0.108
	StdTempAvg	0.09	0.038
	StdDepth	-0.146	0
	StdAvgpH	0.212	0
	StdSurfA	-0.08	0.01
	StdAlt	-0.067	0.123
	StdVarTP	-0.074	0.145
	StdVarTN	0.03	0.488
	StdVarTemp	0.034	0.262
StdRich	~		
	StdAvgTP	0.202	0.01
	StdAvgTN	-0.141	0.088
	StdAvgpH	0.118	0.01
	StdVarTN	0.039	0.457
	StdVarTP	-0.042	0.502
	StdTempAvg	0.009	0.89
	StdVarTemp	0.036	0.349
	StdDepth	-0.163	0
	StdLon	0.24	0
	StdLat	-0.159	0.001
	StdAlt	-0.314	0
LogSecchi	~		
	StdTempAvg	0.015	0.386
	StdSurfA	-0.058	0
	StdDepth	0.074	0
	StdAvgTP	-0.166	0
	StdAvgTN	-0.081	0
	StdLat	0.062	0

Table A4 (cont’d)			
StdAvgTP	~		
	StdTempAvg	0.017	0.638
	StdSurfA	-0.088	0.038
	StdDepth	-0.482	0
	StdLat	0.012	0.731
	StdVarTemp	0.076	0.01
StdAvgTN	~		
	StdTempAvg	0.104	0.025
	StdSurfA	-0.149	0
	StdDepth	-0.383	0
	StdLon	0.295	0
	StdLat	0.24	0
	StdAlt	-0.064	0.031
StdAvgpH	~		
	StdTempAvg	0.228	0.004
	StdSurfA	-0.056	0.247
	StdDepth	-0.251	0
	StdLon	-0.299	0
	StdLat	0.271	0
	StdAlt	0.291	0
StdVarTN	~		
	StdLon	0.251	0
	StdDepth	-0.3	0
	StdLat	0.125	0.006
	StdSurfA	-0.113	0.015
StdVarTP	~		
	StdDepth	-0.399	0
	StdVarTemp	0.171	0
	StdSurfA	-0.103	0.023
StdVarTemp	~		
	StdLat	0.418	0
	StdAlt	-0.304	0
	StdSurfA	0.093	0.036
StdTempAvg	~		
	StdLon	0.376	0
	StdLat	-0.376	0
	StdAlt	-0.268	0
StdSurfA	~		
	StdLon	-0.328	0
	StdLat	-0.307	0

Table A4 (cont'd)			
	StdAlt	-0.133	0.029
StdDepth	~		
	StdLon	-0.281	0
	StdLat	-0.047	0.374
	StdAlt	0.185	0.002
Covariances:			
		Estimate	P(>|z|)
StdAvgChlA	~~		
	StdRich	0.158	0
StdAvgTP	~~		
	StdAvgTN	0.383	0
	StdVarTP	0.528	0
StdAvgTN	~~		
	StdVarTP	0.322	0
StdAvgTP	~~		
	StdVarTN	0.301	0
StdAvgTN	~~		
	StdVarTN	0.394	0
StdVarTN	~~		
	StdVarTP	0.325	0
StdAvgTP	~~		
	StdAvgpH	0.283	0
StdAvgpH	~~		
	StdVarTP	0.184	0
	StdVarTN	0.261	0
StdAvgTN	~~		
	StdAvgpH	0.331	0
StdSurfA	~~		
	StdDepth	0.376	0
StdVarTemp	~~		
	StdTempAvg	-0.055	0.009
StdTempAvg	~~		
	StdSurfA	0.027	0.231
	StdDepth	-0.072	0.001
StdLat	~~		
	StdAlt	0.351	0
	StdLon	-0.494	0
StdAlt	~~		
	StdLon	-0.664	0

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CHAPTER 2

EVOLUTIONARY STABILITY OF COEXISTENCE DUE TO THE STORAGE EFFECT IN A TWO-SEASON MODEL

Abstract

The question of species coexistence has been central to ecology since its beginning. Ever-present environmental variation may be one answer to that question. Previous models have demonstrated that species can exploit this variation to coexist with competitors by having different environmental responses (the storage effect). When traits governing species' environmental response can evolve, however, coexistence is not assured. In this study, I use a continuous time, two-season model to determine the evolutionary outcome of competing species evolving in their seasonal performance trait. I extend the competitive exclusion principle to show that the storage effect can allow no more than N species to coexist on N discrete seasons with no relative nonlinearity. I find a broad region of parameter space where coexistence is evolutionarily stable. The size of this region depends on the period of fluctuations relative to the individual lifespan. Relatively long period fluctuations yield a large coexistence region, but as the period decreases, the region narrows and disappears asymptotically. Finally, I cast my adaptive dynamics technique in terms of Chesson's concept of equalizing and stabilizing mechanisms to demonstrate that the breakdown in coexistence at short periods is due to loss of the stabilizing covariance between the environment and competition.

Introduction

The role of temporal variation in maintaining diversity has long been of interest to ecologists. Hutchinson proposed non-equilibrium conditions as one possible solution to his "Paradox of the Plankton" (1961). He noted that different species take advantage of changing conditions throughout the year and suggested that intermediate time-scale variation would prevent competitive exclusion. This idea was embraced by aquatic ecologists and tested in laboratory experiments (Turpin and Harrison 1979; Sommer 1984; Grover 1991). There was significant theoretical development as well: Armstrong and McGehee (1976) showed that species with nonlinear resource use functions could coexist on a single shared, fluctuating resource. Soon after, Levins (1979) showed that variance itself could be thought of as a resource that species could consume, expanding the competitive exclusion principle. More in line with Hutchinson's verbal model of a varying environment, Loreau (1989) showed that competitors could have niche differentiation in time and thereby coexist.

The notions of species consuming resource variance or partitioning time are intuitively appealing, but the subtleties of coexistence mechanisms have lead to some confusion. Chesson and Huntly (1997) clarified that environmental variation by itself does not necessarily result in species coexistence, a fact that had been understood with respect to the maintenance of allelic diversity in the genetics literature for some time (Gillespie 1973, 1974; Felsenstein 1976). Chesson (1994) classified two distinct mechanisms through which species can coexist in fluctuating environments: relative nonlinearity and the storage effect. Relative nonlinearity occurs when species growth responses are nonlinear relative to each other, so that one performs better at high resource availability and the other at low resource availability. Armstrong and McGehee's (1976) and Levins' (1979) models fit this category, as do subsequent works (Litchman and Klausmeier 2001). The storage effect requires that species respond differently to variation in some environmental factor, such that species occupy different niches in time. Three conditions are necessary for this mechanism to operate: 1) differential responses to the environment so that species perceive good and bad times differently, 2) buffered population growth, usually interpreted to mean resting stages, dormancy or long-lived adults, and 3) covariance between competition and the environment so that there is a relaxation of competition when a species gets its good season (Chesson 1994, 2000).

The models discussed above are ecological and have assumed few species, whose traits do not change significantly, ignoring evolution. However, the ecological mechanisms proposed to explain coexistence may break down when faced with evolution or invasion from a broader species pool (Ellner and Hairston 1994; Shoresh et al. 2008). A robust approach to explaining diversity must include an analysis of the evolutionary stability of a coexistence mechanism. Here I consider both the origin and maintenance of diversity. Diversity can arise in two distinct ways. Assuming reproductive isolation, diversity may originate *in situ* if small mutations lead a single species to a point where it undergoes disruptive selection (an evolutionary branching point; Geritz et al. 1998). Alternatively, large mutations or immigration of other species from the metacommunity may succeed when small mutations fail (a local, but not global, one-species ESS). Diversity is maintained when two species with distinct strategies can each rebound when rare and no other strategy can successfully invade the pair (a multi-species, global evolutionarily stable strategy [ESS]). In my model, diversity is maintained when it arises through either mechanism, with branching points a subset of non-global one-species ESS's, both of which lead to two-species global ESS's.

There are multiple studies demonstrating coexistence due to temporal variability in nature (Pake and Venable 1995; Cáceres 1997; Angert et al. 2009, 2011), implying that evolutionarily stable, fluctuation-dependent coexistence is indeed possible. Modeling studies are less clear, and sometimes suggest the opposite. Kremer and Klausmeier (2013) investigated the evolutionary stability of relative nonlinearity in a seasonal environment and found a broad range of conditions leading to evolutionary stable coexistence and branching; others have found evolutionarily stable coexistence due to relative nonlinearity to be unlikely (Hartig et al. 2014). Litchman et al. (2009) and Edwards et al. (2013) found coexistence of different size classes of phytoplankton given appropriately pulsed nutrient environments based on a trade-off between nutrient storage, growth rate, and competitive ability.

Similarly contradictory results concern the evolutionary stability of coexistence via the storage effect. Snyder and Adler (2011) asked whether the storage effect could be expected to evolve in a model based on the desert annual plant system, consisting of a single generation per year and with lottery competition and evolution in the germination trait. They found that coexistence due to the storage effect was usually evolutionarily unstable and, except for a specific set of circumstances where germination and competition (represented by fecundity in the lottery model) were correlated, would not evolve. In contrast, Abrams and colleagues (2013), showed that in a lottery model with type II functional responses, the storage effect could evolve over a range of tradeoff shapes. This analysis tied germination and competition by considering evolution in overall recruitment. Although they note the possibility for multiple attractors, the analysis mainly concerns the potential for evolutionary branching and not the possibility of evolutionarily stable coexistence of two species generated in allopatry. Similarly, Mathias and Chesson (2013) found that in a desert annual plant-based model with continuous dynamics within years and discrete dynamics between years, coexistence based on a single rain event was eliminated by evolution, but with a more complex environment (two rain pulses per year) the model could produce evolutionary branching. The quantitative genetics literature has also addressed the question. Ellner and Hairston (1994) found that fluctuating environment could maintain genetic variation in a sexual population via the storage effect. Most of the previous papers have considered discrete time models that based on the life cycles of annual plants. These models make specific assumptions (no generational overlap, lottery competition) that may not translate to other systems. As yet, there has been relatively little work on systems with continually reproducing organisms, like phytoplankton and other microbes. Despite the theoretical and practical interest, the role of temporal variation on coexistence in these systems remains unclear.

In this paper I use a minimal model to isolate the role of the storage effect in maintaining diversity in continuously reproducing species. I investigate the time scale of environmental variation relative to the life span of the competitors to see under what conditions the storage effect is evolutionarily stable, whether diversity could arise through evolutionary branching in asexual organisms, and how many species can coexist on a single resource in a variable environment. Instead of focusing solely on branching points I also consider global evolutionary stability. I use a series of models in a simple two-season environment. I begin with a density-independent model to understand the underlying selective landscape, then add density dependence to incorporate competition. I extend the competitive exclusion principle to show that without relative nonlinearity there can be no more species than distinct seasons (in my case, two) and that stable coexistence is unlikely for rapid fluctuations. I then look at how the evolutionary stability of coexistence and existence of branching points depend on the specifics of the environmental fluctuations and species parameters. Finally I decompose the model into stabilizing and equalizing components, as in Chesson's work (Chesson 2000), to demonstrate the disappearance of the storage effect as the period of fluctuations decreases. Together, these results illuminate the conditions under which the storage effect is expected to evolve or be evolutionarily stable and link Chesson's theory and adaptive dynamics.

Model Basics

The model is periodic in continuous time, with an environmental variable $T(t)$ that alternates between two values, representing two discrete seasons. For concreteness I refer to the environmental variable as temperature but the model is appropriate for any environmental parameter that leads to a unimodal growth response, such as pH.

$$T(t) = \begin{cases} T_1 \text{ if } t \bmod \tau < \phi\tau \\ T_2 \text{ if } t \bmod \tau > \phi\tau \end{cases} \tag{1}$$

Here, τ is the period, ϕ is the proportion of each period spent in the first season, and T_1 and T_2 are the temperatures in season 1 and 2 respectively (Figure 2.1A).

Competing species differ only in their optimal temperature, T_{opt}, which will be the focal trait of my analyses. Birth rate μ depends on the difference between the temperature and the species' optimum. I make three reasonable assumptions about the form of this function $\mu(T_{opt}, T)$: 1) It is unimodal with respect to T_{opt}, with a maximum at the point where the trait (T_{opt}) is equal to the temperature (T); 2) it is bounded from below, because birth rate cannot be less than zero; 3) it is continuously differentiable. These assumptions imply a function with a positive second derivative on the outer edges and a negative second derivative in the center. One such function that conforms to all of these requirements is a Gaussian function with width σ:

$$\mu(T_{opt}, T) = e^{\frac{-\left(T_{opt}-T\right)^2}{2\sigma^2}} \tag{2}$$

(Figure 2.1B). This function creates a tradeoff between performance in the two seasons for T_{opt} values between $T_1$and $T_2(\Delta T)$ (Figure 2.1C). Species with trait values outside this range are worse in both seasons, so I don't consider them further. A species with trait value $T_{opt} = T_1$ is best in season 1, but has lower growth in season 2, while a species with trait value $T_{opt} = T_2$ has the opposite problem. The exact shape of the tradeoff depends on of the shape of the birth function, but because of the requirements for the second derivative it will be either convex or convex-concave-convex, depending on the distance between the seasons (Levins 1979). Table 2.1 gives a list of parameters and values for reference.

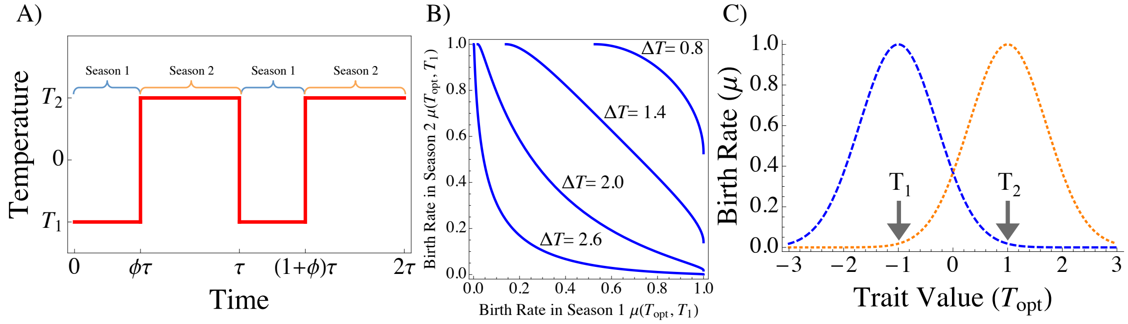

Figure 2.1 Seasonal forcing and traits A) Birth rate (μ) as a function of trait value (T_{opt}) in two seasons (season 1 [dashed line]: $T_1 = -1$ and season 2 [dotted line]: $T_2 = 1$). B) Tradeoff function for a range of ΔT. The curve goes from concave down (indicating the best strategy is a generalist) to concave up (indicating the best strategy is two specialists). Only the portion of the tradeoff function that lies between the two peaks is shown. C) Temperature as a function of time.

Density-Independent Model

I begin with the simplest case of density-independent growth. Species do not interact in this model, so it is not appropriate for questions of coexistence. In addition, populations in density-independent models can blow up to infinity, clearly not a realistic result. However, because the species with the largest growth rate will ultimately come to dominate the community, it gives insights into how this periodic environment selects for traits. As I will later show, it also relates to a density-dependent model with fast fluctuations and serves as a baseline for understanding the density-dependent case.

The instantaneous fitness of species i, g_i is the given by per capita net growth rate

$$\frac{dn_i}{n_i dt} = \mu\left(T_{opt,i}, T(t)\right) - m = g_i \tag{3}$$

where n_i is the density of species i, m is the mortality rate, μ is the birth rate given by equation 2 and $T(t)$ is the time-dependent temperature given by equation 1. In a continuous-time periodic environment, the appropriate measure of overall fitness is simply the time-averaged instantaneous fitness,

$$\overline{g_\iota} = \frac{1}{\tau}\int_0^\tau g_i(t)dt \tag{4}$$

(Metz et al. 1992; Smith and Waltman 1995; Klausmeier 2008). In my two-season model, this is the average fitness in each season weighted by the time spent in each season,

$$\bar{g}_i = \phi\mu\left(T_{opt,i}, T_1\right) + (1 - \phi)\mu\left(T_{opt,i}, T_2\right) - m \qquad (5)$$

Note that fitness here is independent of the period τ.

Figure 2.2 shows how these instantaneous fitness landscapes combine to form the overall fitness landscape for different values of ϕ and $T_1 - T_2$. The optimal trait value is the one that maximizes $\bar{g}_i$. The mortality rate *m* is independent of the trait, so the optimum does not depend on it. Since $\bar{g}_i$ is a weighted mixture of two Gaussians, there is either a single global maximum (Figure 2.2a,e) or two local maxima separated by a minimum (Figure 2.2b-d) (Schilling et al. 2002). When the seasons are equal length ($\phi = 0.5$), there is a single generalist optimum at $T_{opt} = (T_1 + T_2)/2$ for $|T_1 - T_2| \leq \sqrt{2}\sigma$ and two alternative specialist optima for $|T_1 - T_2| > \sqrt{2}\sigma$ (Schilling et al. 2002, Figure 3). That is, similar seasons select for a generalist species while distinct seasons select for specialists. In the perfectly symmetric case of $\phi = 0.5$, the alternative specialists have equal fitness (Figure 2.2b-c), but in general one specialist has lower fitness than the other, and represent a local, but not global optimum (Figure 2.2d). There are two optima for a wide range of ϕ with the global optimum close to T_1 for $\phi > 0.5$ and close to T_2 for $\phi < 0.5$ (Figure 2.4). Therefore, this density-independent model shows the influence of the environmental fluctuations on the optimal trait, but species coexistence requires precisely equal fitness resulting in neutral coexistence. The shape of the tradeoff function also varies as the distance between the optimal temperatures changes (Figure 2.3b). Closer peaks yield a more concave down the tradeoff function and confer advantage to the generalist phenotype. A similar type of tradeoff curve was explored in Levins (1968).

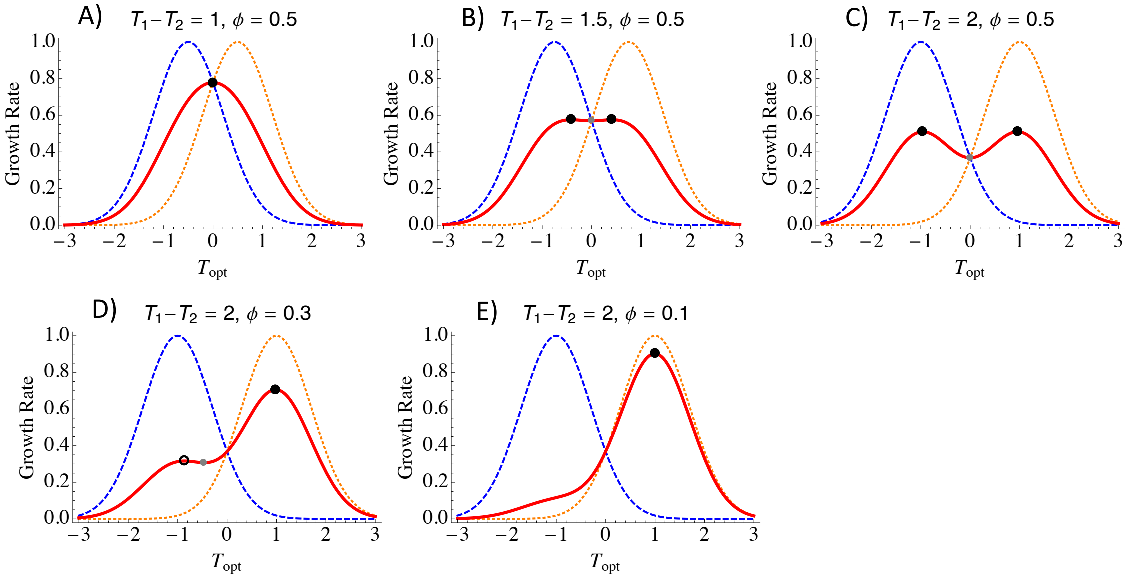

Figure 2.2 <u>Overall fitness surfaces ($\bar{g}$) for a range of ϕ</u> The dashed blue and dotted orange lines indicate the correspondence between growth rate and trait in each season, as in figure 1, while the red, solid line indicates the overall growth vs. trait function. Global maxima are given by large filled circles, local maxima are given by large open points, and minima are given by small gray points.

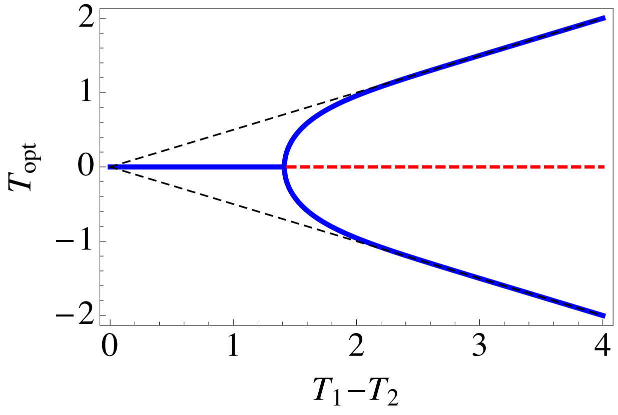

Figure 2.3 <u>The difference between seasonal temperatures and the resulting optimal trait(s)</u> Optimal strategies as the difference between the seasons increases ($\phi = 0.5$). The dashed black line indicates the temperatures and the thick blue line indicates the evolutionary optima. The red dashed line indicates the fitness minimum. The bifurcation point occurs at $\sqrt{2}$.

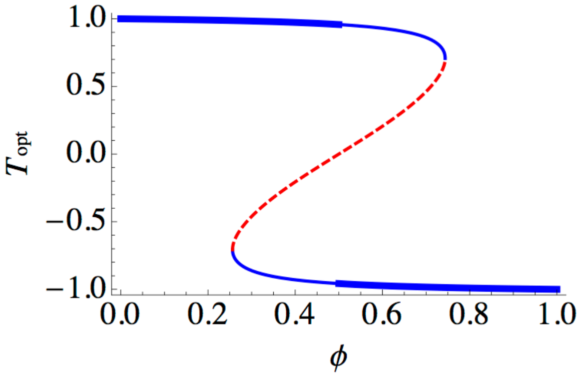

Figure 2.4 Fitness maxima and minima as a function of length of season 1, ϕ ($T_1 = -1, T_2 = 1$). Thick blue lines indicate globally stable strategies, thin blue lines indicate locally, but not globally stable strategies, and the red, dashed line indicates a fitness minimum.

Density-Dependent Model

To address the question of robust species coexistence I need to add density dependence, done here through competition for a single limiting resource. Environmental variability still affects the maximum birth rate, but now birth is mediated by resource availability, which in turn is determined by the density of consumers.

$$\frac{dn_i}{n_i dt} = \mu\left(T_{opt,i}, T(t)\right) f(R) - m = g_i \tag{6}$$

$$R = R_{tot} - \sum_i n_i \tag{7}$$

Here, R is the available resource, R_{tot} is total resource, assuming a closed system, and $f(R)$ is a functional response relating birth rate to available resource. I assume all species share the same functional response ($f(R)$) to avoid relative nonlinearity, which is a separate coexistence mechanism. In numerical examples I use a linear functional response, $f(R) = R$. Modeling the resources with an algebraic equation instead of another differential equation does not affect my results, as long as the dynamics of the resource are much faster than those of the consumer. This is a good assumption for phytoplankton consuming inorganic nutrients and for many other systems.

Ecological Dynamics

To illustrate the ecological dynamics of this model, I consider two specialist species ($T_{opt,1} = -1, T_{opt,2} = 1$) in a slightly asymmetric environment where season one lasts longer than season two ($\phi = 0.6$), for two contrasting periods ($\tau = 0.1$ and $\tau = 10$). I numerically perform invasion analyses, solving the dynamics of a monoculture of each species then calculating the invasion rate of the other. Finally, I show the dynamics of both species together (Figure 2.5–2.6).

In the case of fast environmental fluctuations ($\tau = 0.1$; Figure 2.5), populations and resources do not vary much over a period (Figure 2.5 top row). Each invader grows rapidly during the season that favors it, but the average growth rate can be either positive or negative (Figure 2.5 bottom row). In this case, species 1 outcompetes species 2 because its favored season lasts longer.

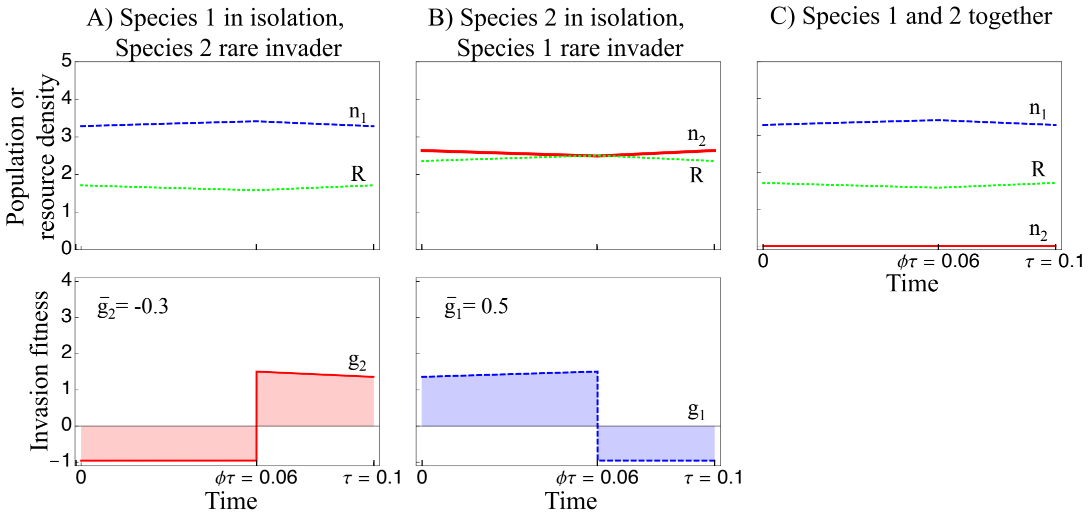

Figure 2.5 Population and invasion rate dynamics for two species and the resource when $\tau = 0.1$ and $\phi = 0.6$. Resource (R): green dotted line, species 1 (n_1): blue dashed line, species 2 (n_2): red solid line. Shading under the invasion fitness graphs indicates that invasion fitness should be thought of as integrated throughout the entire period. Note there is little change in the densities of species or resources. Although species 2 can survive on its own (B), it cannot survive in competition with species 1 (C), as indicated by its negative average growth rate $\bar{g}$ as invader (A).

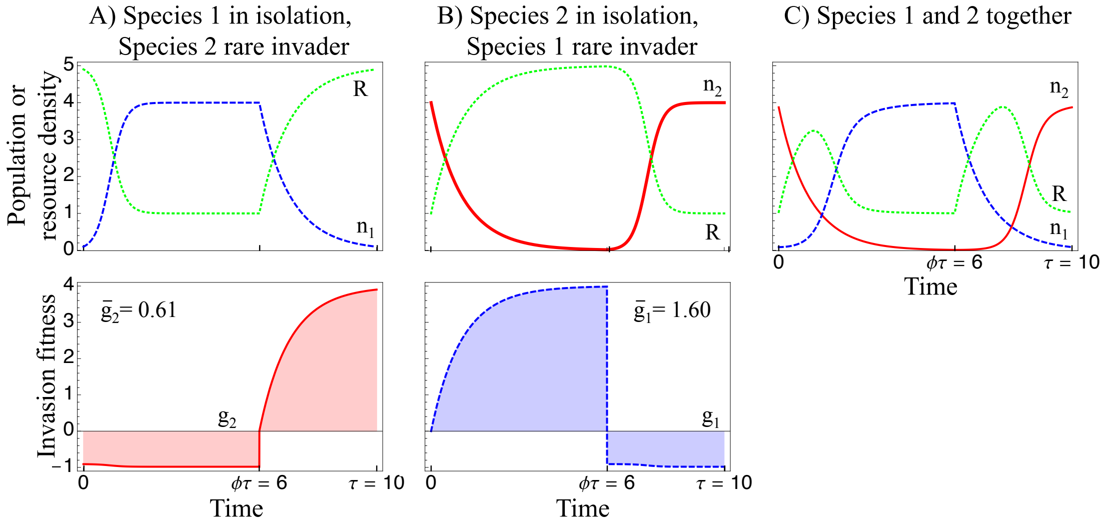

Figure 2.6 Population and invasion rate dynamics as in Figure 2.5, with $\tau = 10$ and $\phi = 0.6$.. At this longer period there is drastic change in the densities of species and resources, and now species 2 can survive on its own (B) and in competition with species 1 (C), as indicated by its positive $\bar{g}$ as invader (A). Although the population dynamics in (A) and (B) look similar to those in (C), note that in competition, the resurgence of a given species is delayed by depletion of resources in the previous season.

In the case of slow environmental fluctuations ($\tau = 10$; Figure 2.6), the dynamics consist of relatively constant periods, interspersed with rapid transitions (Figure 2.6, top row; see also Klausmeier 2010). Each invader grows even more rapidly during the season that favors it because resources are abundant when the resident species is unfavored (Figure 2.6 bottom row). This positive covariance between environmentally determined growth and resource level gives each species an advantage when rare, so that each species can invade a monoculture of the other. This leads to stable species coexistence (the storage effect, Chesson 1994), despite the difference in season length (Figure 2.6c).

Although this system can allow two species to stably coexist, I can show that this is the maximum diversity that can be maintained. To see this, note that the invasion rate is the time-average growth rate as in the density-independent model. This can be broken up into contributions from the two seasons

$$\bar{g}_i = \frac{1}{\tau}\int_0^{\tau} g_i(t)dt \tag{8}$$

$$= \mu\big(T_{opt,i}, T_1\big)\frac{1}{\tau}\int_0^{\phi\tau} f(R(t))dt + \mu\big(T_{opt,i}, T_2\big)\frac{1}{\tau}\int_{\phi\tau}^{\tau} f(R(t))dt - m \tag{9}$$

$$= \phi\mu\big(T_{opt,i}, T_1\big)\overline{f_1(R)} + (1-\phi)\mu\big(T_{opt,i}, T_2\big)\overline{f_2(R)} - m \tag{10}$$

where $\overline{f_j(R)}$ is the average resource-dependent functional response in season j. Each species shares the same average resource-dependent functional responses, so they act as two limiting factors (a two dimensional environmental feedback *sensu* Meszéna et al. 2006). According to the competitive exclusion principle, no more species than limiting factors can coexist (Levin 1970; Meszéna and Metz 1999). Therefore, when all species share the same functional response (no relative nonlinearity), no more than two species can coexist in a two-season environment, since there are in effect only two limiting factors, resources in season 1 and resources in season 2. More generally, no more than *N* species can coexist in an environment with *N* distinct seasons. When the environment changes continuously, in theory there is no limit to the number of coexisting species, but in practice it becomes a question of limiting similarity as explored by Barabas (2011).

In the case of infinitely fast fluctuations however, stable coexistence is impossible. As can be seen in Figure 2.5a-c, the resource is practically constant throughout a period because the populations do not have enough time to react to changes of the season. This means $\overline{f_1(R)} \approx \overline{f_2(R)} \approx f(\bar{R})$ in equation 10, leaving only one limiting factor, $\bar{R}$. Equation 10 can be rewritten

$$\bar{g}_i = \left[\phi\mu\left(T_{opt,i}, T_1\right) + (1-\phi)\mu\left(T_{opt,i}, T_2\right)\right] f(\bar{R}) - m \qquad (11)$$

$$= \overline{\mu\left(T_{opt,\imath}\right)} f(\bar{R}) \; - m \qquad (12)$$

It is apparent that the species with the greatest average birth rate $\overline{\mu\left(T_{opt,\imath}\right)}$ is the superior competitor who will displace all others. Since $\overline{\mu\left(T_{opt,\imath}\right)}$ is merely a rescaled version of fitness from the density-independent model, the density-independent optimum strategy is also the winner in the density-dependent model with infinitely fast fluctuations.

Evolutionary Outcomes

To determine the outcome of evolution I use the techniques of adaptive dynamics (Geritz et al. 1998). Given a resident species with trait value $T_{opt,res}$, I first find the resident species' ecological attractor. Then I consider a rare invader with strategy $T_{opt,inv}$, and calculate its invasion fitness, defined as its growth rate into the environment set by the resident, $\overline{g_{inv}}$. If $\overline{g_{inv}} > 0$ invasion can be successful and if $\overline{g_{inv}} < 0$ it fails. Note that $\overline{g_{res}} = 0$ given the assumption the resident is at its attractor. If invaders arise through small mutations of the resident species, then I need to consider only the derivatives of the invasion fitness function, evaluated at the point where the invader trait is equal to the resident trait. If $\partial\overline{g_{inv}}/\partial T_{opt,inv} > 0$ then invaders with larger T_{opt} can replace the resident (Geritz 2004) (directional selection towards larger T_{opt}); if $\partial\overline{g_{inv}}/\partial T_{opt,inv} < 0$ then invaders with smaller T_{opt} can replace the resident (directional selection towards smaller T_{opt}). A singular strategy T_{opt}^{*} is one where $\partial\overline{g_{inv}}/\partial T_{opt,inv} = 0$, indicating no directional selection. At a singular strategy, if $\partial^{2}\overline{g_{inv}}/\partial T_{opt,inv}^{2} < 0$ then T_{opt}^{*} is a local fitness maximum (stabilizing selection; a locally *evolutionarily stable strategy* [ESS]); if $\partial^{2}\overline{g_{inv}}/\partial T_{opt,inv}^{2} > 0$ then $T_{opt}^{*}$is a local fitness minimum (disruptive selection). An intriguing possibility is when directional selection leads to a fitness minimum, called an evolutionary branching point. This provides ecological conditions that promote the generation of diversity *in situ* (when the assumption of instantaneous reproductive isolation as in asexual species is met). Near branching points, similar species can stably coexist (mutual invasibility), leading to a two-species resident community. These species may evolve further to reach a two-species ESS, which represents evolutionarily stable coexistence.

If invaders include other species that immigrate from the metacommunity, then I must consider all possible trait values not just those similar to the resident's. A strategy that makes $\overline{g_{inv}} \leq 0$ for all potential invaders is a global ESS. A global ESS is a stronger condition than a local ESS, because a local ESS may be invasible by a sufficiently different species (analogous to a local fitness maximum as in Figure 2.2d). This may again lead to a two-species ESS and evolutionarily stable coexistence, but not the *in situ* generation of diversity.

A pairwise invasibility plot (PIP) provides a graphical way to see the outcome of evolution (Geritz et al. 1998). PIPs show the sign of the invasion fitness of an invader with a trait value given on the y-axis, into a resident species whose trait value is given on the x-axis. Shaded areas represent positive invasion fitness, and white areas are negative. Singular strategies occur where the zero-isoclines cross the one-to-one line. The classification of the singular points as described above is given in Figure 2 of Geritz et al. (1998).

Figure 2.7 shows example PIPs for my model, calculated in the limit of large periods using the SSD approximation of Klausmeier (2010) (for a more complete set of PIPs, see supplemental fig. A1). Briefly, this approximation assumes infinitely long periods while maintaining the main transitions between states in the periodic system. For small ϕ there is a single global ESS slightly less than $T_{opt} = 1$ (Figure 2.7a). At $\phi \approx 0.196$ this ESS loses its global evolutionary stability and is invasible by a strategy near $T_{opt} = -1$. Coincidently, a two-species ESS is born at this point (a generic result shown in the appendix of (Geritz et al. 1999)). Figure 2.7b shows this case of a local, but not global ESS. At $\phi \approx 0.368$ a pair of new singular strategies arise near $T_{opt} = 0$, a branching point and a repellor (fig. 7c). At $\phi \approx 0.460$ another pair of new singular strategies emerge near $T_{opt} = -1$, a local ESS and another repellor (Appendix Figure A1). Due to the symmetry of the model, the same transitions happen in reverse past $\phi = 0.5$ (Appendix Figure A1). Therefore in the limit of slow forcing (large τ), there is a wide range of ϕ values that have an evolutionary branching point and an even wider range that leads to a two-species ESS (evolutionarily stable coexistence).

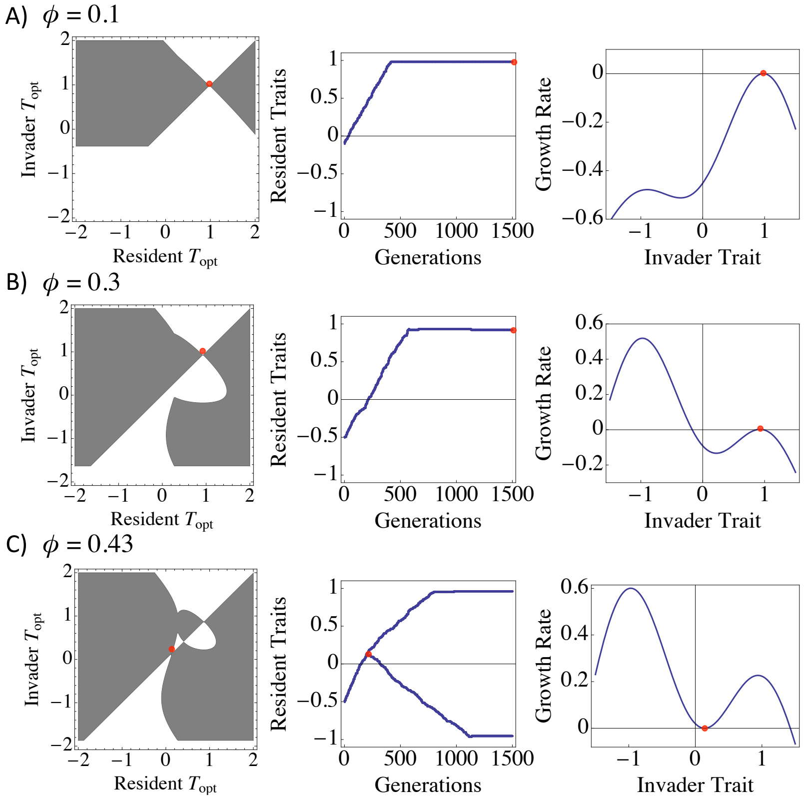

Figure 2.7 PIPs, evolutionary trajectories, and invasion graphs corresponding to the density-dependent model ($\tau = 100, m = 1$). Red dots indicate the same trait value within a row. Regions of the PIP without a main diagonal indicate resident strategies that cannot survive. In the first column, the PIPs, grey indicates positive invasion rate and white indicates negative invasion rates, across a range proportion of time in the first season (ϕ). In the second column, I show the evolutionary dynamics produced by rare, small mutations. Ecological dynamics are allowed to come to equilibrium before a new invader is introduced. Note that the results of evolution by rare mutation are the same in rows A and B. The third column shows the invasion profile at either the final community (rows A and B) or the community at the branching point (row C). The community in row A is uninvasible by any trait value, while the community in row B is invasible by trait values near the other seasonal optimum. The final panel in row C shows the community just at the branching point. As ϕ increases, the outcome progresses from A) only one singular point, a global ESS ($\phi = 0.1$), to B) a local but not global ESS ($\phi = 0.3$), to C) three singular strategies: two attractors, a local ESS and a branching point, with a repellor between ($\phi = 0.43$).

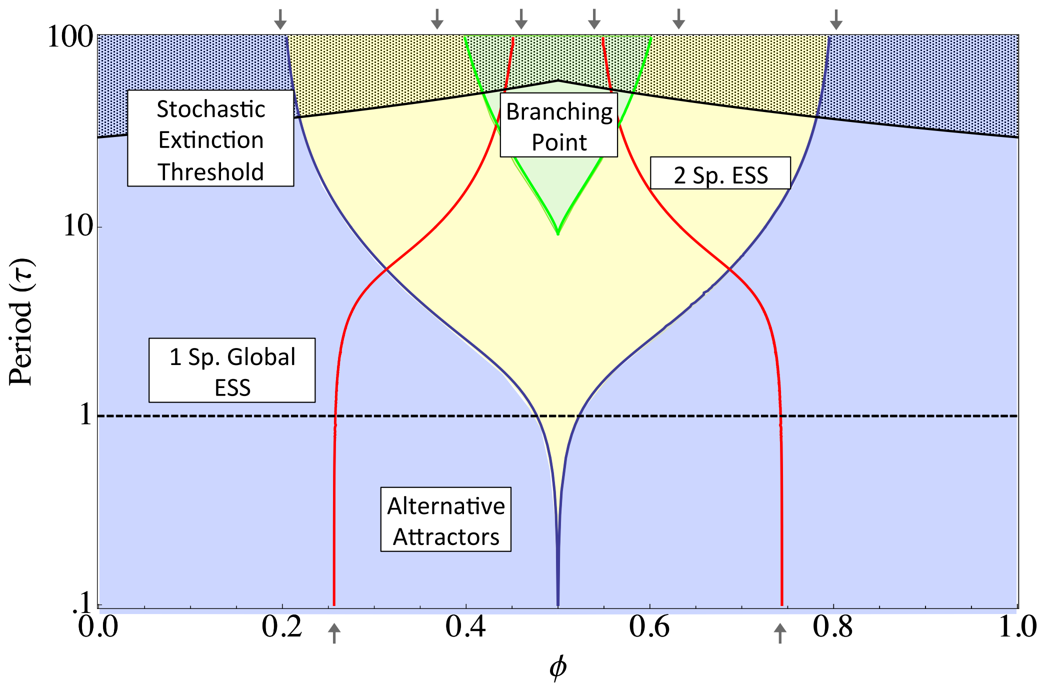

Figure 2.8 Overview of evolutionary outcomes for finite periods ($m = 1, R_{tot} = 5$). In the green region, there is a branching point, allowing the *in situ* generation of diversity. The blue line indicates the loss of global stability of a single specialist: in the yellow and green regions above it, two species can coexist stably. The red line indicates the appearance of a second attractor point (paired with a repellor) where evolution by small mutation can lead result in evolution toward only one of the specialist species despite the existence of another, more globally stable strategy. The black dashed line indicates the period that corresponds to the lifespan of the species in the model. The arrows at the top of the figure indicates where the transitions occur in the SSD approximation ($\tau \rightarrow \infty$), and the arrows at the bottom indicate the transitions corresponding to the density independent case. The shaded region at the top is where the population of either competitor drops below a threshold value of 100 individuals/lake, and thus risks stochastic extinction.

So far I have shown that evolutionarily stable coexistence is widespread for large (effectively infinite) τ but impossible for infinitely small τ. To find out what happens in between, I numerically solve the model for finite τ and locate the boundaries between qualitatively different outcomes as described above (Figure 2.8). For long periods ($\tau > 20$) the results qualitatively match those of my SSD approximation, but as the period gets shorter, the range of ϕ values where a two-species ESS exists narrows, and the branching point region disappears entirely around $\tau = 10$ (an expanded view of this disappearance is given in Appendix Figure A2). As a reference value, the mean lifespan of the competitors in my model is $1/m$ =1. For τ much less than the mean lifespan of individuals, coexistence becomes contingent on finely balanced seasons, while for τ much more, it is widespread. When the analysis is repeated for different values of m and R_{tot}, the picture changes in that for high values of m or low values of R_{tot}, it becomes impossible for species to survive with the generalist strategy and so the evolutionary branching point disappears.

Because the populations in my model can reach very low densities at long periods, I test the robustness of my results by setting an extinction threshold. I used a practical limit of 100 cells/lake with an initial estimate of roughly 10^15 cells/lake when at high densities (Litchman and Klausmeier 2001). I then calculated the corresponding τ and ϕ by solving the expressions $100 = 10^{15}e^{-\tau\phi}$ or $100 = 10^{15}e^{-\tau(1-\phi)}$ (the threshold where 10^{15} cells declines to 100 cells/lake during the off season with a mortality rate of 1) for τ. This effectively cuts off the top portion of figure 8 from ecological plausibility, but it leaves all of the evolutionary outcomes intact. The results agree with Hutchinson's verbal argument that coexistence occurs for intermediate-period fluctuations (Hutchinson 1961), but as Chesson and Huntley (1997) point out it is the covariance, not the fluctuation itself that makes coexistence possible.

When evolutionarily stable coexistence is possible, what are the traits of the coexisting species? Figure 2.9 shows the one-species singular strategies and the two-species ESS trait values over the range of possible ϕ for three different values of τ. While the trait values of the various one-species singular strategies vary widely across ϕ, the traits of the species in the two-species ESS are almost constant whenever it exists, $T_{opt}^{*} \approx \pm 1$ (Figure 2.9), that is, specialists on the two different seasons.

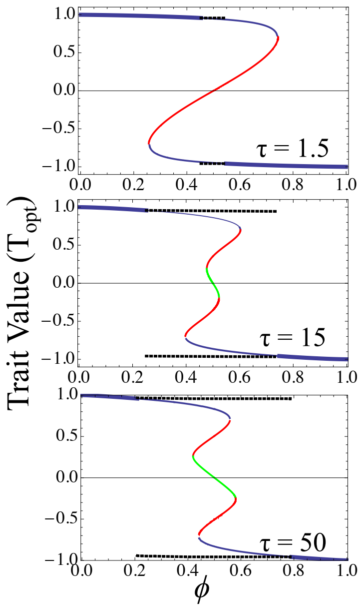

Figure 2.9 Evolutionary equilibria over a range of ϕ for three different period lengths (τ). Thick blue lines indicate a globally stable ESS, dotted black lines indicate the two species ESS, and thin blue lines indicate an attractor strategy that can be invaded (local ESS). Red lines indicate repellor points and green lines indicate branching points. As in figure 8, the region of coexistence increases with the period.

I have seen that the evolutionarily stable coexistence of two specialists is common in this model, particularly for large periods, and when there is a one-species ESS it is one of the specialists. Are there conditions that select for a generalist ($T_{opt} = 0$) instead? In the density-independent model, when the two seasons are similar to each other, the generalist is the only optimum (Figure 2.2a). I varied the difference between the seasons, $|T_1 - T_2|$, in the density-dependent model with ϕ=0.5 and found similar results: for $|T_1 - T_2| < \sqrt{2}$, the generalist $T_{opt} = 0$ is an ESS, while for $|T_1 - T_2| > \sqrt{2}$ two species coexist with trait values that approach T_1 and T_2 as in Figure 2.3 (results not shown). The difference is that these specialists coexist stably in the density-dependent model but only neutrally in the density-independent model.

Quantifying Strength of the Storage Effect

In this section I recast my model in terms of stabilizing and equalizing effects (Chesson 2000) to show that coexistence in my model can be attributed to the storage effect and that the breakdown of coexistence for small period fluctuations can be understood as the loss of the stabilizing effect. The first two requirements of the storage effect listed in the introduction — differential responses to the environment and buffered mortality — can be seen in the population growth equations. The birth rate depends on the environment and on the trait of the individual, leading to differential responses to the environment. Buffered mortality occurs because the rate of population decline in the unfavorable season is limited to $-m$. The final requirement for covariance between the environment and competition is less obvious. In this section I rearrange the growth equation to reveal the role that competition-environment covariance plays in coexistence.

Assuming a linear functional response ($f(R) = R$) for simplicity and to match my numerical examples, my definition of instantaneous fitness (eqn. 6) becomes

$$g_i = \mu_i \, R - m \tag{13}$$

where I have replaced $\mu\left(T_{opt,i}, T\right)$ with μ_i for brevity. Recalling the definition of fitness as time-averaged growth rate (eqn. 4),

$$\overline{g_\iota} = \overline{\mu_\iota \, R} - \overline{m} \tag{14}$$

I can use the fact that $\overline{\mu_\iota \, R} = \overline{\mu_\iota} \, \overline{R} + cov(\mu_i, R)$ to decompose fitness into three terms.

$$\overline{g_\iota} = \overline{\mu_\iota} \, \overline{R} + cov(\mu_i, R) - m \tag{15}$$

The first of these is the average growth of species i on the average resource level, the second is the temporal covariance between growth and resource, and the third is the mortality ($\overline{m} = m$ because mortality is constant).

Now, I can apply this decomposition to evolutionary analyses. First, I can give an expression for the growth rate of the resident

$$\overline{g_{res}} = 0 = \overline{\mu_{res}}\,\overline{R_{res}} + cov(\mu_{res}, R_{res}) - m \tag{16}$$

where R_{res} is the time-varying resource environment set by the resident ($e.g.$ Figure 2.5ab, 2.6ab). Resident fitness equals zero because I assume it is on its attractor. The fitness of a rare invader is

$$\overline{g_{inv}} = \overline{\mu_{inv}}\,\overline{R_{res}} + cov(\mu_{inv}, R_{res}) - m \tag{17}$$

Since $\overline{g_{res}} = 0$, I can compare the invader's growth rate to the resident's

$$\overline{g_{inv}} = \overline{g_{inv}} - \overline{g_{res}} \tag{18}$$

$$= \overline{R_{res}}(\overline{\mu_{inv}} - \overline{\mu_{res}}) + cov(\mu_{inv}, R_{res}) - cov(\mu_{res}, R_{res}) \tag{19}$$

$$= \overline{R_{res}}\,\Delta\bar{\mu} + \Delta cov \tag{20}$$

This breaks the fitness of a rare invader into two parts, similar to Chesson (1994): the difference in average growth rates of the invader and resident ($\Delta\bar{\mu}$) times the average resource left by the resident, and the difference in covariance between their growth rate and the resource level set by the resident (Δcov). In Chesson's work (Chesson 1994), he suggests employing scaling factors to correct for the differing lifespans of competitors, but since the populations I consider here have very similar life histories, I omit such scaling for clarity. Because competition in this model is solely through resources, and the environmental dependence is expressed through the birth rate, this is analogous to Chesson's covariance between competition and the environment. The first term is an "absolute fitness comparison" (sensu Chesson 2000); the second term represents the potentially stabilizing storage effect, which also allows for convergence stability of the generalist.

Since the two parts of this decomposition add up to the growth rate of the invader, I can also decompose a PIP into these two terms (Figure 2.10). The "absolute fitness difference" term ($\Delta\bar{\mu}$) gives rise to a bimodal landscape with peaks near $T_{opt} \approx \pm 1$ (Figure 2.10b), as in the density-independent model. The storage effect term (Δcov) is sometimes negative, but often quite positive (Figure 2.10c), indicating the potential for strong beneficial effects for rare invaders that differ significantly from the resident. At the branching point near $T_{opt}^{*} = 0$, there is almost no Δcov for any invader so the storage effect does not contribute significantly to disruptive selection. This is because the resident creates a constant resource environment for the invader, since it draws down the resource equally in both seasons. The storage effect is strongest when the invader is quite dissimilar to the resident (Figure 2.10c), which stabilizes the coexistence of two specialists. This has an interesting implication for the evolution of the storage effect: the storage effect is not required for divergent selection, but stabilizes coexistence once it exists and allows for convergence stability.

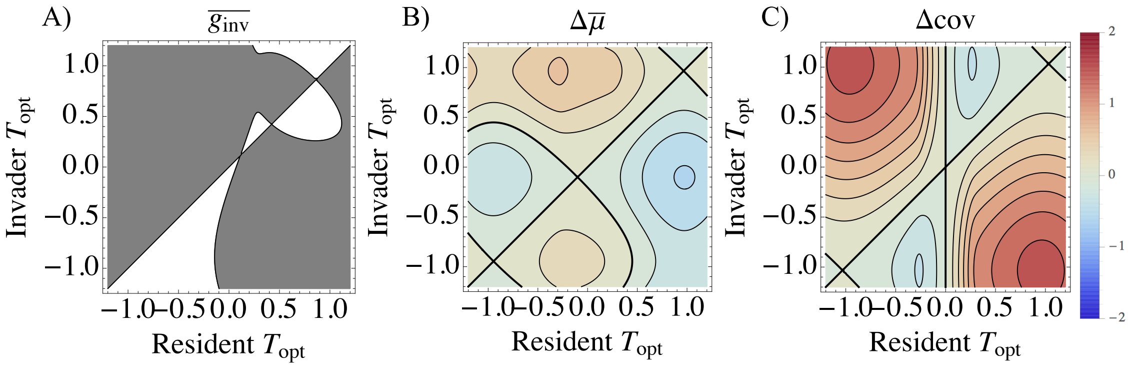

Figure 2.10 Decomposition of the PIP, $\phi = 0.46, \tau = 100, T_1 - T_2 = 2$. After equation 20, panel A = $\overline{R_{res}}$ * panel B + panel C. A) Grey areas are positive invasion rate of the invader into the resident. B–C) Red areas indicate positive values and blue areas indicate negative values. Thicker grey lines indicate zero isoclines and the thinner lines are contour lines.

To understand the breakdown of coexistence for small periods, I vary the period with equal length of seasons ($\phi = 0.5$; a vertical slice down the center of Figure 2.8) and calculate the strength of the storage effect Δcov, evaluated at the two-species ESS. Due to the symmetry of the environment and the species' traits, the "absolute fitness difference" term $\Delta\bar{\mu}$ =0 and both species receive the same storage effect benefit. Figure 11 shows that the storage effect decreases as the period goes to zero, leaving only nearly neutral coexistence at the two species ESS. Any slight deviation from symmetry in the environment ($\phi \neq 0.5$) would tip the balance in favor of one specialist (Figure 2.8).

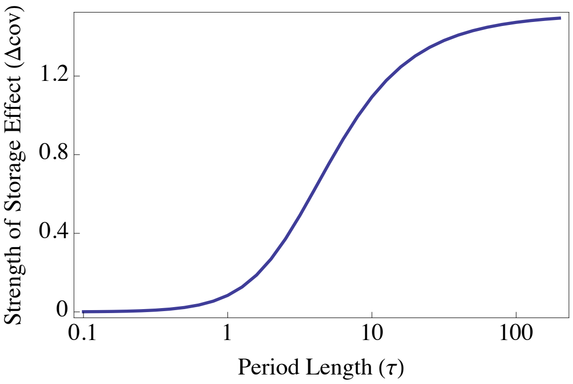

Figure 2.11 The strength of the storage effect at the 2 species ESS goes to zero at low period lengths.

Discussion

In this study I found a broad range of parameters that allow for evolutionarily stable coexistence of two species. Within this range, I found a sizeable region where the storage effect could evolve *in situ* through disruptive selection. I found this even with simple, linear functional responses, whereas studies in the past supporting evolutionarily stable coexistence employed type II functional responses (Abrams et al. 2012). Selection for seasonal specialists can only happen when the two seasons are sufficiently different to create two adaptive peaks instead of a single, seasonal generalist (Figure 2.3). In addition, I showed that there can be at most N species coexisting in N distinct seasons, absent any relative nonlinearity (equations 8-10). Because this result was derived independent of the functional form, it is general: one species per distinct season, providing an extension to the competitive exclusion principle.

The conclusions drawn about the ecological and evolutionary stability of a hypothesized coexistence mechanism can depend greatly on the specifics of the model used to test it. This problem was made evident in the debate over limiting similarity where the choice of model form and functional shape dictated the conclusions about how many species could coexist on a continuous spectrum of resources, detailed by Meszéna et al. (2006). Investigations into the evolutionary dynamics of temporally variable systems seem to have suffered the same fate, as evidenced by the variety of results detailed in the introduction. My paper examines a substantially simpler model of coexistence than those previously employed and so it is easier to examine the consequences of different choices.

Given sufficiently distinct seasons, the proportion of time spent in each determines whether two seasonal specialists can coexist. Just how even the proportion of time spent in each season must be, depends on the length of the period. When period lengths are very long, seasons can be quite skewed and still support the coexistence of two species, but for very short periods, coexistence becomes impossible for all but the most evenly matched seasons (Figure 2.8). The reason for this change in behavior is hinted at in Figures 2.5 and 2.6, where the variation in resource availability changes drastically with the length of the period. Short periods lead to little variation, due to the fact that species densities do not decline instantaneously. When periods change quickly, then populations do not have time to react to the change in seasons, and are still present and consuming resources in their off season. This loss of variation in resource level eliminates the covariance difference between resources and the environment, one of the requirements for coexistence via the storage effect (Figure 2.11). Other studies that included overlapping generations (Ellner and Hairston 1994; Svardal et al. 2015) or different mortality rates for different competitors (Svardal et al. 2011) found that decreasing the length of the period led to increased coexistence. This could be due to the fact that the very long-lived (dormant) stages are able to hide from the selection imposed by the fluctuating environment. This could allow them to experience the fluctuations on a much longer timescale. Decomposing population growth rates into the covariance and fitness difference terms also allowed us to see that the storage effect does not have to be the cause of disruptive selection, but is a stabilizing force for sufficiently differentiated competitors. Thus, the storage effect can stabilize coexistence, but it is not required for the disruptive selection.

The unimodal growth response to traits and the environment assumed by this model may be a common one. Although inspired by temperature optima, this formulation could apply to any system where species have a window of tolerance to an environmental factor. This could be pH (Weisse and Stadler 2006), salinity (Tonk et al. 2007), or even light spectrum (Stomp et al. 2007). While my models are inspired by phytoplankton, this sort of seasonal replacement is also seen in insects (Prigent et al. 2013). I assume a sharp transition between seasons, as is often seen in Mediterranean or monsoon climates, and could be an approximation for temperate lakes, which often freeze and unfreeze suddenly, but my results provide a limiting case for more gradual transitions.

Conclusion

My results complement previous studies, almost all of which employed annual plants (Snyder and Adler 2011; Mathias and Chesson 2013) or sessile marine animals (Kisdi and Meszéna 1995) as their metaphor, and some sort of lottery or discrete time model (Snyder and Adler 2011; Abrams et al. 2012; Mathias and Chesson 2013). In all of these models there is one generation (or less) per environmental fluctuation. In addition, my analysis includes the evolutionary stability of two-species coexistence that cannot be reached via small mutation. This broader definition of evolutionary stability addresses questions of community assembly where the introduction of new trait values comes not from small mutations, but from new invaders.

Figure 2.8 may provide an empirical rule of thumb for interpreting the relevance of this study for real world systems: species with short lifespans relative to the period of environmental fluctuations are more likely to coexist via the storage effect. In the particular example shown, the mortality rate is 1 per unit time, which means that for the species considered, the expected lifespan is 1 unit time. I can identify three regimes in Figure 2.8: 1) For competitors whose lifespans are comparable to the length of the period (within an order of magnitude or so), there is a region of coexistence that cannot be reached by small mutation, but that is nevertheless evolutionarily stable. 2) For longer periods, a region of branching points appears and the region of coexistence reaches a maximum width. 3) For shorter periods, the region of coexistence becomes vanishingly small and relies on perfectly symmetric species, in essence relying on the equalizing effects of similar fitness rather than the stabilizing effect of the storage effect. The model suggests that increasing the period of fluctuations strengthens the stabilizing effect (Figure 2.11). I would expect to see stable coexistence only when the lifespan of the species in question is shorter than the period of the environmental variation, and for the storage effect to evolve would require species that complete several generations for each period of variation.

Table 2.1: Parameters and their default values

Parameter/Variable	Description	Value
μ	Maximum growth rate	
T	Temperature	
n_i	Density of species *i*	
$\bar{g}_\imath$	Average growth of species *i*	
R	Available resource	
R_{tot}	Total resource	5
T_{opt}	Trait value – optimum temperature	$-1 < T_{opt} < 1$
ϕ	Proportion of time spent in season 1	$0 < \phi < 1$
σ	Width of temperature response curve	1
τ	Length of the period	--
T_1, T_2	Temperature in seasons 1 and 2, respectively	-1, 1
m	Mortality	Density independent, 0 Density dependent, 1

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APPENDIX

APPENDIX

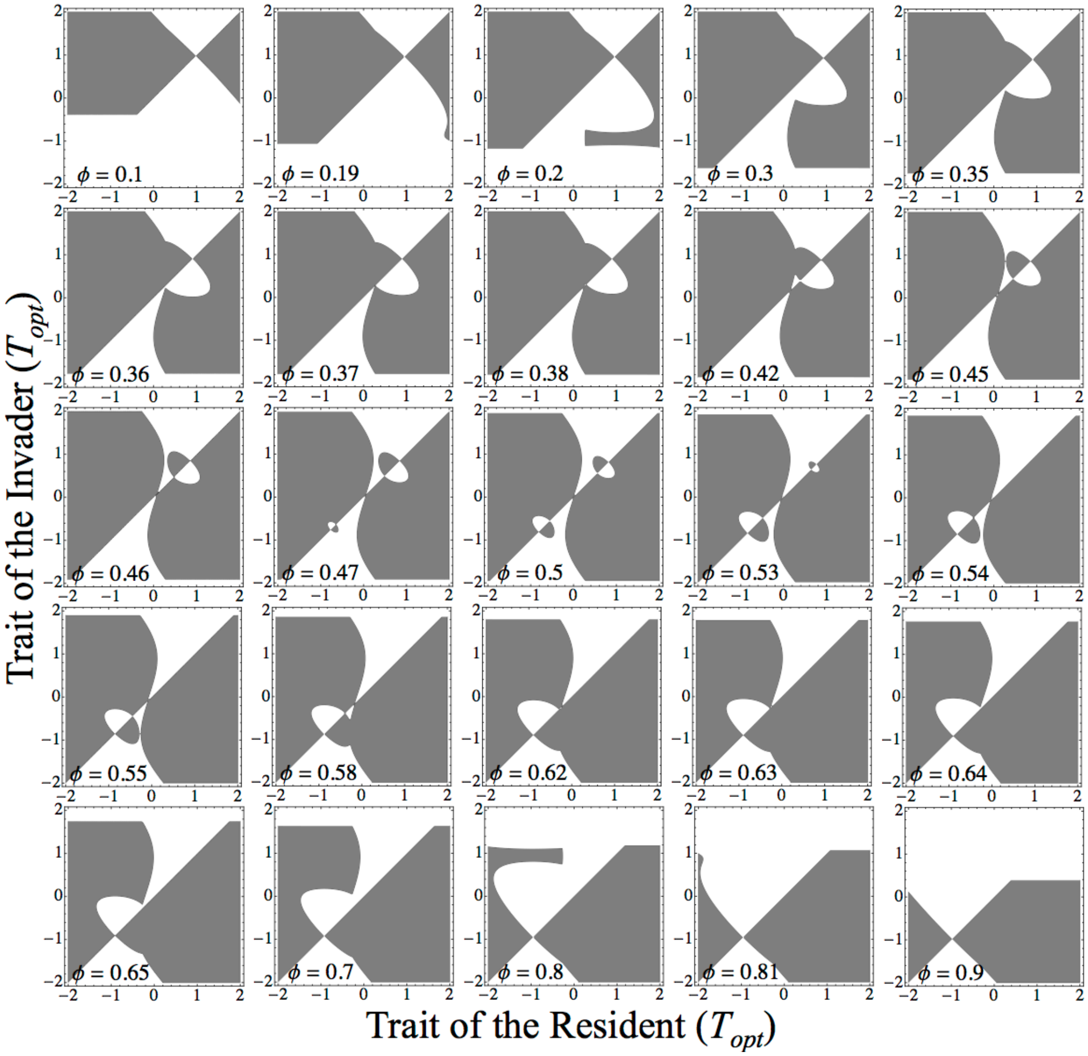

Figure A1 More complete array of PIPs as excerpted in Figure 2.7.

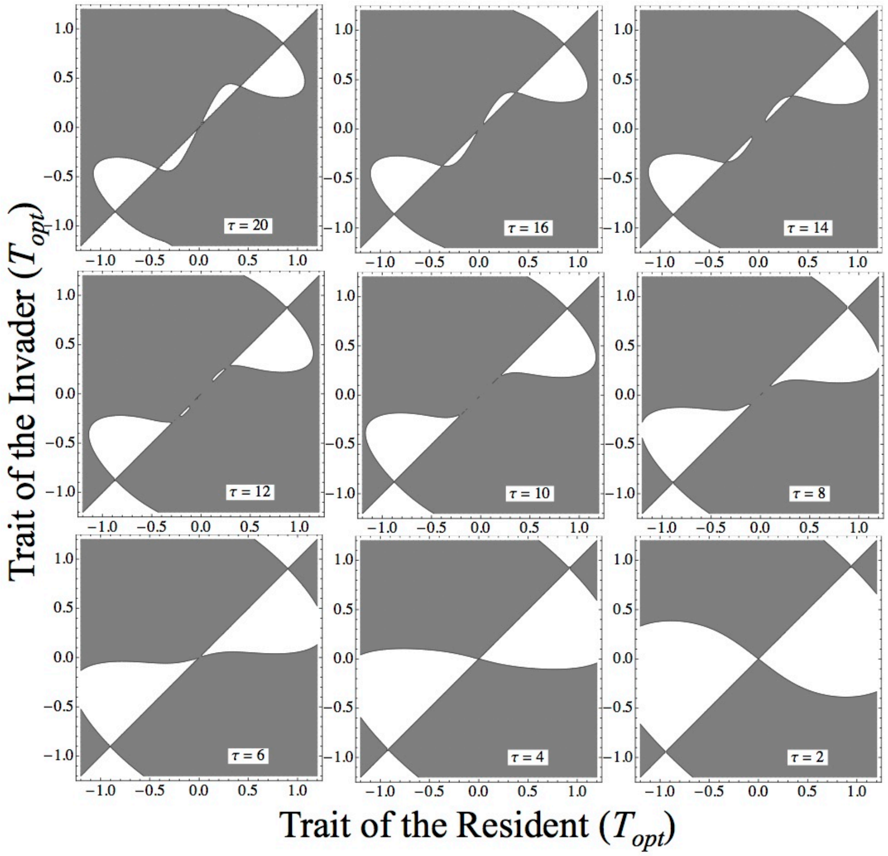

Figure A2 A slice of PIPs at $\phi = 0.5$, showing the disappearance of the branching point as the period decreases. At longer period lengths $\tau > 10$, there are 5 singular strategies, but for $\tau < 10$, the three central singular strategies (branching point, and 2 repellors) merge into a single repellor.

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LITERATURE CITED

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CHAPTER 3

SYNERGISTIC OR INDEPENDENT INTERACTION OF RELATIVE NONLINEARITY AND THE STORAGE EFFECT: HOW THE TYPE OF ENVIRONMENTAL VARIATION AFFECTS THE POTENTIAL FOR DIVERSITY

Abstract

There are many mechanisms that promote species coexistence in the literature of community ecology, but each one accounts for only a small proportion of the overall diversity observed in nature. It is often assumed that many mechanisms work in conjunction to enable diversity. How these mechanisms combine and interact is rarely studied. Here I investigate two mechanisms that rely on environmental fluctuations, relative nonlinearity and the storage effect. I employ two environmental forcing regimes, one that creates distinct seasons and one that changes the environment continuously. In the case of distinct seasons, the two coexistence mechanisms operate independently. In the case of the continuously variable environment, the coexistence mechanisms combine synergistically to allow more diversity than can be accounted for by either acting alone. The increase in diversity can be attributed almost entirely to an increase in the storage effect. We speculate that the difference between these two results is due to the difference between discrete and continuous environmental niche space.

Introduction

Ecological communities are defined by the laws of natural selection and survival of the fittest. Despite this cutthroat existence, ecological communities are typically diverse. Formulating this apparent contradiction in the form of the "Paradox of the Plankton," Hutchinson (1961) inspired many decades of research in coexistence theory when he noted that many species of phytoplankton are able to coexist on what appears to be a small set of limiting resources in an unstructured environment. There is a menagerie of coexistence mechanisms, but each accounts for only a small part of the answer to the paradox. Many mechanisms must work together to explain the sum total of the diversity we see. But the next step, combining mechanisms, is rarely explicitly taken. Different coexistence mechanisms may interact with each other and increase or decrease the possibility of coexistence. In this paper I examine the combination of two of the main mechanisms thought to generate diversity, the storage effect and relative nonlinearity.

The mechanisms proposed to explain coexistence operate in a wide variety of ways. Hutchinson himself proposed non-equilibrium conditions as one solution to his paradox (Hutchinson, 1961). As new coexistence mechanisms have been defined and refined over the years, there have been various attempts to categorize them. Much of the work has been inspired by terrestrial plant communities (Shmida & Ellner, 1984; Wilson, 1990; Tilman & Pacala, 1993). They all cite some combination of spatial and temporal heterogeneity and structure in different forms as well as trophic complexity, multiple limiting resources, and differences in life history as mechanisms that allow coexistence. More recent attempts have tried to link mechanisms together into a single framework. Chesson (2000) categorized mechanisms as either equalizing (competing species are similar and slow to exclude one another) or stabilizing (each competing species has an advantage when rare). He further divided coexistence mechanisms into four classes, storage effects, relative nonlinearities, fitness-density covariances, and variation-independent mechanisms then mathematically showed how each of these operate with respect to species density and fitness through time and space (Chesson, 2008). Another recent review, Edwards et al (in prep), includes the evolutionary stability of each mechanism in its classification scheme. None of these classification schemes considers how coexistence mechanisms might interact.

The two mechanisms I will consider are relative nonlinearity and the storage effect, both known as “fluctuation-dependent mechanisms” (Chesson, 2000). They both require variation in the environment, but take advantage of it in different ways. Relative nonlinearity relies on the competing species having resource uptake functions, at least one of which must be nonlinear, that result in a tradeoff between competition at low resources and growth rate a high resources. Then, if the resources are variable, e.g., a pulsed resource supply, the species with the higher growth rate can take advantage of abundant resources at the beginning of the pulse while the good competitor will eventually drive down the resource level and outcompete the other. The storage effect (Chesson, 1994), relies on differential responses to the environment to promote coexistence. In this case, species experience different environmental optima and rely on sufficient growth in the good time to survive through the bad time.

Both of these mechanisms were originally formulated as purely ecological models, that is, they assumed fixed species traits. A pair of species in ecological equilibrium is not necessarily evolutionarily stable. Evolution may cause species to converge (or diverge) in their traits, leading to the extinction of one of the competitors. For example, competition for two essential resources can allow the coexistence of two species with carefully chosen trait values specializing on different resources, but evolution leads to a single generalist (Schreiber & Tobiason, 2003). An evolutionarily unstable coexistence would be rare in nature since species are constantly experiencing selection. So, understanding the evolutionary stability of coexistence mechanisms is crucial to understanding their capacity to enhance diversity.

The conclusions about the evolutionary stability of relative nonlinearity depend somewhat on whether the models are analyzed in discrete or continuous time. Hartig et al (2014) analyzed a discrete time system with non-overlapping generations and constant resource supply analogous to annual plants without seed dormancy. They found that although there were many pairs of competitors that were dynamically stable without trait change, evolution usually led to the dominance of one intermediate phenotype except in the case of very specific tradeoffs. On the other hand, in continuous time models inspired by phytoplankton dynamics, coexistence was more evolutionarily plausible. Litchman et al (2009), Edwards et al (2013), and Kremer and Klausmeier (2013), all found that when resources fluctuate, there is a large region of parameter space that permits coexistence.

For the storage effect to occur, competing species must fulfill three requirements: 1) differential responses to the environment, where each species perceives a different "good" season, 2) buffered population growth, so that no species dies too much in its "bad" season, and 3) covariance between the environment and competition. This last condition occurs when, as a rare invader, a species is released from competitive pressure when it experiences its good season.

The storage effect has been observed multiple times in nature across multiple taxa (Pake & Venable, 1995; Cáceres, 1997; Angert *et al.*, 2009; 2011). Its occurrence in natural systems implies that we should expect to see evolutionary stability in storage effect models. Again, these models can be divided into discrete and continuous time. Models of discrete time usually mimic annual plant dynamics and have either regular or random fluctuations between year types (often high or low rainfall). Competing species trade off their ability to germinate in these different year types. Work by Abrams et al (2013) shows that under a wide range of tradeoff shapes, this type of coexistence is evolutionarily stable. Continuous time models have either examined continuously varying environment (Barabas *et al.*, 2012) or temperature regime (Kremer and Klausmeier, in prep), or discrete temperature seasonality (Chapter 2). For the continuously variable environment, more extreme temperature differences increase the number of coexisting species (Kremer and Klausmeier in prep), but the actual number that can persist depends on the species niche widths (Barabas *et al.*, 2012). Eventually, if the temperature changes too drastically, the “bad time” for any given species becomes too long and no species can survive. For discrete seasons, the maximum number of coexisting species is set by the number of seasons: resources in each season can be thought of as unique limiting resources. Again, the relative timescales of environmental variation and lifespan come into play; the period of fluctuation must be longer than the lifespan of the individuals to easily allow for evolutionarily stable coexistence. Evolutionary branching and the generation of diversity occur only when the period of environmental fluctuations is much longer than the lifespan of the individual (Chapter 2).

The work that has been done up to this point has largely been examining a single coexistence mechanism at a time, but there are some notable exceptions. Kuang and Chesson have investigated how the storage effect interacts with predation in a series of papers (2009a,b), and found that in models that do not consider evolution, predation weakens the storage effect. Stump and Chesson (2015) have looked the Janzen-Connell Hypothesis (Connell, 1970; Janzen, 1970) concerning how spatial structure interacts with specialist predators and found that the spatial structure in predators was less important than previously thought in maintaining diversity. Recently, Yuan and Chesson (2015) investigated the combination of the storage effect and relative nonlinearity in a discrete-time lottery model with no evolution. They analyzed the system in terms of stabilizing and equalizing forces (Chesson, 2000) and found that while the storage effect provides a strong stabilizing force, relative nonlinearity generally only added to the equalizing effect, which on its own is not enough to ensure coexistence. I am aware of no study in discrete or continuous time that considers the evolutionary consequences of these two coexistence mechanisms working in conjunction.

Here, I look at how the storage effect and relative nonlinearity combine in continuous time with externally forced seasonality. Species compete for a single resource, which is supplied at a constant rate. In this way, this study is analogous to phytoplankton communities competing for a single limiting nutrient and experiencing temperature fluctuations that affect their growth rates.

I examine how the evolutionarily stable strategy changes as the difference between the seasons becomes more extreme. I begin by allowing evolution in the environmental response but allow no relative nonlinearity, to establish a baseline of how many species can exist via the storage effect. Then, I examine the number of species that can coexist by differentiating through relative nonlinearity alone when they cannot diverge in their environmental response. Finally, I combine both mechanisms to see how they work together to promote coexistence. I look at how these coexistence mechanisms operate both in an environment where the temperature varies continuously and where there are two distinct seasons as in Chapter 2 of this thesis. I show that under continuous environmental variation, these mechanisms interact and can produce more diversity than can be accounted for by a simple multiplicative combination of the two.

Interacting Coexistence Mechanisms

For species to stably coexist, as defined by mutual invasibility, they must distinguish themselves from each other in ecologically meaningful ways (Chesson, 1991). These ecologically relevant distinctions can be thought of as differences in traits. Traits can be quantitative, like size or growth rate, or they can be qualitative, like color or the ability to consume a certain type of prey. In either case, I define the set of all possible values of a given trait as a trait axis. To coexist, species must have distinct trait values along at least one trait axis. One trait axis defines a single dimension in trait space. Coexistence mechanism X might enable coexistence through differentiation in trait *a*, while mechanism Y can allow differentiation in trait *b*. If species experience both coexistence mechanisms simultaneously, competitors may differentiate in both dimensions. If mechanism X by itself allows 2 species to coexist and mechanism Y by itself allows 3 species, differentiation in the *a*-*b* plane is expected to produce 6 species if X and Y are independent (Figure 3.1a). Each niche provided by mechanism X can be shared by the three species coexisting through mechanism Y. Figure 3.1a gives a hypothetical example of how this might happen. If mechanism X and Y are not independent, two different cases may result from their interaction. It is possible that mechanisms X and Y share a common cause or experience a tradeoff and that there are regions of trait space that cannot be reached, decreasing the potential for coexistence (Figure 3.1b). I call this collinearity to imply that the two dimensions are correlated in some way and so define less than a full plane. On the other hand, two coexistence mechanisms working in concert may open up trait values that would otherwise be excluded because increasing the dimensionality increases the distance (in trait space) between species (Figure 3.1c). I call these mechanisms synergistic to imply that the two mechanisms working together enhance the potential for coexistence.

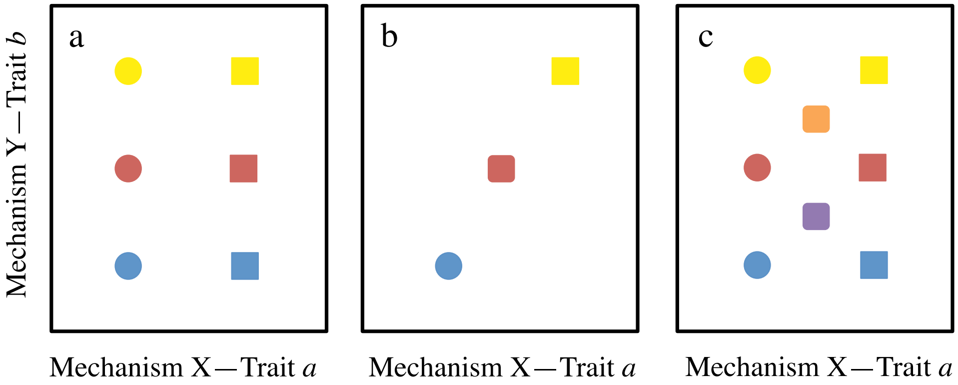


Figure 3.1 The ways in which coexistence mechanisms could interact. a) Independent mechanisms result in multiplicative (2 * 3 = 6) diversity. b) Collinear mechanisms where a tradeoff results in a loss of diversity relative to the independent case. c) Synergistic mechanisms result in increased trait distance between the species in two dimensions, allowing more intermediate species to invade.

Little is known about how coexistence mechanisms interact. Whether independent, collinear, or synergistic effects result probably depends on the specifics of the coexistence mechanisms. The mechanisms examined in this paper, the storage effect and relative nonlinearity, both rely on variation in available resources to operate. In Chapter 2, I showed that when competition is mediated through resources it is variation in those resources that leads to the covariance between competition and the environment that produces the stabilizing effect. Relative nonlinearity also relies on variation in resources that alternately favors a fast grower or a good competitor. I therefore expect any interaction between these two mechanisms to be caused by a change in the dynamics of the resource through time.

Methods

Seasonal Forcing and Population and Trait Dynamics

I begin with environmental variation very similar to that in Chapter 2, and expand to include another more continuous type of seasonal forcing. First, I examine two distinct seasons that switch back and forth

$$T(t) = \begin{cases} T_1 \text{ if } t \bmod \tau < \phi\tau \\ T_2 \text{ if } t \bmod \tau > \phi\tau \end{cases} \tag{1}$$

where T_1 and T_2 are the temperatures in the two seasons, $\phi = 0.5$ and is the proportion of time spent in season 1, and τ is the length of the season. I refer to this as square wave forcing. I also consider environmental forcing that varies continuously between seasons. I refer to this as triangle wave forcing. The triangle wave can conveniently be expressed as a function of sines and arcsines:

$$T(t) = T_{amp}\frac{2}{\pi}\sin^{-1}(\sin(\frac{2\pi t}{\tau} - \frac{\pi}{2})) \qquad (2)$$

where T_{amp} is the maximum temperature reached and the period is τ. Figure 3.2 illustrates the two seasonal forcing models.

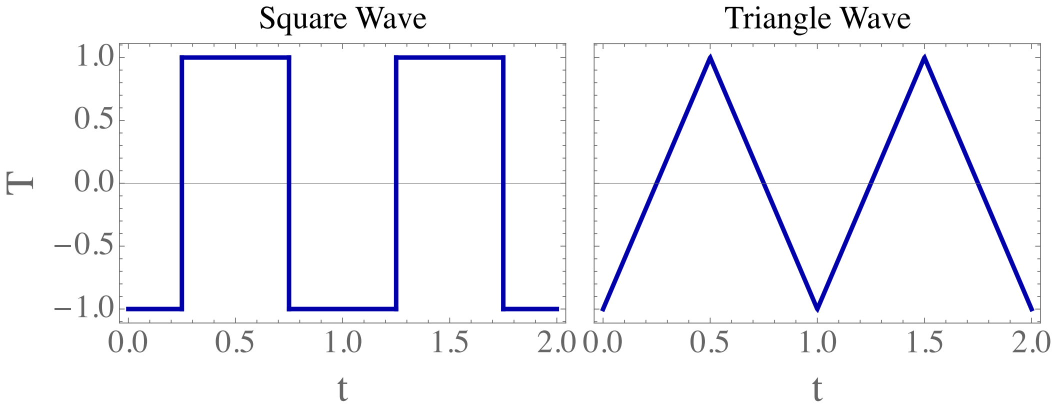


Figure 3.2 Seasonal forcing used throughout this paper for the square and triangle waves. In this case, illustrated at $T_{amp} = 1$.

The maximum growth rate μ of each species depends on the match between the temperature and its temperature trait T_{opt}:

$$\mu(T_{opt}, T) = e^{\frac{-(T_{opt}-T)^2}{2\sigma^2}} \qquad (3)$$

μ is a Gaussian function with a maximum at $T_{opt} = T$ and standard deviation of $\sigma^2 = 1$. Since the temperature can vary continuously (instead of two distinct seasons) it is helpful to look at how μ varies across a range of temperatures (Figure 3.3).

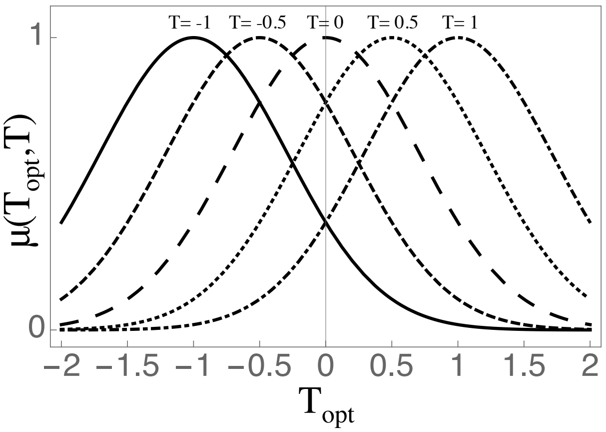


Figure 3.3 Growth rate (μ) as a function of trait (T_{opt}) for a range of values of T: $T = -1$, far left solid line through $T = 1$, far right, dot-dashed line.

The population growth equations (identical to those I use in Chapter 2) give the growth rate of any species n as a function of the total available resources R, which are a function of the total biomass in the system.

$$\frac{dn_i}{n_i dt} = \mu\left(T_{opt,i}, T(t)\right) f(R) - m \tag{4}$$

$$R = R_{tot} - \sum_i n_i \tag{5}$$

where n_i indicates competing species, R_{tot} is the resource supply rate, and m is the death rate. Because I am interested in relative nonlinearity, I must introduce a nonlinear resource dependent growth function. Previously, $f(R) = R$. Here, I introduce a more complicated function that depends on the trait governing the growth-competition tradeoff.

$$f(R) = \frac{r\,R}{K(r) + R} \tag{6}$$

where r is the maximum growth rate and $K(r)$ is the half saturation constant. I use Kremer and Klausmeier's (2013) $K(r)$ function, which allows a variable tradeoff between the half saturation constant and the maximum growth rate.

$$K(r) = \alpha + (\beta - \alpha)\left(\frac{r-\gamma}{\delta-\gamma}\right)^c \tag{7}$$

where α, β, γ, and δ are set to $0.1, 6, 0$, and 5, respectively. The shape parameter c determines the strength of the tradeoff, and is set to create a strong gleaner-opportunist tradeoff at $c = 5$. The trait of interest, r, is high for fast growing, poor competitors and low for slow growing, good competitors. Figure 3.4a shows the tradeoff between r and $K(r)$for a range of r and Figure 3.4b gives resulting resource functional responses for example low and high r species.

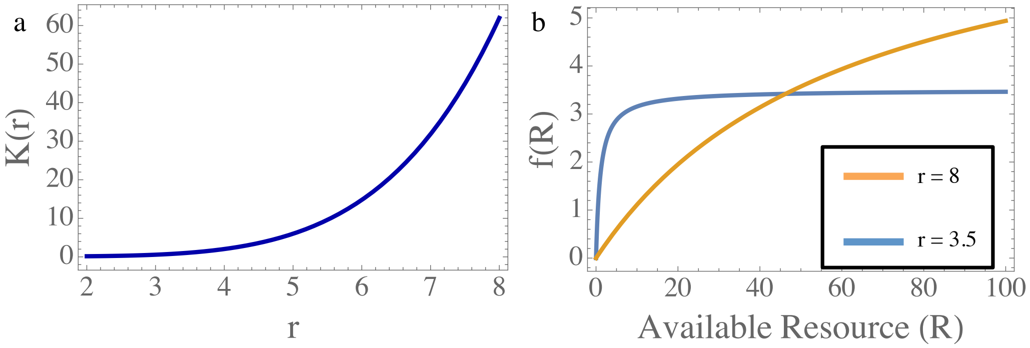


Figure 3.4 Relative nonlinearity in the resource function. a) The tradeoff between r (the relative non-linearity trait) and the half saturation constant K(r). b) Resource functions resulting from two different values of r. The lower value is a better competitor at low resource levels and the higher is better when resources are high.

The temperature difference between the seasons controls the magnitude of environmental variation in this model: a greater difference between T_1 and T_2 indicates a greater temperature range. Any variation in the resource levels is a result of changing population density caused by the changing temperature. For simplicity, and without loss of generality, I center my temperatures around zero, and so refer to the difference between T_1 and T_2 in terms of the absolute value of T_1, or $T_{amp} = |T_1|$. In the following sections I investigate how the magnitude of the variation in the environment, controlled by T_{amp}, affects the potential for coexistence of species sharing the same resource. As I shall show, the magnitude of this variation is the main parameter controlling the possibility for coexistence via the storage effect and relative nonlinearity, but the form of the environmental variation (triangle or square wave) determines whether these two coexistence mechanisms interact.

SSD Modeling Framework

In my analysis I use the Successional State Dynamics (SSD) approximation introduced by Klausmeier (2010). This approach models successional dynamics in communities experiencing periodic forcing. By focusing on the timing of transitions between competing species, SSD takes otherwise stiff numerical systems and makes them analytically and computationally tractable. The key simplification of this technique is to set the length of the period to infinity. This means that transitions between dominant species become instantaneous and the state of the system can be described simply by which species is "visible" or present and affecting the resource abundance. Although this may seem like a drastic shift, it retains many essential features of the differential equations it is based on, including lags between resource and population dynamics (Klausmeier, 2010). It is especially well suited for modeling communities with relatively high densities and fast population dynamics (like phytoplankton). For a comparison between SSD and finite time dynamics, see Figure 2.8, Chapter 2; the SSD results are nearly identical to the long period results. What is lost in flexibility to explore short-period dynamics is more than gained in the computational ability gained to explore evolutionary outcomes in multiple dimensions.

Finding Evolutionarily Stable Communities

To model the evolutionary outcome of competing species I employ the framework of adaptive dynamics (Geritz *et al*., 1998). Adaptive dynamics assumes a separation of timescales between ecological and evolutionary dynamics, so that evolution proceeds through the invasion of a rare mutant into an environment set by the resident at its ecological equilibrium. The mutation steps can be infinitesimally small, analogous to a small genetic mutation in the resident population or large, analogous to invasion by another species or a mutation of large effect.

With multiple traits and multiple species analytical methods become difficult, but I can numerically search for evolutionarily stable coalitions (ESC). An ESC is a set of species with trait values such that when all species are at their ecological equilibrium (when a species' population density is the same at the beginning and end of a cycle) no species with a different trait value can invade. All species in an ESC are at peaks in the fitness landscape, defined by the invasion rate of a rare invader. No point on the fitness landscape of an ESC is greater than zero and all of the peaks are equal to zero. I find the ESC by solving numerically for the combinations of traits where all species are at fitness maxima for a given set of parameters. If I find a coalition where all species are at a maximum but there is another region of trait space that has positive invasion fitness, I add another species in the region of positive fitness and solve again for the fitness maxima. I continue this process until I reach the ESC and no more species can invade. In this paper I focus on the effect of the amplitude of variation in temperature, T_{amp}, on the ESC because I am interested in the role of environmental variance. All of my analyses are done with Mathematica software (Wolfram Research, Inc. 2015).

Over a range of T_{amp}, two kinds of bifurcations can occur. First, an ESC can lose its global stability when region of trait space transitions from negative to positive invasion fitness, adding a species to the ESC (Geritz *et al*., 1999). I refer to this as a seamount bifurcation, since it resembles an island of positive fitness emerging from a sea of negative fitness. To locate this bifurcation, I solve numerically for the T_{amp} where the fitness of a species at the peak of the seamount equals zero. The second type of bifurcation is where a fitness peak becomes a branching point, resulting in a new pair of species that displace the former resident. This occurs when the second derivative of the fitness gradient around the peak goes from negative to positive. I can detect this bifurcation point by solving for the T_{amp} where the second derivative equals zero.

Results

Square Wave

Storage Effect Alone

In Chapter 2, I showed that when the seasons are discrete, the effect of increasing the difference between the seasonal extremes T_{amp} (referred to as ΔT in Chapter 2), is to change from a single seasonal generalist to two seasonal specialists (Chapter 2, Figure 2.3). This effect, shown for the case of no density dependence, but identical for the density dependent case, does not depend on the resource supply. The independence from the resource also means that the results are not affected by the addition of a nonlinear functional response. Figure 3.5 shows that over a range of r trait values, the bifurcation point at which the single generalist's strategy ($T_{opt} = 0$) becomes unstable and branches to two seasonal specialists occurs at exactly the same point for the nonlinear model as for the linear model, $T_{amp} = \frac{\sqrt{2\sigma^2}}{2}$. This point depends on σ^2, which controls the width of the temperature response function and is, set to 1 in this case. Fixing r also shows the effect of the storage effect in isolation. As I showed in Chapter 2, there are at most two species that can coexist on two distinct seasons by the storage effect.

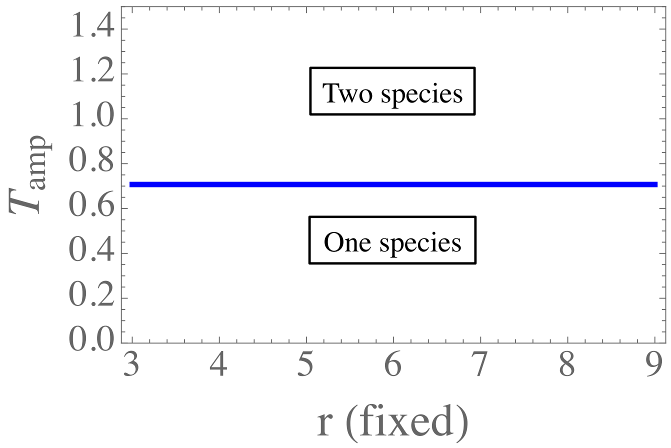


Figure 3.5 The effect of the storage effect alone under square wave forcing. The bifurcation point from one generalist to two specialists does not depend on r.

Relative Nonlinearity Alone

We similarly examine the potential for coexistence via relative nonlinearity by fixing T_{opt} and examining the effect of T_{amp} on the number of species that can coexist by divergence in r. This divergence occurs via the seamount bifurcation. Figure 3.6 shows that over a range of T_{opt} there are at most two species that can coexist due to relative nonlinearity given sufficient environmental variation (T_{amp}). In this case, the switch from a single (low r) species to two coexisting species occurs because of an increase in variance in the available resources. When the single resident species (with a fixed T_{opt}) is present it draws down the resources to its R*, the resource level where its per capita growth rate equals zero. In the season to which the resident is better adapted, it has a low R*, but in the off season, its R* increases because its birth rate decreases. This creates variation in the resource level between seasons. When this variation is large enough (when the bad season is bad enough) the resource pulse created by the bad season is enough to allow an opportunist (high r) competitor to invade. When the T_{opt} is fixed at zero, the resident species has the same R* in both seasons regardless of the T_{amp} and so the resource variance necessary for an opportunist invasion never occurs. For T_{opt} values near zero, the resident species is driven to extinction at T_{amp} values too low for diversification to occur. Thus, in this model relative nonlinearity can allow at most two species to coexist when T_{amp} is sufficiently large and when T_{opt} is sufficiently far from zero.

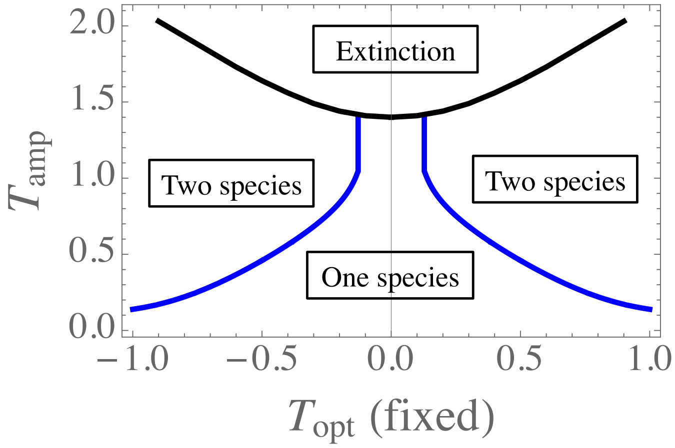


Figure 3.6 The effect of relative nonlinearity alone under square wave forcing The bifurcation point occurs at smaller amplitude fluctuations for more specialized species. When the T_{opt} is fixed near zero, there is no bifurcation point because the species cannot persist at all with large variation in temperature and go extinct.

Storage Effect and Relative Nonlinearity in Combination

Both the storage effect and relative nonlinearity create two temporal niches. If these two mechanisms do not interact, I expect to see no more than four species when T_{amp} is large enough to produce two storage effect niches. Furthermore, I expect that if the mechanisms are independent, the gleaners (low r) and opportunists (high r) in the same season should share the same storage effect niche and therefore have the same T_{opt} trait (Figure 3.1a). Interaction between the mechanisms could result in more or less diversity. If species diverge in T_{opt} within a seasonal niche, it would indicate an interaction increasing the trait diversity. Likewise if more than two species were able to diverge in r this would indicate a synergistic effect of the two mechanisms on species diversity (Figure 3.1c). A decrease in diversity could occur if divergence in T_{opt} prevents the necessary resource variation for diversification in r. This could create a situation where diversification in r could happen if only one of the seasonal specialists were present but not with two.

When I allow both traits to evolve over a range of T_{amp}, the two coexistence mechanisms mostly behave independently (Figure 3.7). When T_{amp} is low there is a small region where relative nonlinearity alone could allow two species to coexist, but in combination with the storage effect, no diversification is possible in r. For higher values of T_{amp}, the gleaner and opportunist species in the same season share the same T_{opt}. Species diverge in T_{opt} exactly as they would with no relative nonlinearity. This is consistent with my result that in a model with two seasons there are exactly two niches due to the storage effect.

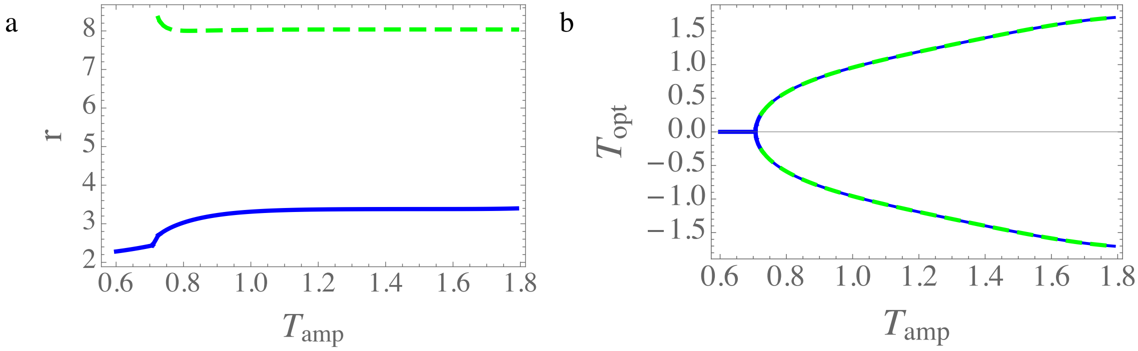


Figure 3.7 The effect of both relative nonlinearity and the storage effect under square wave forcing a) The bifurcation in r occurs shortly after b) the bifurcation in T_{opt}. Once this bifurcation occurs, the gleaner and opportunist species share the same T_{opt} value, indicated by the green and blue dashing in panel b). Green dashed lines indicate the opportunist species and the blue solid line indicates the gleaner.

Triangle Wave

Storage Effect Alone

The effect of increasing T_{amp} on diversification in T_{opt} under a triangle wave temperature function (Figure 3.8) is similar to the results from the square wave (Figure 3.5). Two major differences are apparent: the T_{amp} required for diversification is much higher, and the fixed value of r affects the bifurcation point. Low r values require more variation in the environment to produce diversity. The decrease in diversity at low T_{amp} for the triangle wave relative to the square wave is due to the fact that the distribution of temperatures is evenly distributed by the triangle wave as opposed to the strict bimodal distribution of the square wave. The result, though, is still a maximum of two species within the parameter range that I consider.

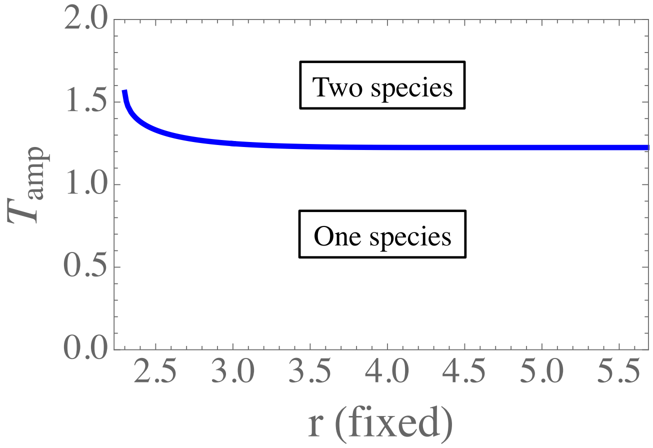


Figure 3.8 The effect of the storage effect alone under triangle wave forcing Unlike under square wave forcing, the bifurcation point from one species to two is affected by the r value of the competing species. With very low r values it requires more environmental variance to support coexistence.

Relative Nonlinearity Alone

With the triangle wave, the effect of relative nonlinearity is quite different from its effect with the square wave (Figure 3.9). In this case, although the bifurcation T_{amp} increases somewhat as the fixed T_{opt} approaches zero, diversification in r can still occur at $T_{opt} = 0$. There is also no extinction threshold within the bounds of the parameters I consider. Still, I see that only two species can coexist on relative non-linearity alone.

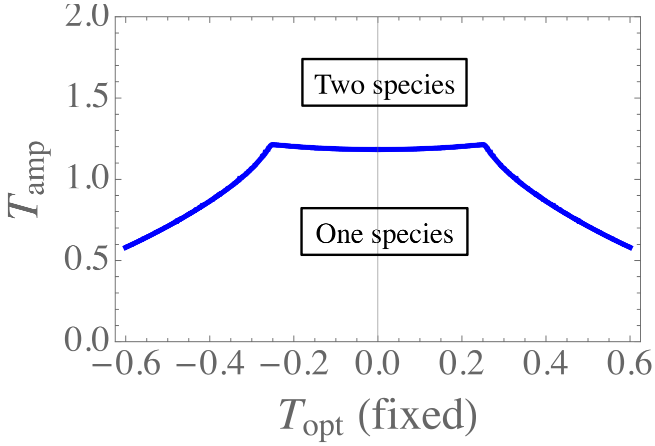


Figure 3.9 The effect of relative nonlinearity alone under triangle wave forcing Unlike under square wave forcing, there is always the possibility of diversification in the r dimension, even when the T_{opt} is near zero. In addition, species with T_{opt} near zero are not at risk of extinction. This is because under the triangle wave forcing the temperature still passes through zero.

Storage Effect and Relative Nonlinearity in Combination

In the case of the triangle wave, as in the case of the square wave, I have at most two niches defined by each mechanism. The expected results for independent mechanisms are the same: four species with one grazer and one opportunist on each side of the T_{opt} spectrum, species on the same side of the T_{opt} spectrum should have the same T_{opt} trait, and each pair of gleaners or opportunists should share the same r value. If the mechanisms are synergistic I expect to see an increase in overall diversity, and if mechanisms are collinear, I expect a decrease in overall diversity.

To understand the evolutionary outcomes, it can be helpful to examine adaptive landscapes and the population dynamics of the evolutionarily stable community at specific values of T_{amp}. In the following set of graphs, I show the population dynamics, environmental forcing, and fitness landscape of a rare invader when the community is an ESC. The contour lines on the fitness landscape are like topographical lines on a map, showing the invasion rates of rare mutants with trait values given by position in the $T_{opt} - r$ plane.

At low T_{amp} ($T_{amp} = 1$, Figure 3.10a), there is no diversification. The single, low r species has a T_{opt} of zero. There is no region of positive invasion rate in T_{opt}. When T_{amp} is slightly higher ($T_{amp} = 1.1$, Figure 3.10b) there are two regions of trait space (near $T_{opt} = \pm 1$ and $r = 9$) where the invasion rate, though still negative, is somewhat less negative than the surrounding trait values: a pair of seamounts. The population dynamics show that the resident species experiences a population drop when the temperature forcing is at its most extreme. As T_{amp} increases, the invasion rate of the species on the seamounts also increases. The critical transition occurs at $T_{amp} = 1.105$. Figure 3.10c shows the evolutionarily stable community at $T_{amp} = 1.2$, where the seasonal generalist gleaner coexists with a pair of seasonal specialist opportunists.

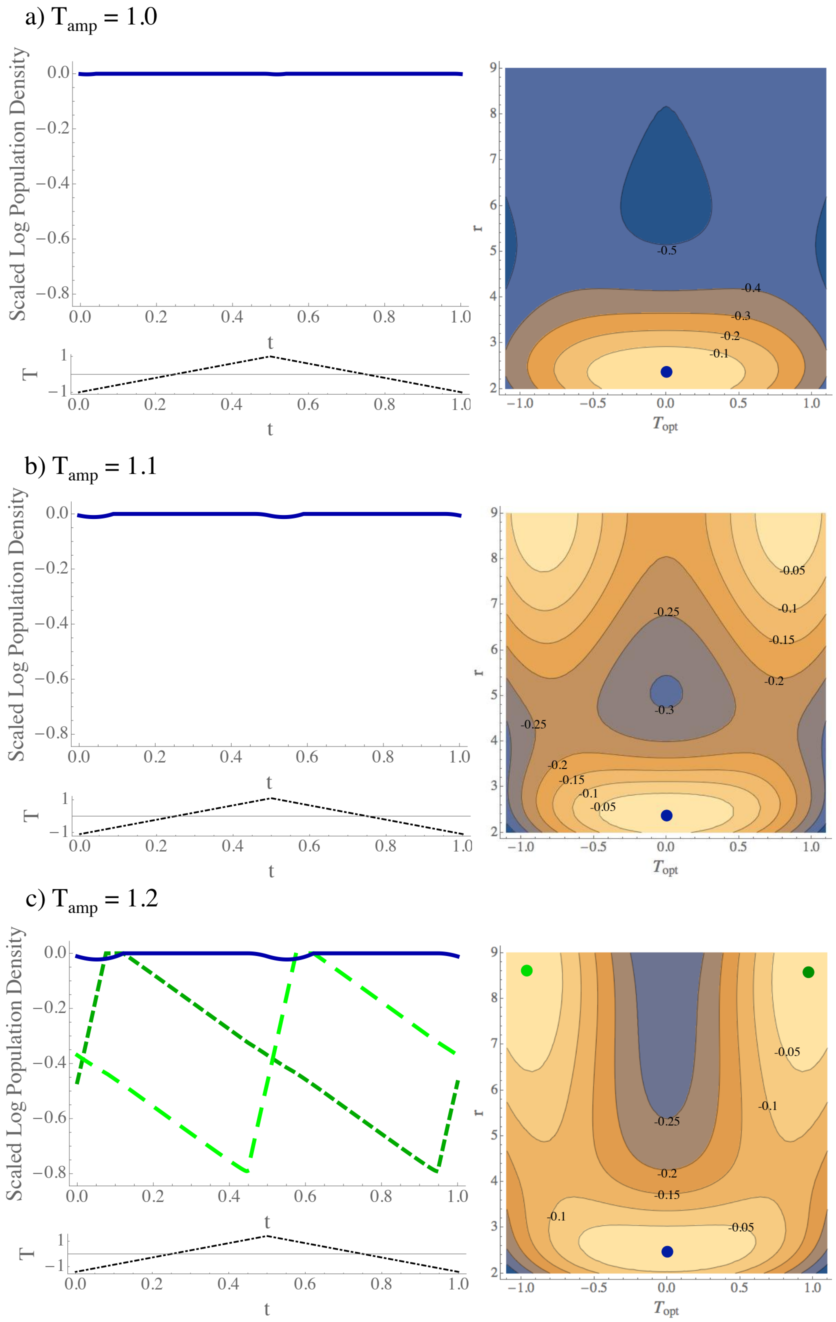
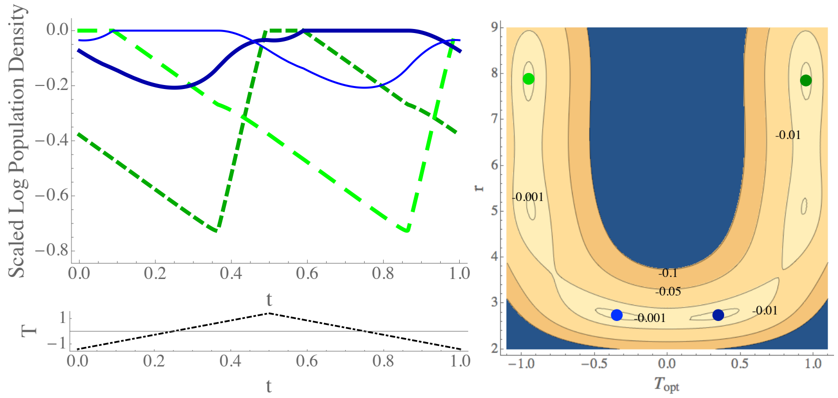


Figure 3.10 Changes in the ESC as T_{amp} goes from 1 to 1.2 The left panels show the population dynamics and the right panels shows the fitness landscape (FL). The color of the dots in the FL correspond to the color of the lines in the population dynamics a) $T_{amp} = 1$ the left panel shows the dynamics of the single species, with the environmental forcing below it. In the FL the contour lines all are less than zero because the resident strategy is the ESC. b) $T_{amp} = 1.1$ there is still only one species in the ESC, but now the population dynamics show that its density dips when the temperature is at its most extreme. The FL shows two seamounts, regions of less negative (but still less than zero) invasion rates at high r and extreme T_{opt}. c) $T_{amp} = 1.2$ three species now form the ESC, with two high r and extreme T_{opt} species joining the low r and central T_{opt} species. The two seamounts are now peaks on the FL.

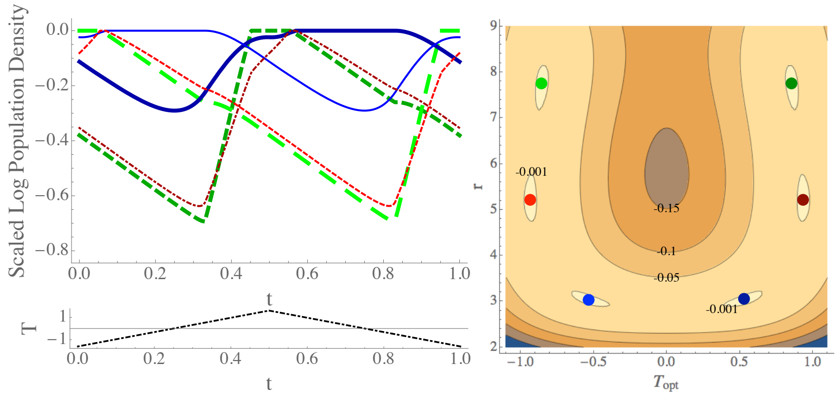
For higher T_{amp}, another critical transition, a bifurcation in the generalist gleaner, occurs at $T_{amp} = 1.302$. Figure 3.11a shows the evolutionarily stable coalition at $T_{amp} = 1.41$ where there are two pairs of gleaners and opportunists. In contrast to the square wave results, where the gleaners and opportunists on the same side of the temperature spectrum shared the same T_{opt} trait, in this case the species do not line up in T_{opt}. This is because the temperature is constantly changing; the opportunist species experience more extreme environmental conditions than the gleaners (see the population and temperature dynamics in the left panels of Figure 3.11).

Further increase in T_{amp} leads to another seamount surfacing at $T_{amp} = 1.424$, as seen "underwater" in Figure 3.11a and "surfaced" in Figure 3.11b. This third species pair, unseen in the square wave analysis, has an intermediate r trait, $r \approx 5$. This pair squeezes between the other two pairs and is only visible for a brief time (left panel, Figure 3.11b). For even greater T_{amp}, this intermediate species pair becomes demographically unstable and goes extinct (Figure 3.11c), this critical transition occurs at $T_{amp} = 1.930$.

a) $T_{amp} = 1.41$



b) $T_{amp} = 1.6$



c) $T_{amp} = 1.95$

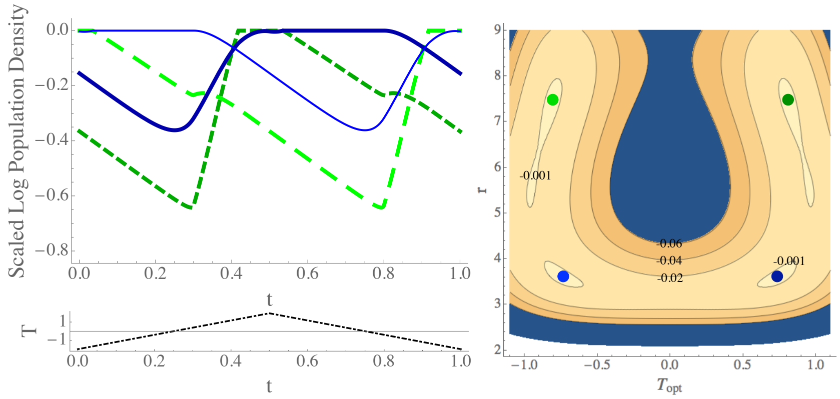


Figure 3.11 Changes in the ESC as T_{amp} goes from 1.41 to 1.95 The left panels show the population dynamics and the right panels shows the fitness landscape (FL) with the temperature forcing below. The colors of the dots in the FL correspond to the colors of the lines in the population dynamics. a) $T_{amp} = 1.41$ the left panel shows the dynamics of the 4 species ESC. Note that the species do not line up in their T_{opt} because they are present at different T values. The fitness landscape shows that there are two small seamounts at $T_{opt} = \pm 1$ and $r = 5$. b) $T_{amp} = 1.6$ there are six species in the ESC with the third pair (red, thin, dotted lines) only briefly visible (left panel). c) $T_{amp} = 1.95$ only four species in the ESC, the third pair has gone extinct and are now seamounts at at $T_{opt} = \pm 1$ and $r = 5.5$.

Figure 3.12 shows that relative nonlinearity and the storage effect have a synergistic effect over large regions of T_{amp}. At high values of T_{amp}, a pair of intermediate r species is able to invade the four species coalition of gleaners and opportunists. This leads to a marked increase in diversity (6 species) for intermediate values of T_{amp}, with a slight decrease in diversity (3 species) for a narrow, lower range of T_{amp} (Figure 3.13).

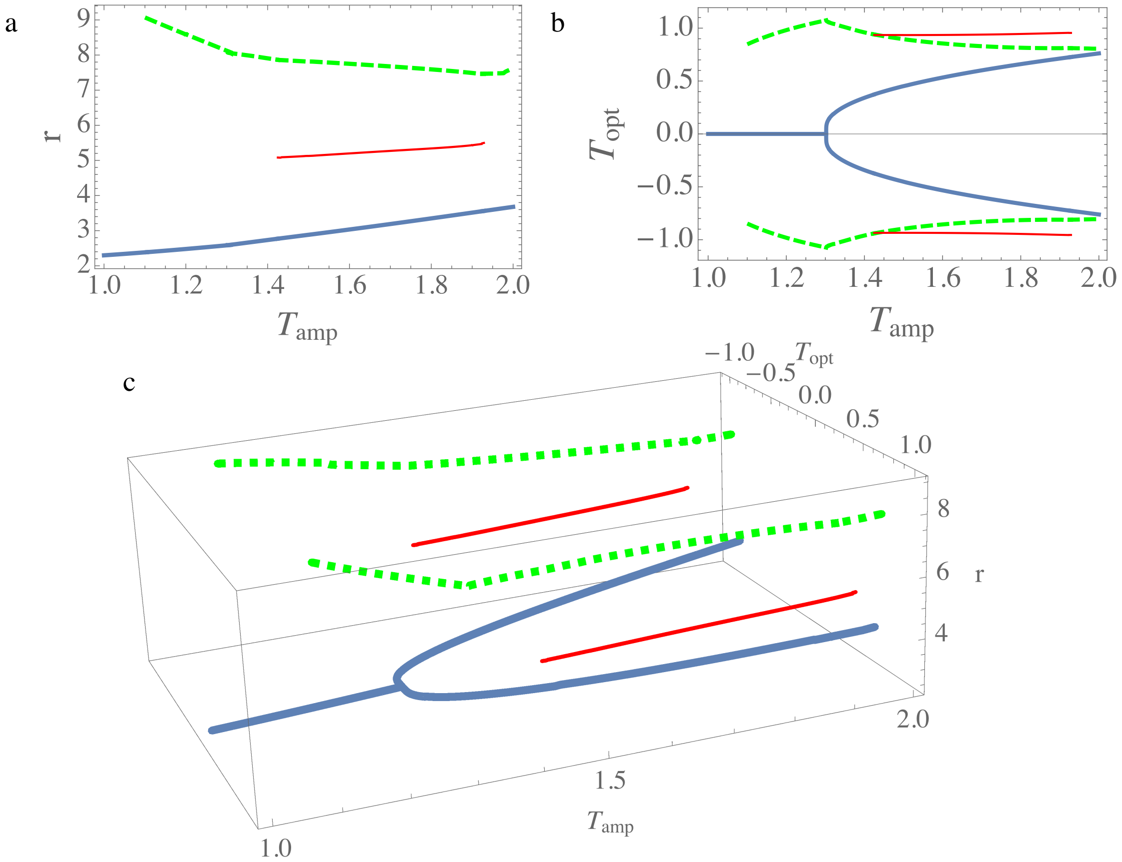


Figure 3.12 Storage effect and relative nonlinearity combined under triangle wave forcing The low r species (blue, solid, thick line) remain closer to generalists in T_{opt}, while the high r species (green, dashed, thick line) become specialists on the more extreme temperatures. The intermediate r species (red, solid, thin line) employs both strategies in T_{opt}, starting at an intermediate T_{opt} at low T_{amp}, and then becoming the most seasonally extreme species for high T_{amp}.

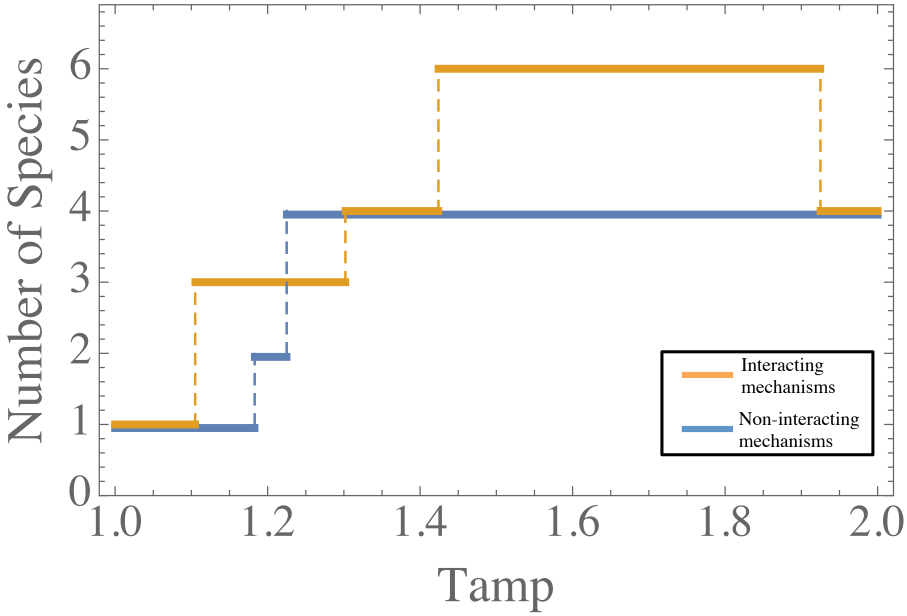


Figure 3.13 Increase in diversity under triangle wave forcing The diversity generated by the interacting relative nonlinearity and storage effect compared to the diversity that would be expected if the two mechanisms were independent. There is a small period of synergy where a seasonal generalist gleaner coexists with two seasonal specialist opportunists at a lower T_{amp} than the independent model would bifurcate. At slightly higher T_{amp}, after the independent model bifurcates in both the T_{opt} and r traits, there is a slight decrease in diversity. When T_{amp} is higher, a pair of intermediate r species can invade, increasing the overall diversity to six.

The Source of the Interaction Between the Storage Effect and Relative Nonlinearity

In this model both relative nonlinearity and the storage effect take advantage of variation in available resources to operate: the storage effect requires covariation between resource availability and the environment and relative nonlinearity relies on variation in resource availability for its stabilizing effect. Since both mechanisms produce diversity through variance in resources, the presence of one mechanism might change the resource variance necessary for the other to function. In this section I will examine how the interaction between relative nonlinearity and the storage effect creates resource dynamics that lead to the invasion of a third, intermediate r pair of species. I will compare the resource dynamics in the square wave and in the triangle wave so that the temperature has the same variance ($T_{amp} = 1.6$ for the triangle wave and $T_{amp} = 0.924$ for the square wave) to see where the additional capacity for coexistence comes from.

For the triangle wave, to approximate the independent case I fix the trait values of the competing species where they would be if the mechanisms did not interact. To calculate the appropriate trait values at $T_{amp} = 1.6$ I first allow evolution and diversification in the T_{opt} trait over a range of r (Figure 3.14a). Then I allow evolutionary diversification in r over a range of symmetric pairs of species with fixed T_{opt} (Figure 3.14b). In this way, I allow both relative nonlinearity and the storage effect to operate independently from each other. Putting the two bifurcation diagrams together yields the trait values that result from independent mechanisms (Figure 3.14c). I can calculate the invasion rate for rare mutants and find a large region of trait space where additional mutants can invade. The positive fitness region does not coincide with the traits reachable by evolution in T_{opt} and r separately.

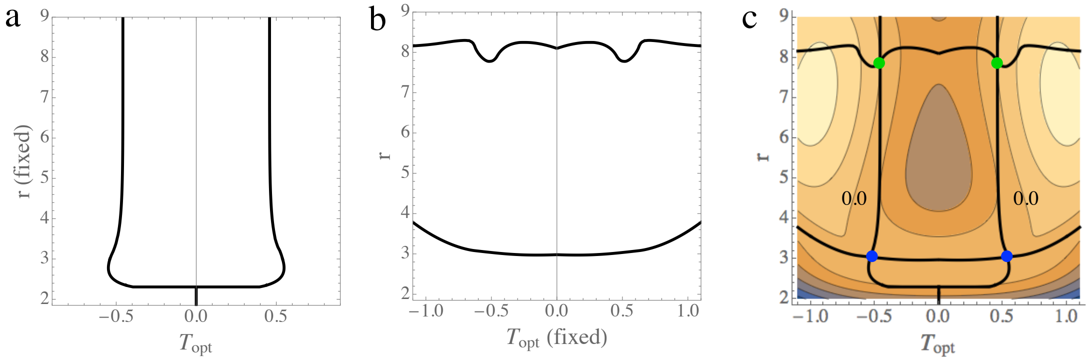


Figure 3.14 The triangle wave function with $T_{amp} = 1.6$ a) Evolution in T_{opt} alone over a range of r. b) Evolution in r alone over a range of T_{opt}. c) The invasion profile for the resulting four species community with the dots representing the species, color-coded as before: greens are the opportunist and blues are the gleaners. A large portion of parameter space has a positive invasion rate. The zero contours are labeled, lighter contours are greater than zero.

The equivalent calculation for the square wave takes place at $T_{amp} = 0.924$ where the variance in the square wave environment is equal to the variance in the triangle wave. Here, I repeat the procedure of allowing evolution in both traits separately and then examining the invasion rate around the four species (Figure 3.16). In this case, I see that there is no region of positive invasibility (Figure 3.16c). As expected, there is more capacity for diversification in the triangle wave model than the square wave model.

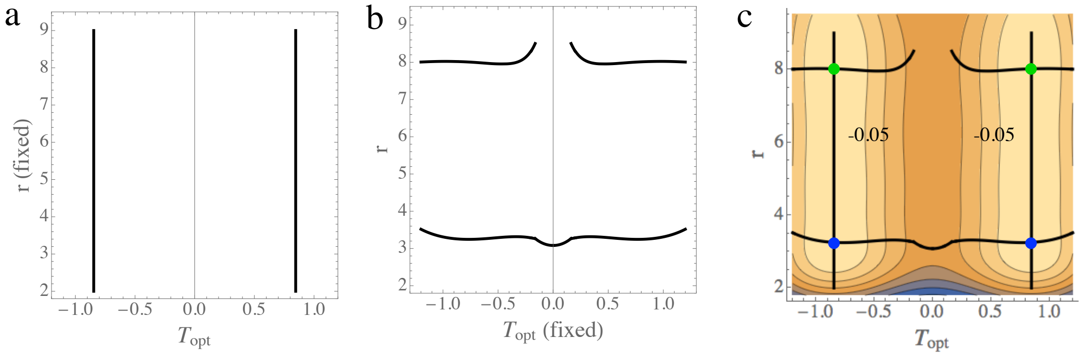


Figure 3.15 The square wave function with $T_{amp} = 0.924$ a) Evolution in T_{opt} alone over a range of r. b) Evolution in r alone over a range of T_{opt}. c) The invasion profile for the resulting four species community. All invasion rates for rare mutants are negative, the largest contour line (-0.05) is labeled. The species are indicated by the blue and green dots.

Where does the increased capacity for coexistence come from? Both mechanisms rely on variation in the resource for coexistence. Relative nonlinearity makes use of variation in the resources directly (Levins, 1979). The storage effect makes use of the covariation between competition and the environment; corresponding, in this model, to the covariance between available resources and the species environmental response, μ (Chapter 2). To see how the synergistic interaction increases diversity, I look at the variance in resources and the covariance between resources and the birth rate of a rare invader over a range of T_{opt}.

The variance in resources is nearly identical between the two models (Figure 3.16 b,e). The variance in the triangle wave model is 45,297.6 while the variance in the square wave model is 45,122.2. This is a difference of only 0.4%, which seems too small to account for the change in diversity. The covariance between resources and species environmental response (the birth rate, μ, Figure 3.16c,f) must be calculated at a specific value of T_{opt}. I calculate this covariance over the range of T_{opt} and find that for the square wave, this value remains nearly zero over the entire range. For the triangle wave, on the other hand, the covariance changes from strongly negative to strongly positive, with high covariance at extreme T_{opt} (Figure 3.16g). This positive covariance corresponds to the region of positive invasion fitness for the triangle wave (Figure 3.14c). This suggests that the storage effect, which requires covariance, is the source of the synergistic diversity effects.

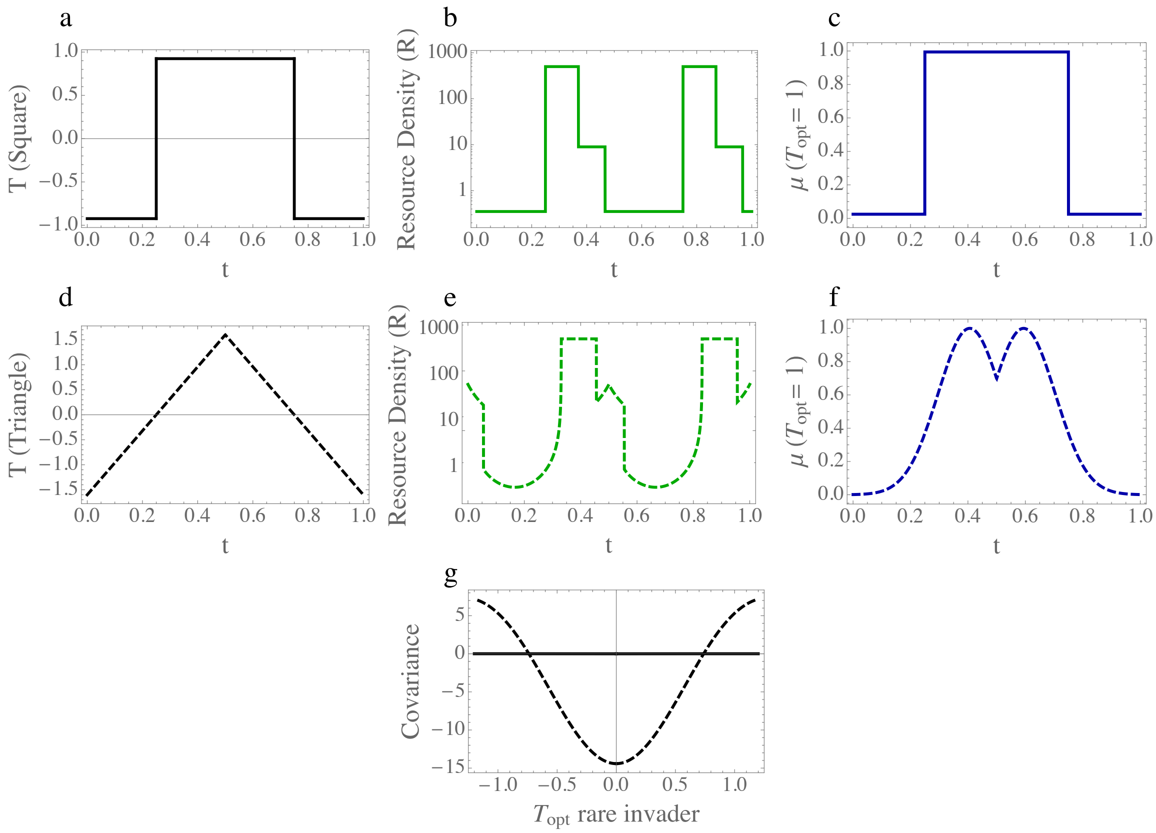


Figure 3.16 Comparison of the resource dynamics in the square wave ($T_{amp} = 0.924$ (a-c)) and the triangle wave ($T_{amp} = 1.6$ (d-f)). Panels (a) and (d) show the environmental forcing. Panels (b) and (e) show the resource dynamics when each community is constructed through independent evolution in T_{opt} and r as described in Figures 3.14 and 3.15. Panels (c) and (f) show the birth rate function of a rare invader species with $T_{opt} = 1.0$. Panel (g) shows the covariance between the resource and the birth rate of a rare invader over a range of T_{opt}, the solid line is the square wave covariance and the dotted line is the triangle wave covariance. When T_{opt} is extreme, there is a positive covariance for the triangle wave but not the square wave. The positive covariance is required for the storage effect to operate.

Discussion

In this paper I simulated the evolutionary outcome of species competing for a single resource under two temperature regimes: square and triangle waves. Species evolved in both their response to the temperature, as well as their ability to take up and compete for the resource. This setup allowed for both relative nonlinearity and the storage effect to shape the diversity in the system. In isolation, each coexistence mechanism could support at most two species coexisting with sufficient variation in temperature. I asked whether, when acting in combination, these mechanisms would interact, leading to an increase or decrease in diversity from the four species I would expect to see.

We saw synergy between the storage effect and relative nonlinearity under the triangle wave forcing but not with the square wave. Within a range of T_{amp}, a third species pair, not present when each coexistence mechanism was working alone was able to invade the triangle-forced system. This pair has a T_{opt} close to the expected species, but an intermediate r. The storage effect works through covariance between the resources and response to the environment, while relative nonlinearity works through variance in the resources. I calculated both of these values for both the square and triangle forcing to understand the source of the additional diversity. Because the extra species seem to be more divergent in r than T_{opt} relative to the rest of the community (Figure 3.12a,b), I expected to see increased resource variance in the triangle forcing and therefore that the synergy worked through relative nonlinearity, but this turned out not to be the case. The variance in resources was nearly identical between the two models but the covariance was much different. The triangle wave forcing had increased covariation between resources and birth rate in the region of T_{opt} where the third pair could invade. Increased covariance but not variance implies that the synergy is working mostly through the storage effect. Yuan and Chesson (2015) drew a similar conclusion from a non-evolutionary model. If one were to examine only the trait distribution of the community one might come to the wrong conclusion about what is driving coexistence.

As I showed in Chapter 2, the square wave forcing creates at most two niches due to the storage effect, one in each of the two seasons. No matter the difference between the seasons, there are still only two seasons. The niche width of the species, σ^2, influences the T_{amp} at which the switch from one species to two takes place, but not the total number of coexisting species. The triangle wave, on the other hand behaves more like a resource continuum. Previous work (Barabas *et al.*, 2012) has shown that coexistence via the storage effect in continuously variable, periodic environments, the environment behaves much like a resource continuum and that the number of species that can coexist is dependent on their niche width. Kremer and Klausmeier (in prep) have investigated triangle forcing at much larger amplitudes and found repeated bifurcations and potentially large amounts of diversity.

The difference between the categorical niche space of the square wave and the continuous niche space of the triangle wave could indicate when coexistence mechanisms might interact. In this case the discrete seasons of the square wave do not allow for any more than two species to take advantage of the storage effect, but the continuous variation in the triangle wave does. It is possible that coexistence mechanisms that rely on discrete functional types will not synergistically interact with other coexistence mechanisms. Competition for substitutable resources (Tilman, 1980; Schreiber & Tobiason, 2003) is similar to my square wave model in that coexistence requires species to specialize on one of the two resources. A coexistence that relies on a tradeoff between predation resistance and competitive ability leads to a similar result

(Koffel et al in review). In fact, this discrete niche space might be seen in any mechanism that has a generalist/specialist tradeoff.

It is possible that further studies will reveal synergistic effects between mechanisms that divide up niche space continuously. Relative nonlinearity is one such mechanism. Resource continuums as in the classic seed-size beak depth diversification in Galapagos finches (Grant, 1972) is another. Squaring niche space can more than square the number of species possible if they can differentiate in both directions like in Figure 3.1c. This is an extension of classical ecological work on species packing, where MacArthur and Levins (1967) postulated, and Yoshiyama and Roughgarden (1977) confirmed, that adding additional dimensions enables closer species packing, with more recent work by Leimar et al (Leimar *et al.*, 2013). Classical mathematics, of course, knew this all along when packing oranges into crates (Gauss, 1831). Still, most species are not oranges, so it remains to be seen how close this analogy runs.

Conclusion

To my knowledge, this is the first study that examines the eco-evolutionary outcomes of combining the storage effect and relative nonlinearity. Understanding how coexistence mechanisms combine is crucial for understanding the maintenance of diversity. This study hints that coexistence mechanisms that rely on limiting similarity and continuous niche space are likely to combine synergistically, while mechanisms that create discrete niches may not. This study was confined to mechanisms that relied on temporal fluctuations to operate. Further research on different types of coexistence mechanisms, those that employ spatial variation or resource gradients or predation, will reveal whether this is a general rule.

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