How Eco-Evolutionary Interactions Mitigate Climate Risk: A Theoretical Perspective

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Abstract

How Eco-Evolutionary Interactions Mitigate Climate Risk: A Theoretical Perspective

Anna C. Vinton

2021

Accelerated rates of climate change are expected to either lead to adaptation and persistence, or extinction. Traditionally, ecological models predict extinction risk based on how environmental change alters a population’s intrinsic growth rate \( r \). However, these predictions often ignore the potential for evolutionary rescue, whereby populations avoid extinction via adaptive evolution. This dissertation sets out to address what allows rapid evolution to rescue natural populations in the face of environmental change. Our current lack of understanding of the role of ecological and evolutionary dynamics, and their combined effect on population responses to climate change, demands further theoretical and experimental work to investigate these processes. I utilize theoretical modeling approaches to investigate the dynamics of small populations that have been reduced due to environmental change, and what allows them to rebound and avoid extinction.

(1) Successful evolutionary tracking depends on how selection acts on key life history traits. The environment may impose selective pressure on specific demographic rates (birth and death) rather than directly on \( r \) (the difference between the birth and death rates). Therefore, when considering the potential for evolutionary rescue, populations
with the same \( r \) can have different abilities to persist amidst environmental change. We cannot adequately understand evolutionary rescue without accounting for demography, and interactions between density dependence and environmental change. Using stochastic birth-death population models, I found evolutionary rescue to be more likely when environmental change alters the birth rather than death rate. Furthermore, species that evolve via density-dependent selection are less vulnerable to extinction than species that undergo selection independent of population density. Resolving the key demographic factors affected by environmental change can lead to an understanding of how populations evolve to avoid extinction. By incorporating these considerations into our models we can better predict how species will respond to climate change.

(2) Propensity for evolutionary rescue varies in complex environments. Natural populations may experience a diversity of selection pressures across space and time due to differences in spatial and temporal environments, as well as in the competition they are subject to. I develop a spatially explicit individual based model to determine how the slope, spatial heterogeneity and patchiness of an environmental gradient as well as the dispersal ability of individuals will alter population extinction risk across a landscape due to environmental change. We find that as expected, the larger the magnitude of environmental change, the more likely a population will go extinct. Furthermore, there is a complex interplay between the spatial scenarios of gradient steepness, patchiness, and heterogeneity. Components that tend to encourage genetic diversity via local
adaption to spatially diverse landscapes tended to allow for persistence. But, there are notable exceptions to this general rule. Too much heterogeneity leads populations to being maladapted to their local environment. In this case, landscape patchiness can serve to allow for environmental refugia. Thus we show that the spatial landscape significantly alters probability of evolutionary rescue, highlighting the importance of spatial realism in predictive models.

(3) Resource scarcity plays a vital role in thermal performance amidst changing temperatures. Consumers and resources both have characteristic responses to temperature change, but how these temperature responses interact in the context of consumer-resource dynamics and adaptive evolution has not been well established. We utilize a consumer resource model to assess how communities will respond to temperature change. Our models demonstrate that within the consumer thermal niche, performance and equilibrium biomass differ. This implies that estimates of thermal stress and extinction risk based solely upon the individual thermal performance is problematic. We find that as consumers reduce a resource, there is adaptive pressure for that resource to grow successfully at lower temperatures where the consumer uptake rate is lower. Lastly we assess the importance of thermal asymmetry of the consumer and resource. If the resource’s thermal performance shifts to warmer temperatures, the consumer’s persistence in low temperatures decreases to reflect the effect of resource limitation at low temperatures. Likewise if the resource’s thermal performance shifts to colder temperatures, the consumer’s ability to persist in the
hottest temperatures also decreases. Thus we must consider the dynamic interplay between temperature and interacting species as this can determine species response to temperature.

Overall, we find that the assumptions we make when modeling environmental change in the life history of individuals, species interactions, and their spatial landscape have significant effects on species ability to survive environmental change. We provide generalizable frameworks to improve our ability to understand and predict how natural populations will respond to climate change.
How Eco-Evolutionary Interactions Mitigate Climate Risk: A Theoretical Perspective

A Dissertation
Presented to the Faculty of the Graduate School
Of
Yale University
In Candidacy for the Degree of
Doctor of Philosophy

By
Anna C. Vinton

Dissertation Director: Professor David A. Vasseur

June 2021
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Introduction

Given that rates of environmental change are increasing, understanding how populations adapt in order to avoid extinction is a necessary and urgent challenge (Thomas et al., 2004). Although there have been attempts to make predictions about how populations will fare, this is extremely difficult because changes in climate alter processes at multiple scales from molecular processes to entire ecosystems. To avoid extinction due to environmental change, a species must either shift its range (Hill et al., 2002), or maintain population viability under the new environmental regime. Rapid environmental changes have been repeatedly shown to accelerate evolution (Gonzalez et al., 2013). Evolutionary rescue occurs when environmental change causes a population to decline, and then the population is able to rebound via adaptive genetic change (Bell & Gonzalez, 2009). However, evolutionary rescue is not equally likely in all populations (Gonzalez et al., 2013).

Responses of natural populations to increased rates of environmental change and their potential for evolutionary rescue will largely vary depending on a long list of variables including species interactions (Osmond & de Mazancourt, 2013), dispersal (Thompson & Fronhofer, 2019), the magnitude of environmental change (Gonzalez & Bell, 2013), initial population size (Bell & Gonzalez, 2009), and standing genetic diversity (Ramsayer et al., 2013). In addition to these components, I have also shown in this dissertation that the way that environmental change alters the demography of species, the patchiness and steepness of the spatial environmental gradient, and feedbacks of temperature effects
on consumer resource interactions all determine the likelihood of evolutionary change rescuing populations from extinction due to environmental change. In this dissertation I develop an array of model frameworks that make it possible to get meaningful insight into these variables which previously seemed intractable. Not only does this work allow us to fine tune the data we might collect and parameters we might use in our models, it also provides new questions to ask regarding evolutionary rescue.

Evolutionary rescue is already known to greatly increase the chances of population persistence and it is clear that the initial population size, genetic variation, rate of environmental change and dispersal are important predictors of its success (Gonzalez et al., 2013). However, until now we have lacked a general understanding of how these predictors are linked to the demographic rates and traits that are under selection during evolutionary rescue. For example, certain types of environmental change may impact mortality while others act on fecundity (or both) and changes may interact with the strength of density dependence, especially when competition for resources comes into play. To address this gap in our knowledge we employ a common model of population dynamics to investigate how different assumptions about the relationship between life-history traits and the environment change the propensity for evolutionary rescue to occur.

Furthermore, how temperature changes across the landscape and what physical barriers exist can also determine whether a population successfully shifts to survive a changing
climate (Årevall et al., 2018; Haller et al., 2013; Polechová et al., 2009). Range shifts therefore do not occur simultaneously for all individuals in a landscape, resulting in alterations to species interactions. For evolution to occur, genetic variation is necessary. The degree of stochasticity and patchiness in the landscape can alter the ability of populations to maintain genetic variability (Lande & Shannon, 1996). Therefore, understanding how environmental stochasticity and patchiness determine genetic variation, as it relates to evolution, is key to forecast climate effects. In my second chapter I use an individual based spatially explicit model to show that incorporating realistic landscapes add complexity to our predictions about what populations might survive environmental change. Theory considering a single spatial variable (e.g. steepness of gradient, patchiness, heterogeneity) don’t always match up with that variable’s effect compared to our assessment of these in chorus. This is of course important as they will occur together in natural systems. Therefore the framework we developed should inform future models taking into account environmental change.

Finally, species interactions (e.g. mutualism, competition, and predation) can limit or expand the biotic range limits of populations (Lavergne et al., 2010; Reznick, 1982). In the case of competition, the optimal phenotype of a species for a particular temperature may differ from the optimal phenotype needed to outcompete another species. Therefore, competition can significantly alter species’ abilities to adapt to ongoing climate change (Osmond & de Mazancourt, 2013). Indeed, simple theoretical and empirical models
incorporating species response to temperature change often exhibit conflicting results (Angilletta, 2009), likely in part due to species interactions (Chown et al., 2010). In my final chapter we take a commonly used metric for assessing species response to temperature, the thermal performance curve, and unify previous approaches in order to incorporate the dynamic interplay between species, temperature, and species interactions. We find that when we incorporate the interplay between consumer and resource temperature dependence we find different extinction predictions that we would have with a more traditional framework. Furthermore, we emphasize the importance of thermal asymmetry, and it’s role in coexistence of a resource and it’s consumer.

Thus, to accurately predict how climate change will alter natural populations, it is vital to incorporate the factors assessed in this dissertation, taking our models and experiments closer to realism. The novel findings presented in this dissertation provide the groundwork on which future investigations into evolutionary rescue and extinction/persistence dynamics can be compared and contrasted. These results further provide a baseline for identifying which natural populations may be most susceptible to environmental change.
Chapter 1

Evolutionary tracking is determined by differential selection on demographic rates and density dependence

Contributing author: Professor David A. Vasseur

Based on the following peer-reviewed article:


Author contributions: ACV and DAV designed the study and conducted data analysis. ACV wrote the manuscript with substantial input from DAV.
Abstract

Recent ecological forecasts predict that ~25% of species worldwide will go extinct by 2050. However, these estimates are primarily based on environmental changes alone and fail to incorporate important biological mechanisms such as genetic adaptation via evolution. Thus, environmental change can affect population dynamics in ways that classical frameworks can neither describe nor predict. Furthermore, often due to a lack of data, forecasting models commonly describe changes in population demography by summarizing changes in fecundity and survival concurrently with the intrinsic growth rate \( r \). This has been shown to be an oversimplification as the environment may impose selective pressure on specific demographic rates (birth and death) rather than directly on \( r \) (the difference between the birth and death rates). This differential pressure may alter population response to density, in each demographic rate, further diluting the information combined to produce \( r \). Thus, when we consider the potential for persistence via adaptive evolution, populations with the same \( r \) can have different abilities to persist amidst environmental change. Therefore, we cannot adequately forecast population response to climate change without accounting for demography and selection on density dependence. Using a continuous-time Markov chain model to describe the stochastic dynamics of the logistic model of population growth and allow for trait evolution via mutations arising during birth events, we find persistence via evolutionary tracking more likely when environmental change alters birth rather than the death rate. Furthermore, species that evolve responses to changes in the strength of
density dependence due to environmental change are less vulnerable to extinction than species that undergo selection independent of population density. By incorporating these key demographic considerations into our predictive models, we can better understand how species will respond to climate change.

Introduction

Environmental change can lead to extinction when population growth rates decline to negative values or when carrying capacities are sufficiently small to generate stochastic extinctions. The ability of a population to persist following environmental change requires a shift back to positive growth rates via ecological or evolutionary mechanisms. The need to understand the mechanisms underlying population rebound has spurred studies about how demographic rescue (via immigration) and genetic rescue (via an increase in genetic variation) (Brown & Kodric-Brown, 1977; Hufbauer et al., 2015; Whiteley et al., 2015) allow for population rebound after an environmentally driven decline. Evolutionary rescue (population rebound due to an increase in density of an adaptive genotype), in particular, provides a lens to investigate extinction which incorporates both the demographic and evolutionary components of population rebound post environmental change (Gonzalez et al., 2013).

The search for what makes evolutionary rescue possible has led to an increasing effort to find experimental, empirical, and theoretical evidence of this phenomenon (Bell & Gonzalez, 2009, 2011; Gomulkiewicz & Holt, 1995; Gonzalez et al., 2013; Johannesson et al., 2011; Lindsey et al., 2013; Lynch et al., 1991; Martin et al., 2013; Martin-Clemente et
al., 2019; Orr & Unckless, 2008; Ramsayer et al., 2013; Zhang & Buckling, 2011). Bell &
Gonzalez (2009) identified four factors which alter the propensity for evolutionary
rescue: initial population size, genetic variability due to standing genetic variation and
mutations, genetic variability due to dispersal, and the extent and severity of
environmental change. These four factors have been confirmed in numerous empirical
and experimental studies (Anciaux et al., 2018; Lindsey et al., 2013; Martin et al., 2013;
Mills et al., 2018; Ramsayer et al., 2013). Although these results have advanced our
understanding of the necessary conditions for evolutionary rescue, we still lack a clear
understanding of the role of the underlying demographic rates in mediating the
outcome (Anciaux et al., 2018), since these demographic rates may have complex
relationships with the four factors described above and with their response to the
environment.

Selection can vary birth and death rates and determine adaptive capability

Environmental change can stress populations and reduce population growth rate by
decreasing the birth rate, increasing the death rate, or some combination of the two
(Aanes et al., 2000; Barfield et al., 2011; Brewer & Peltzer, 2009; Clutton-Brock &
Coulson, 2002; Crump et al., 2004; Dempster, 1983; Mccredie et al., 1983; Sibly et al.,

To generalize across taxa, previous studies investigating evolutionary rescue commonly
model demographic rates using deterministic models that do not differentiate how the
environment acts on the birth and death rates, but rather use a fixed parameter, the
intrinsic rate of population increase, \( r \) (the difference between the birth rate and the death rate at low density) (Lynch et al., 1991). Consequently, information about changes in a particular demographic rate can be lost if \( r \) is the focus of a study.

Populations with the same \( r \), but different underlying demographic rates, can respond quite differently to environmental selection (Holt, 1990). Take the case of two populations, where one has a high birth and death rate, while another has a low birth and death rate. If the difference between the two rates is equal, both populations will have the same \( r \). But, all else held equal, the population with the higher birth and death rate will have a faster rate of population turnover and will evolve in response to selection more quickly than the population with the low birth and death rate. Thus, the potential for successful evolutionary tracking of small populations depends explicitly on birth and death rates, not \( r \), which abstracts away from these rates and obscures the actual speed of adaptation by ignoring the rate of population turnover.

Furthermore, both deterministic (predictable, e.g., adaptive evolution) and stochastic (unpredictable, e.g., genetic drift) processes determine evolutionary rescue (Russell Lande et al., 2003). Although adaptive evolution favors individual traits that are best suited to their environment, stochastic processes can lead to dissimilarities from predictions produced by purely deterministic frameworks (Start et al., 2019; Vellend, 2016). Moreover, demographic stochasticity (the randomness resulting from individual variation in birth and death, as well as variation in the timing of birth and death) influences the ability of evolution to favor adaptation to a changing environment. At
large population sizes, these individual differences average out, yet they remain important at small population sizes (Russell Lande et al., 2003; May, 1973). For this reason, modeling this demographic stochasticity explicitly is especially relevant when considering the ability of populations to rebound from small size. The importance of modeling birth and death rates explicitly has thus been emphasized widely, leading to a wide use of theoretical modeling techniques that incorporate stochasticity into birth and death rates (DeLong & Gibert, 2016; Melbourne & Hastings, 2008; Nåsell, 2001; Ovaskainen & Meerson, 2010). Similarly, population demographers are increasingly able to collect data on how different vital rates change over time, making it especially timely to incorporate these nuances into our predictive models (Coulson et al., 2001; Ouyang et al., 2014; Sibly et al., 2000).

Selection can alter how density dependence acts in populations, determining probability of rebound.

Density dependence can also affect birth and death rates and has been shown to influence the dynamics of many species (Coulson et al., 2001; Ouyang et al., 2014; Reed & Slade, 2008; Sibly et al., 2000). Environmental change may or may not alter the strength of density dependence; this varies across taxa and type of change (Coulson et al., 2001; Owen-smith, 1990; Sibly et al., 2000). For example, environmental change, such as drought, may decrease the availability or accessibility of water-limited resources (Owen-smith, 1990), intensifying density dependence as individuals compete for said resources. Theoretical studies predict that compensatory density dependence, a decrease in growth rate at high densities and increase at low densities, would allow for
a larger population size following environmental change (Chevin & Lande, 2010; Ferguson & Ponciano, 2015; Holt, 1990; Lande et al., 2003), further facilitating adaptation to new environments. Furthermore, the rate of rebound from small population size has been shown to be proportional to the extent of density dependence (Chevin & Lande, 2010; Lande et al., 2003). Thus, establishing the interaction between density dependence and environmental change in different demographic rates is of the utmost importance as the population size following an environmental perturbation determines the probability of extinction. Density dependence, although often difficult to quantify in part due to the time delay in its appearance (Lande et al., 2003; May, 1973) has also been increasingly taken into account by demographers. How density dependence evolves due to selection imposed by environmental change is for the most part only recently being brought into eco-evolutionary models and is absent from models of evolutionary rescue (Martin et al., 2013).

Studies of evolutionary rescue focusing on \( r \) need to be expanded because (a) the underlying demographic parameters and (b) the interaction between environmental change and density dependence may strongly affect evolution. We investigate how evolutionary tracking, and furthermore evolutionary rescue, depends on the way environmental change affects population demographic rates. Here, we incorporate environmental conditions and their effects on density dependence into per capita rates of birth and death, to elucidate their effect on population dynamics and persistence in a stochastic model. We show results using both a fluctuating environment and a nonfluctuating environment with a single environmental shift to emphasize the roles of
ecological and evolutionary tracking and to extend our results to evolutionary rescue.

We find that populations where the environment affects their death rate as opposed to their birth rate are more vulnerable to extinction. Furthermore, when environmental change intensifies density dependence, populations are better able to rebound from small population sizes and evolutionarily track their changing environment.

Methods

Model formulation

We construct a continuous-time individual-based logistic growth model and then consider four ways that environmental change might alter population demographic rates. In all cases, as these are logistic growth models, either the birth or death rate is density dependent. In Cases 1a and 1b, the environment alters the birth rate in a density-independent and density-dependent manner, respectively. In Cases 2a and 2b, the environment alters the death rate similarly, in a density-independent and density-dependent way. We pay particular attention to ensuring that the four cases converge on the same outcome when the environment is static, to best isolate the effects of life history and selection on evolutionary rescue.

Logistic growth

All of our model cases are rooted in the logistic growth equation where $g(N)$ is a function describing the density dependence of the per capita growth rate and $N$ represents the population density:
\[
\frac{dN}{dt} = g(N)N, \tag{1}
\]

\(g(N)\) is equal to the difference between the per capita birth rate \(B\) and the per capita death rate \(D\), and we rewrite Equation 1 as follows:

\[
\frac{dN}{Ndt} = b_0 - b_I - b_D N - (d_0 + d_I + d_D N), \tag{2}
\]

where \(b_0\) and \(d_0\) represent background rates of birth and death, \(b_I\) and \(d_I\) are density-independent modifications to the birth and death rates, and \(b_D\) and \(d_D\) are density-dependent modifications. Consistent with most derivations of logistic growth (Nåsell, 1996, 2001), and without loss of generality, we assume that density-independent and dependent factors tend to reduce per capita birth rates and increase death rates. We fix the values of \(b_0\) and \(d_0\), focusing on the density-independent and density-dependent modification terms as different modes of entry for environmental effects.

**Environmental effect**

We model the effect of the environment on the density-independent and density-dependent modification terms by calculating the mismatch between the environment and the trait of an individual. For simplicity and tractability, we first model the
environment (or optimal trait value) \( \mu_{opt} \) as a simple sinusoidal function of time (see discussion for our reasons for this choice),

\[
\mu_{opt}(t, f) = \cos(2\pi f t)
\]  

(3)

where \( f \) is frequency and \( t \) is time. The effect of the environment on an individual with trait value \( \mu \) is then given by

\[
\varepsilon_{\mu} = |\mu - \mu_{opt}(t, f)|
\]  

(4)

where a large \( \varepsilon_{\mu} \) represents a maladapted individual, and a small \( \varepsilon_{\mu} \) represents a well-adapted individual. We systematically incorporate the environmental effect \( \varepsilon_{\mu} \) into the density-independent \((b_I \text{ and } d_I)\) and density-dependent \((b_D \text{ and } d_D)\) components of the birth and death rates. However, to facilitate comparison among the model cases, we scale our equations so that for any value of \( \varepsilon_{\mu} \) the equilibrium population size (assuming no temporal environmental change) is the same across all of the model cases. This allows us to make an exact comparison of the impact of temporal environmental change on population dynamics, mediated by ecology and evolution. We accomplish this by assuming that a carrying capacity exists; this requires therefore that either the birth or death rate incorporates a nonzero density-dependent effect \((b_D \text{ or } d_D \neq 0)\). We define the carrying capacity for a population in which all individuals are perfectly adapted to the environment, equal to \( K_A \) (with \( K_A = 35 \)). We introduce a second carrying capacity, \( K_B = 18 \) for a population that is two trait units from the optimum \((\varepsilon = 2)\). This
sets a quasi-lower bound for the carrying capacity, since the amplitude of variation in
the trait optima (Equation 4) is equal to one. Demographic and evolutionary
stochasticity may however lead to instances where this is exceeded, but this does not
compromise the integrity of the model.

We then independently solve the parameters \( b_I, b_D, d_I, \) and \( d_D \) given the conditions set
above for the population carrying capacity and assuming that only one of \( b_I, b_D, d_I, \) or
\( d_D \) will incorporate an environmental effect in each instance of the model. When the
environment enters via a density-independent effect on the birth rate (Case 1a) we find

\[
\{b_I, b_D\} = \left\{ \frac{K_B - K_A}{2K_A} \varepsilon_\mu, \frac{b_0 - d_0}{K_A} \right\} \quad \text{and} \quad \{d_I, d_D\} = \{0,0\}
\]  

(5)

When the environment enters via a density-independent effect on the death rate (Case
2a), the solutions for the birth and death parameters in equation 5 are switched. When
the environment enters via a density-dependent effect on births (Case 1b), we find

\[
\{b_I, b_D\} = \left\{ 0, \left( \frac{b_0 - d_0}{K_A} \right) \left( 1 + \frac{K_B - K_A}{2} \varepsilon_\mu \right)^{-1} \right\} \\
\text{and} \quad \{d_I, d_D\} = \{0,0\}
\]  

(6)
Similar to above, the model describing a density-dependent effect on deaths (Case 2b) is found by switching solutions of the birth and death parameters in equation 6. Table 1 provides a breakdown of the model cases.

Stochastic framework

We used the above ordinary differential equation framework to develop a stochastic simulation algorithm (SSA or birth–death process) using the direct method described by (Gillespie, 1977), adapted to allow heritable variation in individual traits. Stochasticity occurs in the model as a result of the random selection of birth and death events (demographic stochasticity), and random mutations during reproduction. This framework is apt for testing our assumptions because true extinctions are possible, and evolution occurs as a result of heritable individual variation that emerges from our assumptions about population demography.

We initialize the model with 35 individuals with traits drawn from a uniform distribution with mean 0 and standard deviation 0.3873, which, under a constant environment is a reasonable approximation to the standing variation that our assumptions generate. We determined this by running our simulations in a constant environment and taking the average standard deviation of trait values in the population. Integration of the model starts by first determining the time until the next event, which is randomly sampled from an exponential distribution with mean $1/E$, where $E$ is the sum of the rates of all possible events (birth and death of all $N$ individuals in the population):
\[ E = \sum_{i}^{N} (B|\mu_i + D|u_i) \]  

(7)

After the current time \( t \) is updated, the specific event that occurs is determined by randomly choosing among all possible events, weighted according to differences in their rates. For example, the probability that the next event is a death of the \( i \)th individual is \( D|\mu_i|/E \). If an individual dies, it is removed from the population and the entire process is repeated. If birth of an individual is chosen, the new individual takes the parent's trait with probability 0.9; otherwise, a mutation occurs and the offspring's trait is equal to the parent's trait plus a random value drawn from a uniform distribution with a range of \(-0.3\) to \(0.3\). This sequence of steps mimics mutation-limited evolution in an asexual population. A similar eco-evolutionary framework is described in DeLong and Gilbert (2016); however, their approach differs slightly from ours because they first aggregate rates of birth and death to the population level and then randomly assign the individual to experience the event. This results in an underestimate in the response to selection, but leads still to the same equilibrium.

Simulations

We conducted simulations across a log-linear range of frequencies \( f \) of environmental change. For each frequency of environmental change, we conducted 512 independent replicate simulations. We ran the model for 500 time steps before recording the trait values of each individual, as well as the population size and all simulations continued for a total of 100,000 time steps or until extinction occurred. Trait–environment correlations were computed for the mean trait and environment value using Pearson's
correlation coefficients. To provide a basis of comparison, we also conducted simulations where mutation-driven evolution did not occur. Simulations were conducted using Wolfram Mathematica v11.0 on a iMac Pro with 18 Xeon W cores.

Lastly, we conducted simulations utilizing an environment that changes in a sigmoidal manner

\[ \mu_{opt}(t) = \frac{t - T_p}{\sqrt{a + (t - T_p)^2}} \]  

where \( a \) is 800 and \( T_p \) or the time at which the environment changes is 600. The slope of the environmental change is determined by \( a \), which we chose to be a similar rate of change to that experienced periodically in the sinusoidal environment with \( f = 0.0015 \). We used this additional case to showcase a more traditional type of environmental change to observe evolutionary rescue.

Results and Discussion

Our results show that evolutionary rescue is affected when the environment influences different demographic rates and processes. We begin by discussing the resulting extinction dynamics when considering populations that cannot undergo evolution, followed by populations that have the capacity for mutation-driven evolution. The four models we consider here are calibrated to produce the same behavior when the environment is held constant; the population will approach an equilibrium density that is determined by the environment, but is consistent across all cases. At equilibrium,
however, the turnover rates (approximated by $\frac{B}{D}$) differ among the models in which
birth rates vary among individuals and those in which death rates vary (see Figure 1).
Consistent differences also emerge among the models incorporating the density-
independent and density-dependent environmental interaction; particularly at low
densities, the effect of trait variation is strongly buffered in the latter cases. These
differences give rise to the results depicted in Figure 2.

Demographic results without mutation-driven evolution

The four models exhibit a consistent ranking of mean persistence time across the entire
range of frequencies of environmental change we considered (Figure 2e). Mean
persistence was greater in populations whose birth rates (rather than death rates) were
environmentally influenced, and when the environment affected the strength of density
dependence. In the absence of evolution, the most persistent populations were of the
form outlined in Case 1b, followed by Case 1a, where there is a density–environment
interaction in the birth rate and where the environment acts on the birth rate
independent of density, respectively. These were followed by Case 2b then 2a (the
populations where the environment altered the strength of density dependence and
acted independent of density on the death rate). This ranking in persistence is easily
explained by the ecological differences among the models, considering in particular
their behavior when population sizes are small (i.e., as populations are near extinction).

First, populations with birth as the responsive trait persist longer than those with death
as the responsive trait due to the greater demographic stochasticity in death models
which increases extinction at small population sizes. The intrinsic growth rate of the population is determined by the difference between the birth and death rate, while demographic stochasticity is determined by the sum of the birth and death rate (Nisbet & Gurney, 2003; Palamara et al., 2016). Although our models are parameterized so that they have the same $K_A$ and $K_B$ for when $B-D=0$, the sum of $B$ and $D$ at these equilibrium points is four times higher in the death models (Case 2a and 2b). Hence, the death models have much higher demographic stochasticity than the birth models (Figure 1), and it is clear that demographic stochasticity increases extinction probability at low population sizes (Lande, 1993; Melbourne & Hastings, 2008). Furthermore, demographic stochasticity increases the variance in population size, as we see in Figure 2 (a,b). High fluctuations in vital rates have been shown to decrease population growth due to an increase in variation in the population growth rate (Jonsson & Ebenman, 2001; May, 1973). Accordingly, species have been shown to be particularly vulnerable to highly variable adult survival, leading to a higher extinction risk (Caswell et al., 1999; Crone, 2001; Jonsson & Ebenman, 2001; Lande, 1988). Although model results emphasize the importance in specific vital rate change due to selection utilizing matrix modeling approaches (Barfield et al., 2011; Coulson et al., 2003), they do not analyze the dynamics of small populations with varied distributions of phenotypes as was the goal in the present study.

Second, at low densities, models where the environment inter-acts with the strength of density dependence maintain higher average (and less variable) population size since maladaptation to the environment has a diminishing impact as population size declines.
(Figure 1b,d). This is reasonable as populations with highly variable growth rates have been shown to be particularly vulnerable to extinction (Lande & Orzack, 1988; Leigh, 1981). Furthermore, it has been shown with a discrete time model that when the environment is embedded in a density-dependent term, it produces a multiplicative effect on population size, and these populations have more strongly bounded populations (Ferguson & Ponciano, 2015). As shown in Figure 1b,d, at low population sizes, the density-dependent environmental effect has lower variation than the density-independent environmental effect, while the opposite is the case at large population sizes. These differences in variation translate into longer persistence times of the models where environmental change alters the effect of density (Case 1b, 2b) relative to those where environmental change alters the vital rates independent of density (Case 1a, 2a). Although the environmental density effect increases variation at high population sizes, it is favorable when populations are small as they are better able to rebound. Researchers have emphasized the importance of density dependence in population growth of course (Chevin & Lande, 2010; Clutton-Brock & Coulson, 2002; Holt, 1990), but the effect of whether or not selection alters said density dependence has been emphasized in this study.

All four scenarios exhibit a rising persistence time as the frequency of environmental variation increases. This is driven by a phenomenon known as “ecological tracking”; when a population ecologically tracks its environment, changes in the environment are re-expressed in the population dynamics as correlated changes in density. Here, where the environment changes sinusoidally, ecological tracking generates population
dynamics that exhibit a noisy cycle at the same frequency as the environment (Figure 3a,c); however, the tracking response of population diminishes as \( f \) increases. In May, 1976; Lande et al., 2003, it is suggested that the system's dominant eigenvalue represents a threshold frequency above which tracking does not occur in the Logistic model, but the exact relationship between tracking and the frequency of oscillations is best described as a continuous sigmoid function (Vasseur, 2007). The stronger tracking response generated at low frequencies of environmental variation leads to greater variation in population density (both above and below the mean) and thus greater extinction risk. This effect has been shown for a variety of ecological scenarios (Heino et al., 2000; Lande et al., 2003; Schwager et al., 2006).

Demographic results with evolution

When the full eco-evolutionary dynamics are present in our models, we find that the persistence ranking of models is maintained; however, all four models demonstrate a \( U \)-shaped (rather than monotonic) relationship between the frequency of environmental change and mean persistence times. This \( U \)-shaped relationship arises due to the interplay between ecological and evolutionary tracking of the changing environment. Evolutionary tracking occurs when changes in the environment are slow enough that they can be re-expressed as correlated changes in the mean or modal trait value(s) of the population. Importantly, evolutionary and ecological tracking are interdependent, here forming a link between ecology and evolution. As evolutionary tracking strengthens, ecological tracking is diminished because a population that adapts quickly does not experience the same extent of variation in its vital rates and parameters (See
Figure 3b,d). As ecological tracking generally has a negative effect on persistence, evolutionary tracking generates a benefit mitigating the population’s response to ecological tracking. Given the assumptions of our model (mutations per birth, mutation effect size, and population size) evolutionary tracking occurs at frequencies of environmental change below approximately $f = 0.005$. Here, it can be seen that the deviation between traits and the environmental optimum tends to decline at low frequencies (Figure 2d), leading to an increase in the population size and mean persistence times. Variation in population size is not only caused by variation of demographic stochasticity between different vital rates, but also by intraspecific trait variation. Since any individual can give birth in dynamic death models, they have more trait variation in the autocorrelated environments, (low $f$) which increases the effect of maladaptation on their death rate. But as the $f$ increases, the effect of maladaptation becomes the same across the models.

The eco-evolutionary dynamic, that is responsible for an increase in persistence times at low frequencies of environmental fluctuation, also leads to a reduction in persistence time at intermediate and high frequencies (Figure 4). This reduction is due to mutational loading (Higgins & Lynch, 2001) which is here exacerbated by the fact that mutations which might be immediately favorable in the population become quickly deleterious as the environment oscillates. This confounding kind of evolution is most likely to occur at intermediate frequencies, where complete evolutionary tracking is unlikely, but random chance allows momentary “misleading” evolutionary changes to occur. Consistent with this idea, we see a slight inflation of the mean and range of
maladaptation in our eco-evolutionary models (Figure 2c) relative to those without mutation-driven evolution. All of our models transition from a detrimental, to a beneficial effect of the eco-evolutionary dynamic near. Determining how this threshold relates to the life-history parameters of natural populations will provide important information about the potential for evolution to buffer populations from extinction in oscillating environments. Note that in Figure 2c, the mean line is slightly decreased at low $f$ for the death models. This is due to the higher trait variation exhibited in these models as previously discussed, causing a larger deviation from the optimal trait condition.

Consequences of environmental effects on different demographic rates
In natural populations, we see that the demographic rates that are selected upon, and how density dependence responds varies. Some populations may respond to environmental change in a density-independent way as in Cases 1a, 2a (Brewer & Peltzer, 2009; Dempster, 1983) while some are likely to show an increase in the intensity of density dependence as in Cases 1b, 2b (Aanes et al., 2000; Coulson et al., 2001), with varied key demographic rates (birth or death). These results emphasize the importance of taking specific demographic parameters into account into our models in the light of evolutionary rescue. Furthermore, these results suggest that environmental change that primarily causes an increase in mortality independent of density will be the most destructive to natural populations (Case 2a). We see dynamics such as this when environmental changes drive populations to physiological limits, natural disasters, severe weather, and pollution. For example, a change in oxygen composition in a marine
ecosystem may affect a population regardless of density (Brewer & Peltzer, 2009), or an increase in heavy metal contamination may similarly increase mortality regardless of population size (Santala & Ryser, 2009).

According to our results, the populations that will benefit the most from evolutionary rescue will be those whose fecundity responds to an environmental change in a density-dependent way. This may be exemplified in cases where the availability of, or access to, resources is altered by environmental change. This leads to an interaction between the deleterious effect of a mismatched environment and competition; as population size decreases and competition for resources is relaxed, the effect on demographic rates weakens. This is similar to the environment by competition covariance that is essential to maintaining positive invasion growth rates in the storage effect (Chesson 2000). Note that density dependence can also decrease due to environmental change in areas where the change is favorable (take the case of invasive species and pests), further increasing persistence potential (Ouyang et al., 2014). From these results, we recommend that long-term studies incorporate fine demographic data when feasible. Further analysis should be done to fine tune the relevant parameters that play a role in evolutionary rescue, so that we may one day be able to predict and promote evolutionary rescue in the wild.

Consequences of our model assumptions

Our modeling framework assumes asexual reproduction and a link between the environment and demographic parameter that is controlled by a single trait. Most
empirical and theoretical work suggests that sexual recombination can lead to an increased rate of evolution, as it is beneficial when mutations are common and have a small effect size (Crow & Kimura, 1965). Recombination can also pose the opposite effect by breaking up favorable gene combinations, or allowing maladaptive traits to persist longer in the population, leading to a greater genetic load on population fitness (Uecker & Herisson, 2016). Thus recent studies show a nonlinear effect of recombination on evolutionary rescue (Uecker, 2017; Uecker & Herisson, 2016). Incorporating recombination to assess any differences in outcome will surely be relevant given the diversity of mating systems in nature. Furthermore, singular step mutations are what allow the population as a whole to track the changing environment, as opposed to a genotype phenotype mapping that is not one to one. This may be representative of populations with a narrow genetic basis for which adaptation to the environment can occur, such as what has commonly been seen in drug resistance (MacLean et al., 2010). That being said, in nature, some cases of environmental change will surely require multiple traits to evolve for the population to persist. The utility of this model though is that it is comparative, it is likely we will see the same trends in a multi-trait model but this will surely be fruitful to investigate as we bring our models towards realism. This will become even more relevant with the incorporation of species interactions. Competition can both inhibit and promote evolutionary rescue in different cases (Osmond & de Mazancourt, 2013) and has shown to be a relevant component in the study of population persistence.
Lastly, the environment in this model lacks environmental stochasticity, which has been shown to play a role in the potential for populations to evolve to track the changing environment (Fey & Wieczynski, 2017; Lande et al., 2003; Ovaskainen & Meerson, 2010). But, because we first utilize a fluctuating environment instead of the single step change commonly utilized in evolutionary rescue studies, we are able to characterize the ability for a population to continuously adapt to a changing environment. In this way, we are able to see populations undergoing evolutionary rescue again and again, in order to better understand the mechanisms underlying this dynamic. In environments undergoing noncyclic changes, the rate and extent of environmental change together form a critical axis on which the success of evolutionary rescue (or more appropriately eco-evolutionary rescue) can be measured. Generally, the potential for eco-evolutionary rescue is assessed using a singular environmental change, for example, from low to high concentrations of salt, or cold to warm temperatures, (Crump et al., 2004; Doebeli & Dieckmann, 2003; McCain & Grytnes, 2010) and the typical pattern of population and trait dynamics are easily explained using the concepts of ecological and evolutionary tracking applied above; when traits are able to track the environmental change quickly enough, ecological changes are dampened enough to prevent extinction. Thus, our model, which incorporates a cyclic environmental change, is a useful predictor of how different assumptions about life history will alter the propensity of eco-evolutionary rescue. We confirm that our results are not an outcome of this cyclic environment, as the same persistence ranking results from a sinusoidal shift in the environment (Figure 5).
The study of evolutionary rescue has increased notably in the past decade, and although we have elucidated a reduced set of relevant factors, the interplay between demography and evolutionary rescue is still largely unknown. We show that models with varied dynamic demographic parameters with the same carrying capacities and initial conditions have different probabilities of undergoing evolutionary rescue following environmental change. Therefore, comparative evolutionary demography provides a lens with which we can understand how different populations may be more or less likely to persist alongside environmental change. As emphasized in previous studies, evolutionary rescue in these models occurs when the rate of environmental change, or the fluctuation frequency, is slow enough for the population to evolutionarily track the changing trait optimum as shown in Figure 3b,d (Lindsey et al., 2013; Perron et al., 2008). Although the current model does not take into account spatially heterogeneous environments or interspecific competition, it provides a starting point to better understand the interplay between evolutionary demography and evolution to a changing environment. We find that changing the demographic parameter that selection acts on, as well as the way in which selection alters density dependence, changes a populations propensity to avoid extinction via evolutionary rescue.

Conclusion

In order to minimize extinction of natural populations alongside changing environmental conditions such as climate change, we must be able to make decisions without complete data describing future phenomena. It is therefore vital to create theory that can aid scientists and wildlife managers alike in understanding how natural populations respond
to escalating rates of environmental challenge. This includes techniques utilizing the population data we already have, to use the past as a proxy for the future, as well as techniques utilizing our understanding of evolution to form ideas of how populations can adapt and how we can help them to adapt to persist into the future.

We show that when evolution is occurring in a system, the extinction probabilities vary given different dynamic demographic parameters. This comes into play in how well a population can evolve to have high fitness in a changing environment and the ability of a population to rebound from small population sizes. Our findings show the importance of explicitly incorporating environmental change and density dependence into equations describing population demographic rates. In our study, the environment provides the selective pressure on individuals, and unlike in previous work, the shape of this selective pressure is shown to differ between commonly used models. This result would not have been shown had we focused on a purely ecological or evolutionary model, this interplay is what allows us to make novel insights into if and how population persistence will be altered by climate change. Furthermore, incorporating selection and trait evolution into models on ecological time scales is an important research priority. This work shows that natural populations that have different key demographic rates will likely respond differently to climate change, and this information should be explicitly incorporated into models that predict extinction due to climate change.
Chapter 1 Figures

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<tr>
<th>Environment enters via:</th>
<th>Density Independent</th>
<th>Density Dependent</th>
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<td>Case 1a</td>
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<td>Death</td>
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<tr>
<td>Case 2a</td>
<td>( d_I = \frac{K_B - K_A}{2K_A} \varepsilon \mu )</td>
<td>( d_I = \frac{b_0 - d_0}{K_A} )</td>
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Table 1. Functional forms for the density-independent \( (b_I \text{ and } d_I) \) and density-dependent \( (b_D \text{ and } d_D) \) modifications to birth and death rates for Case 1a-2b. The birth and death rates for each case are depicted in Figure 1 across a range of environmental conditions.
Figure 1. All four cases yield logistic population growth, but depend on different relationships between per-capita demographic rates of birth (blue) and death (red), (see equations 5 and 6, and table 1). In the upper panels (Cases 1a, 1b) death rate is constant, birth rate is density dependent, and the environment either directly increases or decreases birth rate (1a) or changes the strength of the relationship between density and birth rate (i.e., density dependence) (1b). Each blue line depicts the rate of birth for a particular state of adaptation to the environment, ranging from perfectly adapted $\epsilon_\mu = 0$, as dark blue (top line), to strongly maladapted $\epsilon_\mu = 2$, as light blue (bottom line). The lower panels show the same relationships for Cases 2a and 2b. Colored disks show how the 4 scenarios match to Figures 3 and 4.
Figure 2. Population dynamics of the four model cases without and with a complete evolutionary dynamic (with and without mutation). For population size (a,b) and maladaptation (c,d), the solid lines give the ensemble means of all model replicates and times and the shaded areas show the 25th and 75th percentiles of the distribution. For persistence time (e,f), the solid lines give the means across model replicates and the shaded areas show the 25th and 75th percentiles of the distribution for persisting populations. Maladaptation is measured as the difference between the mean population trait and the environmental value for persisting populations. The blue line represents Case 1b (environmental change alters the birth rate and population response to density), the green line Case 1a (environmental change alters the birth rate independent of density), the orange
line Case 2b (environmental change alters the death rate and population response to density), and the red line Case 2a (environmental change alters the death rate independent of density), as shown in Figure 1.
Figure 3. Ecological tracking occurs when the population size (a) exhibits a correlated pattern of variation with the environment (here $\mu_{opt}$) (panels a and c). In this example all individuals have the same trait value, there is no mutation driven evolution, and $f = 0.0005$. Panels b and d show evolutionary tracking where the mean trait in the population closely follows the environment, thereby dampening the ecological response to the environmental variation.
Figure 4. The quotient between the mean persistence time of populations that exhibited evolution and the mean persistence time of populations that did not undergo mutation driven evolution. For values above one, evolution was beneficial for persistence, for those below one, evolution had a negative impact. Evolutionary tracking increased persistence time for populations when the environmental fluctuation frequency was low.
Figure 5. The proportion of persisting populations over time. These plots portray a typical evolutionary rescue scenario with a sigmoidal environment as opposed to the fluctuating environment shown in the previous figures. The top panels depict the proportion of surviving populations over time out of 512 replicates for Case 1a (green), 1b (blue), 2a (red), and 2b (yellow).
Chapter 2

Evolutionary rescue in complex spatio-temporal landscapes

Contributing authors: Prof. Åke Brännström, Dr. Ulf Deckmann, Prof. David A. Vasseur

Author contributions: ACV UD AB and DAV designed the study. ACV and AB constructed the simulation model. ACV and DV conducted data analysis. ACV wrote the manuscript with input from DAV UD and AB.
Abstract

Genetic variation is the base upon which evolutionary change can occur, and this variation is dependent on the spatial arrangement of individuals as well as the environmental change. Thus, a leading challenge in ecology and evolutionary biology is understanding how complex landscapes influence adaptation to changing environments, and the potential for evolutionary rescue (when a population avoids extinction due to environmental change via genetic adaptation). In order to determine the relevant integrative variables in the current model, we first review the factors that previous studies have shown are important, largely in isolation. We then incorporate these factors into the current model in order to investigate how they interact in concert. We see an overall increase of extinction risk with the magnitude of environmental change as is expected. Furthermore, populations existing on landscapes with steep environmental gradients (high slope) go extinct at lower magnitudes of environmental change than lower sloped gradients. Populations with a higher relative dispersal distance capability were better able to withstand environmental change and thus had a higher overall persistence rate. Autocorrelation, or the similarity between the environment at one location to its neighboring locations, decreases population persistence except in the case of high magnitudes of environmental change, where a refugia effect can allow populations to persist in suitable patches of the landscape. We see an intermediate spatial variation optimizing persistence but there are important interactions between the spatial variables that cause complex results. Thus we show that the spatial landscape significantly alters probability of evolutionary rescue.
Introduction

Evolution can rescue species facing population decline and extinction due to natural or anthropogenic environmental change (Carlson et al., 2014; Gonzalez et al., 2013; Vinton & Vasseur, 2020). Evolutionary rescue occurs when a genetic adaptation allows a population to recover from population decline that would otherwise lead to extinction (Gomulkiewicz & Holt, 1995; Gonzalez et al., 2013). The potential for evolutionary rescue to prevent species extinction is of both pure and applied interest, as it could provide additional tools for managing ecological systems. It is clear that evolutionary rescue cannot help all populations amidst rapid environmental change, so defining the limits of evolutionary rescue is a priority for conservation biology (Bell, 2013). Theory has emphasized that factors including spatial environmental heterogeneity (Schiffers et al., 2013), gene flow (Schiffers et al., 2013), and ecological interactions (Osmond & de Mazancourt, 2013; Vinton & Vasseur, 2020) can each influence evolutionary rescue on their own. However, unlike in simple models that treat these variables exclusively, in a natural system these factors play a role in concert. Furthermore, the spatial heterogeneity in these models lacks realism (Urban et al., 2016), and fails to take the role of spatial autocorrelation, environmental heterogeneity, and slope (the steepness of environmental gradients) into consideration simultaneously. Although studies of environmental change primarily focus on a shift in an average environment, changes in these spatial parameters are also important as climate change is predicted to increase spatial autocorrelation in some environmental conditions such as temperature (Di Cecco & Gouhier, 2018).
It is clear that spatial heterogeneity is one of the factors that drive evolutionary change (Doebeli & Dieckmann, 2003; Haller et al., 2013; Heinz et al., 2009; Payne et al., 2011). Environmental change is often reduced to changes in the average environment, although it has been shown that other environmental aspects such as spatial variation plays an important role in population dynamics and persistence (Fey et al., 2019). High environmental variation has been shown to increase extinction via increases in population fluctuations (Vasseur et al., 2014) and by increasing the chance of genetic maladaptation (Higgins & Lynch, 2001), while other theory shows that spatial variation decreases extinction risk by increasing the standing genetic variation and allowing a more rapid response to selection (Gralka & Hallatschek, 2019). Although previous work typically represents environmental heterogeneity utilizing simple spatial structures such as discrete metapopulations, some have shown the importance of more complex spatial structures such as spatial gradients and the spatial autocorrelation of the landscape, for a population’s trait evolution (Haller et al., 2013). This encourages the incorporation of different kinds of heterogeneity in future models addressing evolutionary rescue.

Evolutionary rescue in complex landscapes may also depend on spatial autocorrelation, which describes the extent to which the environment at one location is dependent on neighboring environments (Legendre, 1993). Climate models predict an increase in spatial autocorrelation in temperature due to climate change (Easterling et al., 2000; Field et al., 2012; Meehl, 2004). Spatial autocorrelation is of course ubiquitous across natural environments (Legendre, 1993), and can play an important role in extinction
propensity (Schmidt, 2004). While spatial autocorrelation is still largely not assessed in eco-evolutionary models with environmental perturbations, we do know that temporal variation in the environment is often positively correlated, and the increase in this autocorrelation has been shown to both increase and decrease extinction risk, depending on the spatial structure of the population, as well as the form of density dependence (Petchey et al., 1997; Ripa & Lundberg, 1996; Schwager et al., 2006; Vasseur & Yodzis, 2004). Furthermore, temporal autocorrelation has been shown to have a role to increase extinction propensity (Koenig & Liebhold, 2016; Schmidt, 2004) via processes such as the Moran Effect (Liebhold et al., 2004). This has been analyzed in metapopulations but less so in individual based stochastic continuous contexts (but see Haller et al., 2013).

There is no research that we know of that addresses the impact of spatial autocorrelation on evolutionary rescue, but spatial autocorrelation has been discussed in an evolutionary branching context which provides us with some null hypotheses to test regarding the effect on evolutionary rescue. In this evolutionary branching context, spatial autocorrelation has been shown to favor trait divergence via refugia effects (Cenzer & M’Gonigle, 2019; Haller et al., 2013). Moreover, there has been work incorporating spatial autocorrelation to assess the ‘Inflationary Effect’ (Gonzalez & Holt, 2002). Here it is shown that spatial autocorrelation can inflate average population abundance and in some cases can even allow persistence of a population when its
average growth rate is negative. One could then hypothesize that complex spatio-temporal patterns might better support populations on the brink of extinction.

Furthermore, another important spatial aspect that alters the persistence of populations is the existence and extent of a spatial gradient. Spatial gradients are common in nature at small scales (e.g. height in the intertidal zone, or in a forest canopy) and at large scales (altitudinal gradients in alpine systems, latitudinal gradients). Spatial gradients may offer enhanced support of trait variation that, during or following a shift in mean environmental conditions, can lessen the extent of adaptation that is required to ensure population persistence. In models with an environmental gradient, range limits correspond to the realized niche of each species, where population growth is negative at some point along the gradient. With a shifting spatial gradient, commonly used in models of species’ responses to climate change (Polechová et al., 2009), the potential of the establishment of beneficial mutations depends on the spatial gradient, and how that gradient changes through time. Typically the environmental gradient has been modeled as continuous and linear, although the type of environmental gradient has been shown to be important when considering trait evolution (Haller et al., 2013). Adaptive evolution has been shown to be maximized at intermediate slopes (Doebeli & Dieckmann, 2003). This is because initially, environmental gradients induce trait diversity due to local adaptation, which allows for evolution, but once the gradient slope is too high, individuals are not able to remain locally adapted due to dispersal.
A key aspect determining the importance of spatial variability, autocorrelation and gradients for persistence is dispersal, as it determines the role of gene flow, and thus local adaptation across space. Dispersal can increase gene flow, allowing for more genetic variation within a population, potentially allowing a population to adapt to a changing environment (Ronce, 2007). However, a high rate of dispersal can also lead to migrational meltdown, due to a decrease in fitness that is caused by a high incidence of local maladaptation (Ronce & Kirkpatrick, 2001). This relationship between dispersal, local adaptation, and persistence in complex landscapes is not well understood, but vital to understand how population abundance varies alongside a changing environment.

Ecological theory predicts that when the environment is spatially heterogeneous but temporally invariant, persistence and diversity are maximized at intermediate dispersal rates (Holyoak & Lawler, 1996; Kerr et al., 2002). This unimodal relationship arises from a well-known tradeoff: increased dispersal allows for faster recolonization after local extinctions but also synchronizes dynamics, increasing the likelihood that extinct or near-extinct patches are neighbored by others with a similar fate and diminishing the pool of potential re-colonists. A different outcome has been observed in studies of local adaptation and gene flow (Lenormand, 2002). High levels of gene flow can impede local adaptation, reduce local fitness, and in some cases even cause population extinction, resulting in a positive relationship between gene flow and maladaptation. High levels of gene flow and dispersal also lead to the synchronization of traits in metapopulations, which increases the likelihood of global extinction (Heino et al., 2000; Molofsky & Ferdy, 2005). Lastly, while dispersal in spatially heterogeneous habitats can reduce population
growth rates, dispersal in the presence of environmental change can enhance population growth (Schreiber, 2010).

Theory surrounding evolutionary rescue has emphasized the importance of factors including temporal and spatial environmental heterogeneity, spatial autocorrelation, environmental gradients, in isolation, and in the absence of realistic spatial landscapes. Unlike in simple models that treat these variables exclusively, in a natural system these factors all play a role in concert. Interactions among these factors could change the outcome of evolutionary rescue. Here we develop a stochastic individual based model to examine the interactive effects of the movement of individuals along a temporally changing spatial gradient on evolutionary rescue. We aim to address how local adaptation to different types of heterogeneous environments influences a population’s ability to undergo evolutionary rescue. Investigating these joint influences on evolutionary rescue will aid in defining which key factors, alone or in concert, limit adaptation to a changing environment, bringing scientists closer to predicting populations’ propensity for evolutionary rescue in the wild.

Methods

Model Overview

Individuals are initialized on a 2D continuous heterogeneous landscape, allowing us to test the role of different types of environmental heterogeneity on evolutionary rescue. Similar to Haller et al (2013), we vary the linear slope of the environmental gradient (the
gradient occurs on one axis), as well as the patchiness (autocorrelation and variation) of the landscape in two dimensions (see Landscape Generation). Furthermore, we vary the magnitude of a sudden environmental change, to observe evolutionary rescue directly. Individuals in this model have constant birth rates, while their death rate is determined by the difference between their trait value, the environment they are located in, and the density of individuals around them. Selection acts on the differences among individuals’ traits and reproduction is asexual with new traits generated via mutation.

Population Dynamics

The carrying capacity $K$ for an individual with trait $u$ in location $(x, y)$ is determined by the difference between the individual’s trait and their environment. Thus, $u_0(x, y)$ is the optimal phenotype, or the environment (trait that produces largest $K$),

$$K(u, x, y) = K_0 N_{\sigma_k}(u - u_0(x, y)).$$  \hspace{1cm} (1)

$N_{\sigma_k}(z)$ is a Gaussian function that determines the effect of being maladapted in the current environment,
\[ N_{\sigma_k}(z) = \exp \left( -\frac{z^2}{2\sigma_k^2} \right). \]  

The optimal phenotype, or \( u_0(x, y) \), is as follows: \( S \) determines slope, and \( \alpha \) as a centering constant. \( \Phi_{v,a}(x, y) \) determines patchiness, where \( v \) determines variance and \( a \) determines autocorrelation, and \( p \) is the press perturbation (see Landscape Generation).

\[ u_0(x, y) = \alpha + Sx + \Phi_{v,a}(x, y) + p. \]  

The strength of competition is given by the effective number of individuals competing with individual \( i \). The strength of competition increases with both trait and spatial proximity,

\[ n_{\text{eff}}(u_i, x_i, y_i) = \frac{1}{2\pi \sigma^2} \sum_{j=1}^{N} N_{\sigma}(u_j - u_i)N_{\sigma}(x_j - x_i)N_{\sigma}(y_j - y_i). \]  

The death rate is given by the strength of competition divided by the carrying capacity experienced by individual \( i \) at location \((x, y)\),

\[ d_i = \frac{n_{\text{eff}}(u_i, x_i, y_i)}{K(u_i, x_i, y_i)}. \]
Birth rates are held constant at \( b \). Reproduction is asexual, and the offspring trait \( u(x, y) \) is given by the parent trait with the addition of a mutation, which has a magnitude drawn from a normal distribution with mean 0 and standard deviation 1.5. Thus, the trait value is heritable in our model. The natal dispersal is the only form of movement, offspring location coordinates \( (x, y) \) are each given as the parental \( x \) and \( y \), with the addition of a dispersal magnitude drawn from a normal distribution with mean equal to 0 and standard deviation equal to 1.5 or 2 depending on the dispersal treatment. The boundary conditions of this landscape in the \( y \) direction are reflecting so if an individual is chosen to disperse outside of the landscape they are reflected back within the boundary. In the \( x \) direction this landscape is continuous, and if an individual disperses past the boundary they are placed on the opposite end of the landscape. See (Mazzucco et al., 2018) for further discussion of boundary choice impact on evolution.

Landscape Generation

We generate a 100x100 patch landscape which is spatially autocorrelated using the spectral method of generating a Gaussian Random Field (Liu et al., 2019). In short, we specify the character of the landscape in the frequency domain by fixing the rate of decay of the power spectral density according to \( f^{-a} \) where \( a \) determines the slope of the log-log power spectrum. We then add to each frequency a white noise component and take the real part of the inverse Fourier transformation of the generated 2-dimensionsal power spectrum. Larger values of \( a \) produce a greater spatial autocorrelation (a value of zero generates no spatial autocorrelation). Actual values of the autocorrelation function
can be determined using the Wiener-Kinchin theorem – but in this manuscript we
describe the autocorrelation using the parameter \( a \). We then normalize the landscape to
have mean 0 and scale the variance according to the necessary treatment and incorporate
any spatial gradient. Thus the patchiness term \( \Phi_{v,a}(x, y) \) that we incorporate is
calculated based on the \( x \) and \( y \) location of landscape, and the variation and
autocorrelation terms as in Table 1. Importantly, the spatial autocorrelation patterns
generated by this method supports our choice of boundary behavior (see Figure 1).

Demographic Events

We developed a stochastic simulation algorithm (SSA or birth-death process) using the
direct method described by Gillespie (Gillespie, 1977) adapted to allow heritable variation
in individual traits. This framework differs from ordinary differential equation (ODE)
models in which true extinctions are never possible, and there is an assumption that trait
distributions have fixed variances. This allowed us to analyze the effect of dispersal and
local adaptation in small populations, investigate how trait variation plays a role in
population persistence, and compare the results from the stochastic model to the ODE
model at large population sizes.

The total birth \( B = \sum_{i=1}^{N} b_i \), and death \( D = \sum_{i=1}^{N} d_i \), rates are equal to the sum of the
respective individual probabilities. The total event rate \( (E) \) is the sum of \( B \) and \( D \), \( E = B + D \). Waiting time to the next event is drawn from an exponential distribution with
mean \( 1/E \). The probability of a birth and death events are \( B/E \) and \( D/E \) respectively.
An individual is chosen for reproduction with probability $b_i/E$. When an individual gives birth, their offspring trait is equal to the parent trait with a probability of mutation. If a death is chosen, an individual is chosen for removal with probability $d_i/E$. Dispersal occurs in this model at the same time as a birth. When an individual gives birth, the placement of their offspring on the landscape is be determined by the dispersal kernel.

Simulations

We begin simulations at $T = 0$ with 700 individuals that are randomly placed on the landscape. At $T = 450$, a sudden press perturbation occurs across the landscape with a magnitude of 9-16 depending on the treatment. The simulation continues until $T = 1,100$ or extinction. Our sample sizes for each treatment range from 30 to 75 replicates depending on the treatment, and we sampled every 10 time steps.

Survival Analysis

We use survival analysis (a multivariate Cox regression model) to examine main and interaction effects of treatments on the time to extinction. Because our gradient of perturbation treatment has a non-linear effect that supersedes other model treatments (all simulations persist at small magnitudes and all go extinct at high magnitudes) we conduct the survival analysis only for perturbation magnitude 12. Furthermore, we look only for interactions among the spatial parameters to limit complexity of the model. We present a Cox regression model where survival over time is predicted by dispersal, and
the interaction between the spatial components using the formula

\[
\text{survival}(\text{time}) \sim \text{dispersal} + \text{autocorrelation} \times \text{standard deviation} \times \text{slope}
\]

to assess the significance of the interactions between autocorrelation, standard deviation, and slope.

Results and discussion

Increasing magnitudes of environmental change hinders evolutionary rescue

Evolutionary rescue occurs when some individuals have a high enough fitness, post environmental perturbation, that they are still able to reproduce and rebound to repopulate the landscape (Figure 2). We confirm the treatments where evolutionary rescue is occurring by comparing the treatments with and without mutation driven evolution (Figure 3). Our results show that increasing perturbation size decreases the likelihood of evolutionary rescue, (Figure 4) consistent with theoretical and experimental findings (Bell, 2013). It is widely accepted that the amount of genetic variation required to adapt to persist increases with the rate and severity of the environmental change (Burger & Lynch, 1995; Gomulkiewicz & Holt, 1995; Lynch & Lande, 1993; Orr & Unckless, 2008). Thus, successful evolutionary rescue is contingent upon the relationship between standing genetic variation, mutation rate, generation time, and speed of environmental change (Lynch & Lande, 1993). Our model considers both the important of genetic variation prior to the environmental perturbation and mutation-limited evolution after
and we focus our discussion of the effects of the spatial environment on those key characteristics.

Therefore, there are clear interactions between the perturbation magnitude and our environmental treatments (Figure 2), as high perturbation magnitudes swamp out effects. Furthermore, in order to focus our discussion on evolutionary rescue, we henceforth focus on a single perturbation magnitude, 12 in order to discuss the effects of our other treatments. This perturbation treatment is high enough that without mutation driven evolution populations will go extinct, and thus there is opportunity for evolutionary rescue in populations that can undergo mutation driven evolution. We find that dispersal has a main effect that is independent of the environmental treatments (Table 2). We briefly summarize our statistical findings from perturbation 12 with mutation driven evolution (Table 2) before discussing each variable on its own: Our higher dispersal treatment was better able to withstand perturbations and thus had a higher overall persistence rate. The effects of standard deviation and autocorrelation are non linear are vary greatly due to the interactions between our environmental treatments. Detailed discussion of these finding as well as their interactions follows. We find that the effects of slope are less pronounced but we do see some notable subtle trends, such as populations existing on higher slope treatments go extinct at lower perturbations than lower slope treatments.
Dispersal distance promotes evolutionary rescue in changing environments

Greater dispersal distances result in a higher likelihood of evolutionary rescue across all of our treatment combinations (Table 2, Figure 5). We find that higher dispersal distances increase the trait variation shortly after perturbation (Figure 6); this may be due to an improved ability of individuals to reach their desired environmental conditions both before and after perturbation. Given that our environmental treatments incorporate a gradient (slope) across the landscape, the population can recover its pre-perturbation fitness by quickly dispersing down the gradient; while this mechanism is insufficient on its own (Figure 7) it assists populations in recovering quickly. Others have shown that the effect of environmental change is regulated by dispersal and subsequent density dependent fitness of migrants (Uecker et al., 2014). Although theoretical predictions convey both positive and negative influences of dispersal on evolutionary rescue (Bourne et al., 2014; Thompson & Fronhofer, 2019), experimental evidence using yeast and bacterium both find only a positive effect of dispersal on evolutionary rescue due to the beneficial effect on genetic diversity (Bell & Gonzalez, 2011; Perron et al., 2008). In theory dispersal can have a negative effect of persistence due to an increase in ‘migration load’, or the process of spreading locally adapted genetic traits to areas where they are no longer well adapted, decreasing the overall fitness of populations (Bourne et al., 2014). Bourne et al (2004) finds that under environmental conditions that select for generalist phenotypes, or phenotypes that can utilize a variety of resources or live in a variety of environments, then dispersal rate increases population persistence. But under conditions that favor a specialist phenotype, dispersal was only able to outweigh the risk of migration
load in a specific range of parameters, notably an intermediate selection strength. Thus far there is no experimental evidence of migration load preventing ER, although this is likely an important factor (Carlson et al., 2014).

Steep environmental gradients promote genetic variation while reducing population size

Although not significant in our Cox regression model (Table 2), we see notable trends of slope which likely plays an important role in combination with our other spatial parameters. The higher slope treatment appears to have a higher survival post perturbation than the low slope treatment (Figure 4-5). Functionally an increase in slope increases the change in environmental value (trait optimum) across the landscape and therefore yields more genetic variation in the population prior to the environmental perturbation (Figure 6). As we can see from Figure 6, the higher slope treatment has a higher range of trait values, presumably allowing for faster adaptation across the landscape. Presumably this would mean that when the environmental perturbation hit, there is more trait variation for selection to act on and allow for evolutionary rescue. A stronger gradient across space also generates a greater amount of environmental variation at local scales – within the dispersal kernel of an individual. Greater slopes may provide a greater opportunity for ‘newborn’ individuals to occupy a favorable environment in the post-perturbation environment. But, a higher slope also decreases the population size prior to perturbation (Figure 8), as this increase in the environmental change across the landscape decreases the ability for individuals to be locally adapted (increasing the chance of migration load as discussed previously). It has been shown that
the population size prior to the environmental change plays an important role in the time with which evolutionary rescue has to occur (Gomulkiewicz & Holt, 1995). At small population sizes vulnerability to demographic stochasticity, Allee effects, and inbreeding depression play a larger role. Thus the decrease in population size might outweigh the benefit of higher genetic diversity in some cases, leading to a non-significant effect.

Increasing autocorrelation reduces overall persistence alongside environmental change

For populations experiencing a perturbation magnitude of 12, we find that higher autocorrelation leads to a lower chance of evolutionary rescue, and thus a lower chance of survival (Figure 5). This is likely due to the fact that autocorrelation homogenizes local environments. While this can be good for survival of offspring (since their trait is likely to be similar to their parents), it can hinder evolutionary rescue because, after a perturbation, offspring from an individual would likely need to disperse further to find favorable environmental conditions. This finding fits in with previous knowledge about increasing the extinction probability with increasing [temporal] autocorrelation, although outside of the current manuscript not much is known about the role of spatial autocorrelation and evolutionary rescue. When considering trait evolution, Haller et al. (2013) found that autocorrelation had the ability to provide refugia, allowing for the survival of individuals in highly variable environments, although we don’t see evidence of this playing a role in population persistence when averaging across our environmental treatments. The role of demographic stochasticity likely overcomes any
refugia effect, as trait evolution is only one part of the ability of a population to rebound to persist alongside environmental change.

Intermediate environmental variation increases probability of evolutionary rescue

Furthermore, we find that an intermediate amount of variation optimizes persistence (Figure 5). Our results confirm that there is an intermediate heterogeneity that most benefits population persistence due to environmental change. This is likely because when heterogeneity is too low, there is not enough resulting genetic variation to persist alongside an environmental perturbation (Burger & Lynch, 1995). But when heterogeneity is too high, maladaptation increases because many individuals experience environmental conditions that are too different from their traits. That being said, recent studies show that this varies between whether the environmental perturbation is a press perturbation like the one used here, and a continuous environmental change; given a continuous environmental change, Orive et al. (2019) found that evolutionary rescue could not be predicted by the genetic diversity at the prior to the environmental change, which largely contrasts this previous work, as they found the most important quantity to be the de novo mutation rate. Thus expanding this work to assess different types of environmental change is surely necessary. The most common hypothesis regarding the effect of spatial variation is the intermediate heterogeneity hypothesis. Haller et al found that intermediate heterogeneity lead to maximal evolutionary divergence. Thus if this equated to resilience against perturbations due to the ability to undergo evolutionary rescue, an intermediate heterogeneity in the form of variance would optimize persistence.
probability. (Peniston et al., 2020) found that temporal variation although bad for persistence in low risk scenarios was beneficial in high risk scenarios, and this could very well be the case for spatial variation.

Interactions among the treatment effects can determine the likelihood of evolutionary rescue

While there are perturbation magnitudes that lead to autocorrelation and variance playing a significant role in survival, there are also the converse. Both variance and autocorrelation have a duplicity of effects – they can be both bad and good for persistence. Variance can be beneficial because it can promote the maintenance of trait variation in the population prior to any perturbation; however, variance also reduces the average fitness of the newborn individuals because they randomly disperse to a new location separate from their parent location, and thus increased variation tends to reduce average fitness. So, its possible that the positive and negative effects of variance and autocorrelation cancel out at some perturbation magnitudes. Autocorrelation can be beneficial because it increases the likelihood that a newborn finds an environment that is similar to its parent’s environment (and since newborns and parents have related traits) this should help to increase the fitness of newborns. At the same time however, autocorrelation will tend to make nearby locations more similar, reducing the likelihood that after the perturbation, there will be habitat that are similar to an organisms current (but maladapted trait). Autocorrelation essentially reduces the effectiveness of spatial variance at the local scale. Furthermore it may be difficult to see some interactions
because there is too much stochasticity to see treatment effects. This is a real possibility that the stochastic approach used here, with limited population size during the bottleneck caused by the perturbation, limits our ability to see any differences caused by the treatments. We also see this is a real thing in nature; demographic stochasticity takes over at small population sizes and this can swamp any signal of the differences in treatments.

Here there are significant interactions between autocorrelation and standard deviation, autocorrelation and slope, standard deviation and slope, and autocorrelation, standard deviation, and slope (Table 2). We find the role of autocorrelation to be the most important when there is high standard deviation (Figure 10), could not be seen when combining all the standard deviation treatments. This is likely because the higher autocorrelation treatment individuals remained in the lower temperature patches “refugia” longer before being able to successfully disperse to the warmer sections of the landscape. This is because of the “lethality” of such a high environmental variation, the uneven distribution and patchiness that autocorrelation causes is beneficial. (Haller et al., 2013) found this to be the case when considering evolutionary branching of traits and termed this as a refugia effect, and surely trait evolution and evolutionary rescue must be related. Ultimately though the statistical significance of the role of autocorrelation in our data wavers depending on the environmental treatment. Thus, our effect seems less than what was found in evolutionary branching in (Haller et al.,
2013), and this is likely due to the importance of small population sizes in evolutionary rescue.

This leads to the interaction between the importance of autocorrelation and different slope and standard deviation treatments. Similarly, increasing the slope and increasing the standard deviation both increase environmental heterogeneity, thus slope and standard deviation each have a smaller effect when the other is high. For example, at low standard deviation and no autocorrelation, we see a switch of the benefit of slope (Figure 11). That is, persistence decreases with increasing slope at low standard deviation, then the higher slope has higher time to extinction at high standard deviation (Figure 11). Autocorrelation to some extent has the ability to reduce this heterogeneity by clumping values together, allowing individuals to clump in these refugia islands. The complexities associated with the interactions between these environmental treatments are surely useful to continue to analyze as some of them have clear effects on population persistence.

Spatial variation and evolutionary rescue

The spatial complexities incorporated in the present study, although producing complicated dynamics associated with evolutionary rescue, we argue bring us closer to a realistic framework that we would see in nature. Some environmental components may change continuously over space as in our slope treatments, such as a toxic soil component that decreases slowly as one moves away from the source, salinity over
large geographic distances in a body of water, and elevational temperature change (Doebeli & Dieckmann, 2003). Because we see various environmental gradients in nature, it is apt to further incorporate different types of environmental gradients into our models of evolutionary rescue. Furthermore, we see autocorrelation in these environments where a slope in an environmental parameter occurs. For example, in a mountain range we would see autocorrelation in elevation and thus temperature, thus temperature across a landscape can be more or less autocorrelated depending on the local landscape conditions (e.g. Asakereh et al., 2020). An important question is, does this autocorrelation in nature fall into the realm that can hinder evolutionary rescue as we find in the present study. It may be that high elevation species are a good example of this, as climate change has already served to reduce their population sizes (Vardaro et al., 2018). The refugia that exist to support populations can likely be beneficial depending on the magnitude and type of environmental change as this could determine the likelihood of local extinction within refugia.

Studies of evolutionary rescue range from not incorporating the spatial environment or incorporating space implicitly (Bell & Gonzalez, 2009b; Uecker et al., 2014; Vinton & Vasseur, 2020), to incorporating space explicitly (Kirkpatrick & Peischl, 2013; Schifffers et al., 2013). The explicit evolutionary rescue studies to date to our knowledge are limited to simple spatial treatments. Kirkpatrick and Peischl (2013) look at how fine grained the spatial environment relative to dispersal is in their model and its role in adaptation. They find that the probability of a mutation fixing declines with migration, and further
find that there is a limit to how large environmental change can be for mutation to allow populations to adapt. Our results also confirm these complexities of dispersal and mutation, although in our model individuals only disperse at birth, similar to a wind dispersed seed or larval dispersal of sessile crustaceans and mollusks. Our high dispersal treatment outperforms our low dispersal treatment (Figure 7), but it may be that if we incorporated more dispersal treatments we would also see a unimodal relationship between persistence and average dispersal distance. Furthermore, Schiffers (2013) points out that when there is environmental heterogeneity, populations may only be able to rebound to persist in a fraction of the landscape, so that evolutionary rescue is only partially effective. We see this in our plots of rebound (Figure 8), where the population size in the higher slope treatments does not reach the original population size, as higher slope treatments have a higher range of environmental values across the landscape. Ultimately incorporating complex types of environmental heterogeneity adds complexity to the outcome of evolutionary rescue, and more work needs to be done to address this and bring our predictions closer to realism.

Conclusion

Evolutionary rescue has been shown previously to have two main predictors, genetic diversity and initial population size (Bell, 2013). But these studies use idealized populations, and lack direct application to populations in realistic spatiotemporal environments. Furthermore, they lack consideration of the role of density dependence as we do here. Thus we provide a novel framework to improve our understanding of evolutionary rescue, including species response to temperature, invasive species,
antibiotic resistance, and the chemical control of agricultural pests. Ultimately we find that not incorporating spatial heterogeneity into our understanding can lead to a gross difference in persistence predictions and more specifically our predictions of what populations can undergo evolutionary rescue.
Chapter 2 Figures

<table>
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<tr>
<th>Slope</th>
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<th>Perturbation magnitude p</th>
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Table 1. Environmental treatments (with and without mutation-driven evolution).
| Variable                        | Coef   | $e^{\text{Coef}}$ | Se(Coef) | z      | Pr ($>|z|)$ |
|--------------------------------|--------|-------------------|----------|--------|------------|
| Dispersal                      | -1.55  | 0.21              | 0.12     | -12.66 | $<2e^{-16}$ *** |
| Autocorrelation                | 0.96   | 2.60              | 0.45     | 2.094  | 0.036 *    |
| Standard Deviation             | 0.030  | 1.030             | 0.014    | 2.091  | 0.037 *    |
| Slope                          | 1.22   | 3.40              | 0.85     | 1.45   | 0.15       |
| Autocorrelation x Standard Deviation | -0.017 | 0.98             | 0.0073   | -2.35  | 0.019 *    |
| Autocorrelation x Slope        | -0.85  | 0.43              | 0.40     | -2.094 | 0.036 *    |
| Standard Deviation x Slope     | -0.026 | 0.97              | 0.013    | -2.071 | 0.038 *    |
| Autocorrelation x Standard Deviation x Slope | 0.015 | 1.015 | 0.0064 | 2.34  | 0.019 *    |

Table 2. Cox regression statistical results for perturbation magnitude 12.
Figure 1. Autocorrelation and environmental variation alter the optimal trait value of an individual across a landscape. Landscape treatments here are shown for slope 1. The standard deviation increases from the bottom panel to the top panel, and autocorrelation increases from the left to right panel. The color represents the environmental value, otherwise known as the optimal trait value.
Figure 2. Evolutionary rescue occurs when the population is able to adapt to the new environment and rebound in population size alongside environmental change. Plots show population dynamics for a treatments with slope 1, low standard deviation (25) and no autocorrelation (0) with a perturbation magnitude of 10. Each panel is a different snapshot in time, from the time right before the perturbation magnitude hits \( t = 400 \), to 400 time steps later \( t = 800 \). Individuals are superimposed on top of the landscape, and their color is their corresponding trait value and thus gives us information about their fitness on the landscape. Immediately after the environmental perturbation hits \( t = 450 \) the population size decreases drastically, and where they survive and how they repopulate depends on the landscape treatment.
Autocorrelation increases →

Slope 1 and 1.2, High Dispersal

Slope decreases

Mean persistence probability

Time

Perturbation size
9
10
11
12
13
14
15
16

Slope 1 and 1.2, Low Dispersal

Slope decreases

Mean persistence probability

Time

Perturbation size
9
10
11
12
13
14
15
16
Figure 3. Persistence probability varies between environmental scenario. Plots depict the average persistence probability across time for each autocorrelation case. Autocorrelation increases from left to right. The top row depicts environments with slope 1, the bottom row is slope 1.2. Each color represents a different perturbation magnitude. The different standard deviation replicates are averaged into each autocorrelation treatment.
Figure 4. Time to extinction decreases with perturbation magnitude, and varies between environmental scenarios. Plots depict time to extinction for each perturbation magnitude, as well as the mean and variation of the time to extinction for each perturbation treatment.
Figure 5. Survival amidst environmental change depends upon the spatial case as well as dispersal. Plots depict a survival analysis for perturbation magnitude 12. The top left panel shows different survival predictions based on autocorrelation value binned by autocorrelation value, for which we determine a $p$ value which when significant tells us that the survival predictions for each treatment are significantly different using a log rank test ($p = 0.055$). The top right panel shows survival by standard deviation case ($p = 0.029$). The lower left plot shows survival by the steepness of slope ($p = 0.034$). The bottom right panel shows survival by dispersal standard deviation, ($p = 3.68 \times 10^{-52}$).
Figure 6. Phenotypic diversity varies with a combination of the slope steepness and dispersal distance. These plots depict the mean trait range over time, which is represented by the difference between the average maximum and minimum trait value of individuals in a population. The mean trait range is thus shown over the vertical axis and time is shown over the horizontal axis. The top panels incorporate mutation driven evolution and the bottom has no mutation driven evolution. Each colored line represents a perturbation magnitude, and the solid lines represent treatments with slope 1 and the dashed lines represent treatments with slope 1.2.
Figure 7. High dispersal distance increases persistence probability most when mutation driven evolution occurs. The plots depict the mean persistence probability over time. The solid line represents populations in the high dispersal treatment and the dashed line represents populations with low dispersal. Light green depicts environmental treatments that progress from no autocorrelation to high autocorrelation as dark green.
Figure 8. Steep slope gradients reduce population size. These plots show the mean population size over time. Populations in an environment with a low slope is depicted by the solid line and high slope is depicted by the dashed line.
Figure 9. Autocorrelation becomes beneficial at high magnitudes of environmental change. These plots depict a survival analysis for perturbation magnitude 10-15 where the color depicts autocorrelation. We determine a \( p \) value which when significant tells us that the survival predictions for each treatment are significantly different using a log rank test: Perturbation 10 \( p = 0.000010 \), Perturbation 11 \( p = 0.032 \), Perturbation 12 \( p = 0.055 \), Perturbation 13 \( p = 0.25 \), Perturbation 14 \( p = 0.33 \), Perturbation 15 \( p = 0.00050 \).
Figure 10. Autocorrelation is beneficial for all environmental perturbation magnitudes when environmental variation is high. These plots depict a survival analysis for perturbation magnitude 10-15, where standard deviation is high. Each color is a different autocorrelation treatment. We determine a $p$ value which when significant tells us that the survival predictions for each treatment are significantly different using a log rank test: Perturbation magnitude 10 $p = 0.020$, magnitude 11 $p = 0.35$, magnitude 12 $p = 0.38$, magnitude 13 $p = 0.56$, magnitude 14 $p = 0.053^*$, magnitude 15 $p = 0.015^*$. 
Figure 11. The effect of slope changes depending on the autocorrelation scenario. These plots depict a survival analysis grouped by slope treatment for no autocorrelation and low standard deviation $p = 0.13$, no autocorrelation with high standard deviation. We determine a $p$ value which when significant tells us that the survival predictions for each treatment are significantly different using a log rank test: $p = 0.030^*$ (upper panel), high autocorrelation and low standard deviation $p = 0.74$, and high autocorrelation low standard deviation $p = 0.012^*$ (lower panel).
Chapter 3

Interactions between consumer thermal performance and resource limitation yield insight into the shape and structure of realized thermal performance curves.

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Author contributions: ACV and DAV designed the study and conducted data analysis. ACV and DAV wrote the manuscript.
Abstract

As temperatures rise across the globe, many species may approach or even surpass their physiological tolerances to withstand high temperatures. Thermal performance curves, often measured under ideal laboratory conditions, are commonly used to determine the physiological or demographic limits of persistence ($T_{min}$ and $T_{max}$); however, this approach fails to consider how interactions with other factors (e.g. resources, water availability) may buffer or magnify the effect of warming. Recent work has demonstrated that the breadth and shape of a consumer’s thermal performance curve changes with resource densities, highlighting the potential for interactions and leading to a potential ‘metabolic meltdown’ when resources decline during warming (Huey & Kingsolver, 2019). Here, we further develop understanding of the interaction between temperature and resource density on thermal performance, persistence, and population dynamics by analyzing a pair of consumer-resource dynamic models. We find that the coupling of consumer and resource dynamics relaxes the potential for metabolic meltdown via a reduction in top-down control of resources as consumers approach $T_{max}$. However, we also show that when both consumers and resources have vital rates that depend on temperature, asymmetry between their responses can generate the necessary conditions for metabolic meltdown. Last, we define the concept of an ‘operational’ thermal performance curve that takes into account the dynamic interaction between consumers, resources and temperature, and we describe an important role for this concept moving forward.
Introduction

Given the quickening pace of environmental change marking the Anthropocene (Zalasiewicz et al., 2017), it is becoming increasingly important to understand how species respond to temperature change. This includes not only responses at an individual or population level, but at the level of whole communities (Urban et al., 2016) where interactions may be rewired. Much of the recent work on of the impact of warming and temperature variability has relied upon the use of thermal performance curves (TPCs). TPCs describe the response of some performance metric across a gradient of temperature, but held constant prior to and during the assessment of performance (Angilletta, 2009). These curves are commonly unimodal with the mode, or optimal value ($T_{opt}$), skewed toward a warmer temperature and the lower and upper thermal limits of performance defined as $T_{min}$ and $T_{max}$. For many species, thermal performance has been measured as Malthusian fitness ($r$) and in this case the upper and lower thermal limits of performance define a niche axis consistent with Hutchinson’s definition (Holt, 2009). Hutchinson defined an ecological niche to be an n-dimensional hypervolume, incorporating the abiotic aspects of a species environment, and the biological aspects of the environment, with the assumption that these axes are independent from each other (Hutchinson, 1957).

Although TPCs have been widely used to predict the persistence and distribution of species under future climate scenarios (Deutsch et al., 2015; Fey et al., 2019; Levy et al., 2015), they are poorly suited to this task. TPCs are generally measured under idealized
conditions that are not common in nature (Schulte et al., 2011), and following a period of acclimation which ensures that any adaptive plasticity has been expressed (Kremer et al., 2018). These idealized conditions embody non-limiting conditions (e.g. food, water, resource concentrations) and more broadly assume that all axes of a species Hutchinsonian niche are at non-limiting values. Any dependence among temperature and other niche axes will result in a poorly performing extrapolation of the TPC to natural conditions. Indeed there are many examples where niche axes are known to interactively determine the viable niche conditions for species (Chase & Leibold, 2003; Soberón & Peterson, 2020) in fact anything except an exact hypercube in niche space prescribes some form of interaction among niche axes (Blonder, 2018), and it is generally well accepted that the fundamental niche is convex shape in the n-dimensional niche space (Soberon and Peterson, 2020).

Recently, Huey and Kingsolver (2019) recognized an important and likely general interdependence among the responses of a consumer population to temperature and resource density. Motivated by data from an empirical study by Brett et al. (1971), which showed a decline in the $T_{opt}$ of individual growth of salmon as the food concentrations provided to fish declined, Huey and Kingsolver (2019) demonstrated that this interdependence is generated by well-studied differences in the temperature dependences of ingestion (unimodal) and metabolism (exponentially increasing). Recognizing the potential for a decline in resource density to exacerbate the detrimental
effects of warming as consumers near their $T_{max}$, they coined the phrase ‘metabolic meltdown’.

To resolve the potential for a generalizable interdependence of resource density and temperature on performance, we embed the temperature dependence of ingestion and metabolism into a dynamic consumer resource framework, where resource densities are responsive to top-down consumption effects. We consider two different scenarios describing the dynamics of resources, and using a combination of analytical and numerical methods, we describe how the interdependence of temperature and resources affects thermal performance, dynamics and persistence. In the first scenario, resources are not directly impacted by temperature, but the thermal performance of the consumer generates indirect effects on resources via consumption. In the second, both resources and consumers depend directly on temperature, and indirect effects arise through their interaction. It is in this scenario that we find the greatest potential for metabolic meltdown due to the potential for strong interactions to arise among the two niche axes (temperature and resource density). Using this understanding we describe a method to operationalize the thermal performance curve to include the potential for joint effects of resources and temperature and describe how such operational TPCs may improve our ability to use the growing library of idealized TPCs as cornerstones in climate change research.
Background

The use (and misuse) of thermal performance curves

Studies that utilize Thermal Performance Curves (TPCs) show that individuals and populations have a multitude of responses to changing temperatures. These responses range from the production of heat shock proteins (Ketola et al., 2004), to changes in dispersal ability (Nowakowski et al., 2020). Thus, TPCs are widely used to describe the response of biological processes to temperature in order to assess thermal plasticity and adaptation (Schulte et al., 2011). Furthermore, this dependence of organisms to temperature has been used to make predictions about where we will find certain species as climate change progresses (Sinclair et al., 2016). Experimental evidence shows that TPCs often take the same general unimodal shape (often with a left skew) across the tree of life (Angilletta, 2009; Schulte et al., 2011): As temperature increases, vital rates increase, reach an optimum and decrease (Huey & Kingsolver, 1989). However, TPC optimum height, width, and shape can be altered by factors including species interactions, evolution and plasticity (Chevin et al., 2013).

Researchers have estimated individual and population fitness using TPCs to integrate across the environment, as TPCs underlie the climate envelope approach (Pearson & Dawson, 2003). Thus they utilize the TPC and the corresponding environmental temperatures to derive a predictive result of where the species will occur (e.g. Deutsch et al., 2008; Tewksbury et al., 2008). To do this they use presence-absence data to solve for a version of the “realized niche”, or the subset of the fundamental niche that species
actually exist in (Wiens et al., 2009). Laboratory studies that produce TPCs for predictive use create what would be close to a fundamental temperature niche, as they do not incorporate species interactions prior to the matching up a species temperature niche and the environment. To further increase the disconnect between laboratory and field derived TPCs, in the laboratory constant thermal environments are used, and this can cause discrepancies when projecting into natural environments that vary diurnally or seasonally (Khelifa et al., 2019). Thus, neither of these approaches use TPCs that can produce an accurate depiction of where species can occur once one takes into account species interactions.

Thus there is a fundamental disconnect between the two TPC approaches, given that species interactions are a major component of the first, and a real challenge is to integrate these two approaches.

Consumer resource models with temperature variation

Consumer resource interactions are the underlying basis of every community. Thus, how temperature change alters these interactions is of great interest, and studies show that there are varying impacts. A multitude of studies show that warming decreases consumer persistence (Huey & Kingsolver, 2019; O’Connor et al., 2011; Wolfshaar et al., 2008), but the assumptions made in these models vary. The traditional TPC used for consumer resource systems typically only consider direct dynamic temperature effects on the consumer, with resources at constant temperatures. Thus here, the traditional Hutchinsonian niche axes for the consumer would appear as two independent axes,
temperature on one, and resource biomass on the other. Moreover, a historical mismatch between theoretical models incorporating TPCs and field data has been prominent (Angilletta, 2009), and is likely in part due to models neglecting species interactions (Chown et al., 2010). Thus although useful, knowing a TPC is not enough to accurately predict species response to changing temperature, because along with climate change comes other interacting changes, importantly changes in species interactions including consumer response to resource availability.

Both field and theoretical work (Brett, 1971; Huey & Kingsolver, 2019) have found that lower resource availability can alter the temperature optimum as well as thermal limits of species. (Huey & Kingsolver, 2019) showed that a reduction in resource availability in concert with warming temperatures could exacerbate the detrimental effects of warming and coined the term ‘metabolic meltdown’ to describe this effect. Thus, this work predicts a compounding effect of temperature increase on consumers due to resource scarcity. There are many reasons to suspect that resource densities might decline as a consequence of warming (e.g. warming temperature decreased Northern Pike prey (Artic Char) which prefer colder water temperature (Winfield et al., 2008); warmer winters decrease insulating snow cover in the artic, reducing plant survival and reproduction which are resources for rodent and bear populations among others (Bokhorst et al., 2011); However many alternatives are also likely. In systems where a consumer and its resources are coupled by a strong interaction, they become dynamically linked. In this case, the co-dependence of consumer and resource densities
can provide additional constraints on the realm of possibilities and better guide our understanding of the potential for metabolic meltdown.

Issues of the intrinsic growth rate and carrying capacity in consumer resource models

Much of the early theoretical work addressing temperature change and population viability takes a simplistic view, where temperature change maps linearly onto a biological parameter (e.g. intrinsic growth rate ($r$), carrying capacity ($K$)) (Vasseur, 2020). Thus the metabolic theory of ecology has led some to develop dynamic modeling attempting to illustrate how temperature alters population dynamics. (Gillooly et al., 2001; Vasseur, 2020), but this understanding is still in its infancy. Here the effects of temperature are scaled by the Arrhenius relationship (a formula for the temperature dependence of reaction rates), and there is an approximately exponential increase or decrease in biological rates across biologically relevant temperatures. This provides a useful framework to compare species at a community level, but is not necessary useful to estimate the biological rates of individuals or populations (e.g. Eppley, 1972). At a species level, the relationship between biological rates and temperature have been more successfully shown using skewed unimodal curves (Angilletta, 2009). Still, there are no studies incorporating unimodal responses in complex food web models (Vasseur, 2020). Thus, the scale (e.g. individual, population, community) at which we are analyzing the effect of temperature determines the utility of previous thermal frameworks.

Nonetheless, at all scales of biological organization, the non-linear effect of temperature often produces non-intuitive variation in population dynamics. This is in part due to the
co-dependence of many biological parameters on temperature. Here we focus on a common codependence that has slowed progress in our ability to accurately predict temperature dependence, the relationship between the intrinsic growth rate ($r$), and the carrying capacity ($K$). It is clear that temperature can have a varied effect on $r$ and $K$. When considering the role of density dependence, in order to make realistic predictions of how populations respond to temperature change it is thus vital to utilize frameworks that incorporate $r$-$K$ codependency.

Metabolic theory has demonstrated that warming leads to an increase in most vital rates (Gillooly et al. 2001; Brown et al. 2005) and the resultant effects at the population and community level are the consequence of differences among these rates. Vasseur and McCann (2005) suggested that the biomass of both consumers and resources will decline at warmer temperatures when consumers’ vital rates increase more rapidly with warming than those of their resources. Experimental work has confirmed this idea, finding that warming can lead to an increase in consumer (top-down) control on resources while also reducing the total biomass of zooplankton and algae in experimental mesocosms (O’Connor et al., 2009). Notably, O’Connor et al. (2009) only found an effect of warming in the presence of nutrient enrichment, suggesting that resource limitation may play a key role in mitigating the response of communities to warming. Unfortunately, theory has contributed little to resolving the effects of temperature on community properties and dynamics, due mainly to the lack of synthesis about the effects of temperature on the resource carrying capacity ($K$; as
discussed later). Since $K$ controls the equilibrium abundance of basal resources in many theoretical frameworks, it has a strong impact over the potential effects of warming. That said, (Dell et al., 2014b) showed that this condition could be violated if the consumer attack rate is influenced by the resource response to temperature. Furthermore, studies have suggested that warming can alter functional responses in consumer resource systems (Mohaghegh et al., 2001; Wang & Ferro, 1998). Thus, we not only must take a dynamic view of how temperature interacts with resource availability, but also how we account for $K$ and $r$ co-dependencies.

Using theoretical models, (Amarasekare, 2015) similarly found that the consumer’s ability to persist is influenced by the response of the resource to temperature, and unlike most previous models, they did not make the assumption that resource and consumer traits change independently or monotonically with temperature. Unimodal responses to temperature are demonstrated in a wide array of studies, and are thus important to utilize in our dynamic models (Dell et al., 2011).

Thermal asymmetry in community dynamics

When incorporating unimodal temperature response curves in consumer resource models, new challenges arise with $K$, as we begin to get what is termed ‘thermal asymmetry’. This occurs when the temperature response of one species is different from the other (Dell et al., 2014). This has been researched by invoking differences in the species temperature optimum, the rate of vital rate change in response to
temperature, and/or a difference in overall magnitude of response to temperature (Dell et al., 2014; Kordas et al., 2011; Pörtner & Farrell, 2008). This asymmetry can alter how the two (or more) species interact, and thus alter the community response to temperature. This means that if we don’t incorporate the interactions between temperature, each species, and then the species together, our understanding of equilibrium biomass, \( K \), and \( r \) will be flawed.

Thermal asymmetry is currently common in nature, and will likely be ubiquitous in natural systems as the climate changes, and new species come into contact (Dell et al., 2014). For example, we may see climate warming altering the phenology of prey reproduction, leading to a mismatch with the predator reproduction that optimizes predation (Durant et al., 2019). If a consumer and resource responded to temperature change in the same way, we would expect an increase or decrease in the rate of interaction as temperature changes (until thermal physiological limits are reached). Thus, the outcome of dynamics such as equilibrium density and coexistence would not change with temperature. However, if asymmetries in how the two species respond to temperature exist, this prediction may not hold (Dell et al., 2014; Rall et al., 2010; Sanford, 1999). For example, (Harley, 2011) showed that predator (sea star) increase due to temperature led to a significant decrease of their sessile prey (mussels). This is because the thermal response slope of the prey is much steeper than the predator, so as temperature changes, the prey is depressed, and so the predator and prey do not shift in unison with temperature change. Thus it is clear that use of TPCs to make
predictions lacking this insight are flawed. Specifically, here we focus on the case where asymmetry is brought about by interacting species having a different temperature optimum, or temperature at which their biomass is optimized (e.g. Kordas et al., 2011; Pörtner et al., 2006).

Model development and analysis

Modeling the temperature-dependence of consumer populations

We begin our analysis by focusing on the dynamic equation representing the per-capita rate of population growth of an ectothermic consumer and the temperature dependence of its constituent rates. The per-capita rate of change within a consumer population \( C \) can be described by the difference between gains from consumed biomass and losses due to respiration, with the effects of temperature \( T \) embedded in two vital rates (Vasseur & McCann, 2005),

\[
\frac{dC}{C dt} = (1 - \delta) f (R, T) - m(T) \tag{1}
\]

Here \( 1 - \delta \) describes the fraction of consumed biomass that is assimilated, \( f (R, T) \) is the functional response and \( m \) represents the rate of respiration. It has been well established that both the functional response and the respiration rate \( m \) respond to changes in temperature \( T \) and a variety of functional forms have been considered. The effect of temperature on \( m \) is well described by the metabolic theory of ecology (Brown et al., 2004) and has been well established (Ehnes et al., 2011). As temperature
increases (to an upper boundary), so do reactions, meaning the kinetic energy is higher, thus changing the speed of cellular respiration.

The functional response provides a way to conceptualize a trophic interaction, describing how per capita prey consumption rate of a predator changes as a function of prey density (Solomon, 1949). All three of the Holling-type functional responses have been demonstrated to respond to temperature (Brett, 1971; Daugaard et al., 2019; Dell et al., 2014; Englund et al., 2011; Gresens et al., 1982; Laverty et al., 2017; South & Dick, 2017; Uszko et al., 2017). The most commonly used form, and the form we investigate, Type II, represents a hyperbolic increase of intake rate and food density. For this functional response, attack rate and handling time have been shown to exhibit a hump-shaped relationship with temperature (Englund et al., 2011). Henceforth we use a Type II functional response:

\[
    f(R, T) = I_{max}(T) \cdot \frac{R}{R + R_0}
\]

(2)

We assume a positive exponential relationship between \( I_{max}(T) \) and temperature, but that any scaling relationship between \( R_0 \) and temperature is negligible, meaning that \( R_0 \) is essentially invariant of temperature (for further discussion see (Vasseur & McCann, 2005). This form of the functional response is analogous to the Holling type II, where \( I_{max} \) is the inverse of handling time. Attack rate and handling time show inverse sensitivity (hump-shaped) to temperature. Thus since attack rate and handling time have inverse scaling, the product of them has no scaling.
Furthermore, given that it has been shown that attack rate increases and handling decreases with temperature increase, (Vasseur & McCann, 2005) assumed that these followed metabolic scaling laws and applied the idea using a macroecological perspective to describe equilibrium biomass across a temperature gradient. This model scaled $r$, $I_{\text{max}}$ and $m$, where $I_{\text{max}}$ is the rate of ingestion under resource saturated conditions (equal to $h^{-1}$). However, this doesn’t apply well to individual populations which are known to exhibit unimodal responses in response to temperature.

We arrive at the following relationships for describing the maximum feasible metabolizable energy, otherwise known as the maximum uptake ability of the consumer. This is an upper bound describing what is biologically possible:

$$I_{\text{max}}(T) = e^{-(T-T_{\text{opt}})^2/\beta}$$

(3)

We describe the other component of the functional response, the respiration rate of individuals in response to temperature change as:

$$m(T) = m_a e^{mbT} + m_c$$

(4)

The shape of these temperature dependencies reflect simple conceptual, rather than mechanistic, representations. Notably, we use a symmetric gaussian function to
describe the temperature dependence of consumption, with breath parameter $\beta$ and modal value at $T_{opt}$. We use an exponential model of the respiration rate rather than the Boltzmann-Arrhenius model, as they are close in shape, but the exponential is much reduced in complexity allowing us to maintain model tractability. See (Amarasekare & Savage, 2012) for a more complete and biologically justified thermal dependence of these parameters.

By setting $m_a$, $m_b$ and $m_c > 0$, the per-capita growth rate $\frac{dc}{cdt}$ (Equation 1) is negative at the extremes of temperature, and provided that $(1 - \delta) I_{\text{max}}(T)$ exceeds $m(T)$ for some value of $T$, produces an asymmetric unimodal function that represents a population’s thermal performance curve (Figure 1). These are not the only assumptions that can be used to generate TPCs of this shape-this result also arises through differencing the two appropriately parameterized exponential functions (Amarasekare & Savage, 2012).

The curves depicted in Figure 1b (given by Equation 1) are equivalent to empirically described TPCs measured at the population level (Deutsch et al., 2008; Huey & Kingsolver, 1989). These studies typically measure the density-independent (intrinsic) growth rate of population growth by ensuring a non-limiting supply of resources and holding temperature constant over many generations. While this works well for organisms with fast generation times, physiological measures of thermal performance are commonly used for slower-growing organisms (Angilletta, 2009; Khelifa et al., 2019).
Experimental evidence shows that TPCs often take the same unimodal, left-skewed shape across the tree of life (Angilletta, 2009; Huey & Kingsolver, 1989; Schulte et al., 2011). The lower temperature at which the curve is equal to 0 is $T_{\text{min}}$ and the upper is $T_{\text{max}}$ and the difference between the two defines the thermal breadth. For measurements of the TPC based on the intrinsic growth rate, the range of temperatures between $T_{\text{min}}$ and $T_{\text{max}}$ defines the Hutchinsonian niche (Holt, 2009).

We investigate the role of resource density on the thermal performance of a consumer by incorporating the complete functional response into this relationship. The relationships shown in Figure 1 assume that resource densities are saturating, i.e. $R \rightarrow \infty$; however, at non-saturating resource densities $R/(R_0 + R)$ is less than 1, resulting in scalar reduction in the functional response (Equation 2). This scaling can have important effects on the thermal performance curve (Equation 1) due to the differencing of the two non-linear functions describing consumption and respiration. (Huey & Kingsolver, 2019) described this role of resource density on thermal performance as it related to empirical data of a salmon system from (Brett, 1971). They explore the combined effect of climate change and food level on mean net energy gain in a constant thermal environment. They find that reduced food intake reduces both maximum growth as well as $T_{\text{opt}}$ (metabolic meltdown), qualitatively coinciding with Brett’s experiments. Figure 2 shows this outcome using the model formulation described above (Equations 1-4). It is also noteworthy that the assimilation fraction $\delta$ has a similar effect; assuming that the assimilation efficiency is not temperature sensitive (there is experimental evidence of
this being the case: (Alexander et al., 2012; Klepsatel et al., 2019; Xu & Ji, 2006), but see: (Krishnan & Chockalingam, 1988; Kukal & Dawson, 1989), increasing delta will result in a TPC that is scaled downward with a smaller thermal range $(T_{\text{max}} - T_{\text{min}})$.

Kingsolver and Huey (2019) suggested a meltdown effect could occur if increasing temperatures occurred in concert with reductions in resource quantity – since the latter move both $T_{\text{opt}}$ and $T_{\text{max}}$ to lower temperatures. It is of note that while $T_{\text{opt}}$ is a curved function of resource density, the envelope that is traced by $T_{\text{min}}$ and $T_{\text{max}}$ is symmetric. This means that, in our model, consumers can most effectively exploit resources at the temperature that is midway between $T_{\text{min}}$ and $T_{\text{max}}$ under resource saturated conditions. If we use the language of $R^*$ (Tilman, 1977), it means that their $R^*$ is lowest at the temperature midway between $T_{\text{min}}$ and $T_{\text{max}}$, not at $T_{\text{opt}}$.

(Huey & Kingsolver, 2019) is an important advance in our understanding of the role of resource limitation, but this framework lacks the ability to analyze dynamic temperatures. In many systems the consumption of resources generates a dynamic response – and thus it is reasonable to assume that resources will not be fixed across temperatures, but will respond to the increasing or decreasing pressure of consumption, and to the direct effects of temperature on resource density. In nature we see both direct and indirect effects of temperature such as this. For example, temperature has been shown to increase the tadpole growth of a gape-limited predator, who thereby alter predator prey interactions through changing prey size (Anderson et al., 2011).
accommodating both direct and indirect effects of temperature, we take (Huey &
Kingsolver, 2019) further to investigate the interplay between resource scarcity and
temperature increase. We do so by incorporating dynamic temperatures and dynamic
resource availabilities into our models. Because this allows us to study feedbacks caused
by direct and interact effects of temperature, we come closer to being able to predict
the effects of climate change.

Below we couple the consumption framework described above to two different models
of resource dynamics to consider how the dynamic interplay between resources and
consumers determines a consumer’s realized TPC. We describe first a model were
resources are supplied in a chemostat (Weston & Yang, 1969), with supply
concentrations and flow that are not sensitive to temperature. This model allows us to
investigate the dynamic consequences of resource supply on consumer performance
and equilibrium. In our second model we assume a biotic resource growing logistically
and with its own temperature-sensitivity. Here we investigate how both the dynamic
interplay of resource supply and the direct and indirect impacts of temperature impact
consumer performance and equilibrium dynamics. An important part of this is the
asymmetry between consumer and resource responses to temperature (Betini et al.,
2019).

Dynamic Consumer-Resource models
Model 1: Chemostat Model

We begin our analysis of temperature-dependent consumer-resource dynamics using a chemostat model of resource supply, where resources are assumed to be non-living nutrients. Here resources are provided at an inflow density $S$ and flow rate $D$ and neither parameter is sensitive to temperature. Combined with the resource functional response (Equation 2), the equation for resource dynamics is given by:

$$R'(t) = D[S - R(t)] - f(R,T)C(t)$$  \hspace{1cm} (5)

Together, with Equations 1-4 this generates an ordinary differential equation system that exhibits two possible equilibria solutions ($\xi^{R,C}$) corresponding to a resource only equilibrium ($\xi^{+,0}$) and a mixed consumer-resource equilibrium ($\xi^{+,+}$). These equilibrium solutions and their stability can be solved analytically; we provide these in appendix A1. For this model, one of the two possible equilibria is always stable (except at the transcritical bifurcation points).

When the combination of the resource supply concentration ($S$) and temperature ($T'$) fall outside the range allowing positive consumer growth (the shaded envelope defined in Figure 2b) the resource-only equilibrium is stable and is unchanged by temperature (Figure 3). This occurs at both low and high temperatures. At temperatures where the resource supply combination and temperature permit consumer growth, resources are consumed to an equilibrium concentration at which the per-capita rate of consumer
growth, \( \frac{dc}{cdt} \), is equal to zero. This is the curve tracing \( T_{min} \) and \( T_{max} \) in Figure 2b and is shown again by the resource equilibrium in Figure 3.

The equilibrium dynamic for the consumer population is an asymmetric unimodal function which has a skew that is opposite the TPC (Figure 1), peaking at values nearer to \( T_{min} \) than \( T_{max} \). An important contributor to this difference in skew and location of the optima is the greater rate of consumer biomass turnover occurring at warmer temperatures (Figure 4). Turnover, measured as production/biomass is a U-shaped function with asymptotes at \( T_{min} \) and \( T_{max} \) (due to the fact that biomass \( \to 0 \)). Turnover is lowest at temperatures near \( T_{min} \) and then increases approximately exponentially with warming. With increases in turnover, more biomass is lost to conversion inefficiency. Coupled with higher rates of metabolism at warmer temperatures, this leads to a peak in the equilibrium consumer biomass peaks at temperatures below \( T_{opt} \) and gradual declines in equilibrium consumer biomass with warming.

Model 2: Consumer-resource model with logistic growth

The logistic model of resource dynamics has been a mainstay for the study of population and community dynamics (e.g. Rosenzweig & MacArthur, 1963). However, there has been considerable debate about how to implement a temperature-dependent version of the model due to the lack of empirical data on the temperature sensitivity of \( K \) (see Vasseur, 2020 for a review). Early attempts assumed that \( K \) was invariant (Vasseur &
McCann, 2005) or that, due to the increased metabolic requirements of individuals in warmer temperatures, that $K$ would decline with warming (Bernhardt et al., 2018; Savage et al., 2004). An empirical synthesis on the effects of temperature on model parameters found only four studies measuring the effect on $K$, and these unequivocally supported a decrease with warming – albeit over a restricted range of ‘biologically relevant’ temperatures (Fussmann et al., 2014).

More recent work has stressed the non-linear and often unimodal shapes of temperature dependence on biological rates as reason to investigate the same functional dependence for $K$. Since $K$ is the result of the joint expression of many biotic and abiotic processes, the manner in which these processes align can lead to a variety of different functional forms over the biologically relevant range (Lemoine, 2019; Uszko et al., 2017). As we endeavor to describe temperature’s effect at the scale of communities, it is important to consider a broader range of temperatures, including those that could lead to negative rates of population growth. In fact, Vasseur (2020) recently demonstrated that doing so elucidates an important constraint on the functional form of $K$.

Thermal performance, as measured by the per-capita rate of population growth are well-defined for both positive and negative values and there has been some debate on how best to incorporate these negative values in forecasting risk (Woods et al., 2018). From the perspective of dynamic models, negative rates of population growth have a
clear interpretation. However their incorporation into the logistic model is challenged by the fact that a transition to negative values leads to an inversion of the effect of density dependence. To see this, consider the sign change of the second term in \( r \left(1 - \frac{N}{K}\right) \) when \( r \) transitions from positive to negative values. The effect of this sign change is that density dependence contributes positively to population growth during periods of decline, when in fact, density dependence should continue to have a negative effect.

(Mallet, 2012) suggested an alternative framework for the logistic model (the \( r - \alpha \) model) to cope with the issue of negative population growth; however, Vasseur (2020) showed that it is unnecessary to switch to an alternative framework when the appropriate constraints are considered. Vasseur (2020) demonstrated that when temperature or another environmental variable causes \( r \) to decline from positive to negative value, \( K' \) must also transition from positive to negative value. While it may seem illogical to prescribe a negative carrying capacity, it is important to note that negative carrying capacities never constitute stable equilibrium points in the Logistic model, but instead accurately guide the population dynamics to extinction during periods of stress. The observation that \( r \) and \( K' \) must share the same intercepts, combined with our confidence in the temperature dependence of \( r \), allows us to rigorously accept that \( K' \) must be, in its simplest form, a unimodal function of temperature that is positive across the domain \( T_{min} \) to \( T_{max} \). The extent to which \( K' \) can differ from \( r \) has been explored only to a limited extent (see Vasseur 2020).
So, landing on a set of constraints for $r$ and $K$, we model the dynamics of consumers and resources, where resources grow logistically as:

$$\frac{dR}{dt} = r(T)R(t) \left[ 1 - \frac{R(t)}{K(T)} \right] - f(R, T)C(T)$$

(6)

With the temperature-dependent intrinsic rate of resource growth given by the difference between a symmetric unimodal “growth” function and an exponentially increasing “maintenance” function similar to those used in Equations 3 and 4:

$$r(T) = b_{max}e^{-(T - T_{opt} - \delta_T)^2/\beta} - (d_0 + d_1 e^{d_2T})$$

(7)

Here, we use the same optimum, $T_{opt}$, as specified for the consumer’s ingestion rate (Equation 3); however, we add the parameter $\delta_T$ to represent the potential for thermal asymmetry among the resource and consumer.

The temperature dependent carrying capacity $K(T)$ is given by:

$$K(T) = \frac{r(T)}{\gamma}$$

(8)
Where $\gamma$ represents the additive effects of negative density-dependence on the birth and death of resources. Here we do not assume temperature effects on the strength of density-dependence; however, (Vasseur, 2020) showed that if warming strengthens density-dependence $K(T)$ peaks at a lower temperature than $r(T)$ (similar to the patterns shown for the consumer in the chemostat model).

This model has three possible equilibrium states: a trivial equilibrium ($\xi^{0,0}$), a resource-only equilibrium ($\xi^{+,0}$), and a mixed equilibrium ($\xi^{+,+}$). Analytical solutions for these equilibria and their stability are provided in Appendix A2. In contrast to the chemostat model, this model can also produce a mixed equilibrium point which is unstable, resulting in a stable limit cycle.

Figure 5 shows the dynamics of the model using a sample parameter set for which there is no thermal asymmetry among the resource and consumer. As temperature increases from low values, the system transitions from the trivial to the resource-only equilibrium that tracks $K(T)$ until the combination of temperature and resource density permit consumer growth. Here the community transitions to the stable mixed equilibrium but with further warming undergoes a Hopf bifurcation to limit cycles. As the system approaches upper limiting temperatures, this sequence of events is reversed until neither the consumer or resource can maintain growth.
We see in Figure 5, as consumers consume and thereby reduce a resource, there is adaptive incentive for that resource to grow successfully at lower temperatures where the consumer uptake rate is lower. Prior research assumes that resource densities are fixed (Huey & Kingsolver, 2019). But clearly, consumer demands change with temperature (e.g. (West & Post, 2016)) and that puts a changing pressure on the resource. Thus, there is a clear interplay between the optimal temperatures of consumer uptake rate, and the optimal temperature for resource biomass. We can also think about this in the case of escape abilities of the resource. It has been previously hypothesized that the ability to avoid predation across a wide range of temperature is more important to survival than any single predation attempt of a consumer, that is, that there is stronger selection on avoiding predators than predator success (Dell et al., 2011). Thus, we emphasize the importance of top down effects and how they play into questions of how TPCs are limited resource availability. Note that the parameters for this example have a slightly wider thermal performance for the resource than the consumer (under saturating conditions). Since resource density and temperature jointly limit growth, the effective or realized thermal performance of a consumer will always be narrower than its resource.

For any combination of resources and consumers governed by this model, for which a mixed equilibrium is possible, the pattern of transitions across the temperature axis is consistent. The only exception to this is the appearance/extent of cycles, which are dampened or do not emerge when consumers are parameterized such that they have a
more prudent impact on their resources. This can be envisioned as a relative reduction in $R_0$; we show an example of this in the Appendix (Figure A2).

*Logistic growth of resources and thermal asymmetry*

We assess the importance of thermal asymmetry on the thermal performance and dynamics of the consumer by adjusting the optimum ($T_{opt}$) of the resource’s “growth” function relative to the optimum for consumer ingestion ($\delta_T$). This parameter shifts both the $r(T)$ and $K(T)$ functions in accordance with Equations 7 and 8 and therefore moves the envelope of temperatures over which the resource can achieve a positive equilibrium density (Figure 6). This has important effects on the consumer’s upper and lower thermal tolerances for growth. If the resource’s thermal performance shifts to warmer temperatures, the consumer’s $T_{min}$ increases to reflect the effect of resource limitation at low temperatures. Likewise if the resource’s thermal performance shifts to colder temperatures, the consumer’s $T_{max}$ also decreases.

The effects that dynamic resources (here growinglogistically) have on the operational thermal performance curve of the consumer are shown in Figure 7. Where the consumer’s growth isocline nears its asymptotes on the temperature axis, the effect of temperature on consumer growth is directly constrained by the consumer’s thermal traits. In contrast, if resource densities lead to intersections in the flatter regions of the consumer’s isocline, consumer growth is indirectly constrained by the resource’s thermal traits. As we show in Figure 6, it is very possible for the upper and lower
temperature bounds to be constrained differently (e.g., by the direct effects of
temperature, or by the indirect effects of temperature on resource density). The shapes
of the consumer’s thermal performance under these scenarios can be visualized by
plotting the intersection of equilibrium resource densities in the absence of
consumption (here $K(T)$) against the curve depicting the consumer’s break-even
resource density as a function of temperature. In the cases where $T_{min}$ and $T_{max}$ are
limited differently, the operational TPCs (Figure 7b) can exhibit clear changes in shape-
from the classic skewed unimodal to those more closely representing an inverted
parabola.

Discussion

Hutchinson’s niche and thermal performance curves

Hutchinson’s niche concept can be formally conceptualized as the set of all
environmental states at which the low-density rate of birth exceeds the rate of death, or
more simply, $r \geq 0$ (Holt, 2009). While there is great potential for various
environmental factors to interact in the determination of $r$ (e.g. water availability
(Colchero et al., 2009) and temperature (Bosque et al., 2001), few factors can be linked
by mechanistic processes. Moreover, many environmental factors may be intrinsically
nested such that changes in one factor can influence others, thereby generating both
direct and indirect effects on $r$. Temperature is one such factor that can have direct
impacts on $r$ and indirect impacts through a myriad of other environmental factors,
including the density of resources. We explore two cases where temperature and
resource density interact; in both cases resources respond dynamically to changes in our focal (consumer) population, but vary in their assumption about whether resource dynamics exclude or include the direct impact of temperature.

Metabolic meltdown is unlikely when consumers are dynamically coupled to their resource

Our results suggest that metabolic meltdown is an unlikely scenario for consumers that have strong dynamic coupling to their resources. During metabolic meltdown (Huey & Kingsolver, 2019), declining resource densities reduce $T_{\text{max}}$ while warming occurs, increasing the likelihood of population decline and extinction. In our models, where the dynamics of resources are tightly coupled to those of the consumer, there is always a relaxation of top-down control as the consumer nears the limits of its thermal niche ($T_{\text{max}}$ or $T_{\text{min}}$) which generally allows equilibrium resource densities to increase. For the chemostat model of resource dynamics, metabolic meltdown cannot occur given that resources are not directly impacted by temperature; any temperature-driven decline in consumer density will result in an increase in resource density. In the case where resource dynamics are governed by logistic growth, there are a limited number of scenarios where metabolic meltdown could occur. Meltdown requires that both of the traces in Figure 7a are descending functions of temperature at $T_{\text{max}}$. This is likely to occur when consumers have TPCs optimized at warmer temperatures than their resources.
Our model assumes a strong coupling of consumer and resource densities; however few systems are isolated from the effects of additional interaction with other species. In instances where other factors beyond temperature and the focal consumer impact resource densities, metabolic meltdown may be far more likely than we predict. For example, when one or more other competing consumers share in their resource demands, resource densities may remain static or decrease as our focal consumer nears its $T_{max}$. This may be particularly prevalent in cases where climate invaders or invasive species are better suited to warmer conditions. For example, temperature change has been shown to reduce vertical niche segregation in deep cold lakes of species including whitefish and vendace (Gjelland et al., 2007). These fish both feed on zooplankton, and thus the areas of overlap due to temperature increase will likely lead to a depletion in zooplankton, even though some zooplankton have been shown to increase given increasing temperature (Carter & Schindler, 2012; Rolls et al., 2017).

The thermal performance and equilibrium biomass don’t always correspond

Our models demonstrate that within the thermal niche of a consumer, performance (as measured by the TPC) and equilibrium biomass differ distinctly. This implies that estimates of thermal stress and extinction risk based solely upon the TPC may be problematic. For the chemostat model, equilibrium biomass peaks at lower temperatures relative to the peak in performance due to the increase in turnover at warmer temperatures. While the results of the logistic-resource model are more complex due to the appearance of limit cycles, the disconnect between performance
and extinction risk is likely still quite large. Given our large reliance on thermal 
performance curves as a predictor for stress in warming and increasingly variable 
environments (Vasseur et al. 2014; Deutsch et al. 2008; Tewksbury et al. 2008; Sinclair 
et al. 2016), more work is needed to better understand how changes in biomass due to 
environmental and demographic stochasticity, complement the information provided by 
TPCs.

Oscillations are an important feature of strongly-interacting pairs of consumers and 
resources and our model that incorporates logistic population growth demonstrates 
cycling over a broad range of parameter space. These results are consistent with 
previous modeling and experimental work by (Uszko et al., 2017) and (Fussmann et al., 
2000) and while these model cycles can be dangerously large in amplitude, natural 
oscillations tend to be more stable (Jensen & Ginzburg, 2005; Roy & Chattopadhyay, 
2007). It is also important to note that a change in parameters (specifically the ratio of 
$R_0/K$ – see Yodzis & Innes, 1992) can greatly reduce their magnitude and the domain 
over which they appear. In this paper our focus is on the dynamics expressed near the 
consumer’s persistence boundaries (transcritical bifurcations) which always take the 
form of a stable equilibrium point. However, where cyclic dynamics exist near to the 
upper critical value $T_{max}$, they may contribute importantly to extinction risk. Further 
experimental work on consumer-resource cycles in warming environments is necessary 
to better understand this phenomenon.
The importance of thermal asymmetry

In our logistic resource model, we assume that $r(T)$ and $K(T)$ have perfect thermal symmetry – which implies that density dependence in the resource population is not affected by temperature (see Vasseur, 2020). Given that the biotic resource populations modeled by the logistic equation are likely themselves limited by a very similar set of constraints that we describe here for consumers, it is likely that density-dependence will be altered by the thermal environment. This would lead to an asymmetry between the optimal values of the $r(T)$ and $K(T)$ functions similar to those which emerge from the models here. Imposing this restriction at the resource level would tend to exacerbate the asymmetry between the maximum of the TPC and of equilibrium biomass at the consumer level.

Asymmetry among the responses of consumers and resources has been a subject of recent interest (Dell et al., 2014b; Smith & Amarasekare, 2018) particularly given that evolutionary responses may be more rapid for some species relative to others. We find that thermal asymmetry between a consumer and its resource can reshape the ‘operational’ TPC, and lead to a compression of the thermal niche by affecting either $T_{min}$ or $T_{max}$. Most notably, if the consumer’s thermal niche is matched to warmer conditions than the resource’s thermal niche, there is a much greater likelihood for metabolic meltdown – even for specialist pairs (Figure 6). We see some trends in the literature of how this asymmetry manifests. In the case of asymmetry in the breadth of the TPC, there is evidence both that prey, or lower trophic level organisms have a lower
$T_{\text{min}}$ (Dell et al., 2011), which they deem to be because avoiding predation across a range of temperatures is more critical to survival than individual attempts of consumers to catch food, we also see this incentive in Figure 5. When it comes to $T_{\text{max}}$, some studies show that prey has a higher $T_{\text{max}}$ than predators (Petchey et al., 1999; Sentis et al., 2013; Voigt et al., 2003), while some show that the consumer, or higher trophic levels have the higher $T_{\text{max}}$ (Franken et al., 2018). Furthermore, we could extend this to host-pathogen interactions, where it has been shown that infection increases with host/parasite thermal tolerance mismatch (Nowakowski et al., 2016). Parasites tend to have wider tolerance than hosts, so hosts become more at risk when temperatures shift (Cohen et al., 2017). Infection has also been shown to decrease $T_{\text{max}}$ (Greenspan et al., 2017). When it comes to asymmetry in the TPC optimum as we address with our model, there is not a clear pattern of thermal asymmetry of the optimum of different trophic groups, as in cases sometimes the predators might have a higher optimum and sometimes the prey might (Dell et al., 2011). But the variation in $T_{\text{max}}$ indicate that given enough data on $T_{\text{opt}}$ we might find general predictions.

Conclusion

It is of growing importance to have a mechanistic understanding of how communities respond to environmental change. We focus on temperature as not only are the majority of earth’s diversity ectotherms, but it is clear that temperature change has a large impact on a variety of life on earth. Drawing from niche theory we produce a novel ‘operational TPC’ and assess how it changes with varying thermal asymmetry of
consumers and their resources. By characterizing species response to temperature in
terms of deviation from their optimum temperature, as well as the feedback of
temperature response between a consumer and resource, we provide a predictive
framework for species coexistence that can be generalized and can incorporate the
added complexity of more species. We thus establish the basis for a mechanistic
understanding of how communities might respond to temperature change. There is a
lack of understanding of equilibrium species abundance across temperature and thus
experimental work informed by theoretical work such as this is warranted as climate
change leads us to new temperature
Chapter 3 Figures

Figure 1. a: Changes in the $I_{max}$ (blue) and $m$ (yellow) across temperature. b: changes in $I_{max} - m$ as a function of temperature (green) and for the same function when half of the ingested biomass is not assimilated (orange). The difference among the two non-linear functions in 1a results in the skewed unimodal functions in 1b that are typical of thermal performance curves. Here $T_{opt} = 25$, $\beta = 150$, $m_a = 0.01$, $m_b = 0.1$, $m_c = 0.05$, and $\delta = 0.5$. 

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Figure 2. Resource Scarcity decreases optimal temperature for consumer growth. As the density of resources declines, the ingestion rate decreases, leading to changes in the intercepts and optimum of the TPC; the lower threshold temperature ($T_{min}$) and upper threshold temperature ($T_{max}$) converge under resource limitation and at the same time the optimum shifts toward lower temperatures due to the interplay of the non-linear functions governing ingestion and maintenance (panel a). In panel b the filled area represents combinations of temperature and resource density that generate a positive per-capita growth rate and the black line represents the zero-growth isocline of the consumer. This isocline can be separated into the lower $T_{min}$ and upper $T_{max}$ critical values of the thermal performance curves in panel a. The optimum temperature for
growth at each resource density is given by the dotted line in panel b. Parameters are as given in Figure 1.
Figure 3. Equilibrium densities of the consumer-resource dynamic model when resources are supplied by a temperature independent chemostat. Here solid (dotted) lines correspond to stable (unstable) equilibria. Transcritical bifurcations occur where the two equilibrium branches exchange stability (here at approximately 10 and 30.5°C). The u-shaped equilibrium branch for the resource population is the same curve shown in Figure 2b. The equilibrium densities and their stability are analytically solved in Appendix A1. Parameter values are as in Figure 1 and $S = D = 1$. 
Figure 4. Consumer biomass turnover rate for the chemostat-resource model. Turnover is given by the ratio between consumer production and equilibrium biomass. This ratio has vertical asymptotes where the consumer equilibrium reaches is lower and upper critical values. Away from these asymptotes, the turnover rate increases with temperature reflecting an increase in biomass expended for consumer respiration and lost due to consumption.
Figure 5. The dynamics of the consumer and resource when the resource’s dynamics are given by the logistic model with temperature sensitive parameters $r$ and $K$ (Equation 7-8). Stable equilibrium branches are shown as solid lines and unstable branches as dashed lines. The exchange of stability between equilibrium branches ($\xi^i$) occurs at transcritical bifurcations. The coexistence equilibrium ($\xi^3$) loses stability (and regains stability at Hopf bifurcation points which generate limit cycles (with amplitudes shown by the shaded regions). Parameters are: $b_{max} = 1, d_1 = 0.01, d_2 = 0.1, d_3 = 0.05, \gamma = 0.5, R_o = 0.5, \beta = 150, m_a = 0.01, m_b = 0.1, m_c = 0.05, e = 0.5, \delta_T = 0, T_{opt} = 25.$
Figure 6. The effect of thermal asymmetry on the dynamics of consumers and resources.

The shaded areas depict which of the dynamical regimes is the stable outcome for each combination of temperature and thermal asymmetry (positive values shift the resource’s thermal performance to warmer temperatures. In the unshaded area, neither resource nor consumer can persist ($\xi^{0,0}$); in the lightly shaded area only the resource persists ($\xi^{+,0}$); in the next darkest region resources and consumers persist at a stable equilibrium ($\xi^{+,+}$) and in the darkest region resources and consumers persist and exhibit stable limit cycles. These results were generated by numerically solving for the equilibrium conditions.
Figure 7. Panel a shows traces of the resource equilibria across temperature (in the absence of consumers) for the chemostat (blue) and logistic (red) resource models. The manner in which these resource supply curves intersect the consumer growth envelope (shaded region) determines the thermal performance of the consumer population, measured as the maximum per-capita growth rate (panel b and c). For the logistic model, we show two values of thermal asymmetry. As the resource carrying capacity $K(T)$ curve shifts to higher temperatures ($\delta T = 11^\circ C$), $T_{min}$ of the consumer’s TPC changes nearly the same amount; however $T_{max}$, which is constrained by the consumer’s thermal performance, exhibits very little change. Similarly, shifts to lower optimum values show the alternative set of constraints. The equilibrium dynamics for models with $\delta T = 11^\circ C$ and $\delta T = -22^\circ C$ are shown in Appendix A3.
Appendix

Appendix A1

Model 1 Analysis

The consumer-resource model, assuming chemostat resource renewal is given by:

\[
\frac{dC}{dt} = (1 - \delta)f(R, T) \cdot C - m(T) \cdot C
\]

\[
\frac{dR}{dt} = D(S - R) - f(R, T) \cdot C
\]

where

\[
f(R, T) = I_{\text{max}}(T) \cdot \frac{R}{R + R_0}
\]

This model has two equilibrium solutions, and we categorize them based on the presence or absence of the consumer and resource:

Resource only \((\xi^{+,0})\): \(R = S\) and \(C = 0\)

Coexistence \((\xi^{+,+})\): \(R = R_0\left(-1 + \frac{1 - \delta}{(1 - \delta) - I_{\text{max}}(T)^{-1} \cdot m(T)}\right)\) and

\[
C = \frac{(D - D \cdot \delta)((S - S\delta) - I_{\text{max}}(T)^{-1}m(T)(R_0 + S))}{m(T)((1 - \delta) - I_{\text{max}}(T)^{-1}m(T))}
\]
Appendix A2

Model 2 Analysis

The consumer-resource model, assuming Logistic resource renewal is given by:

\[
\frac{dC}{dt} = (1 - \delta) f(R, T) \cdot C - m(T) \cdot C
\]

\[
\frac{dR}{dt} = r(T) R \left( 1 - \frac{R}{K(T)} \right) - f(R, T) \cdot C
\]

where

\[
f(R, T) = I_{max}(T) \cdot \frac{R}{R + R_0}
\]

This model has three equilibrium solutions, and we categorize them based on the presence or absence of the consumer and resource:

Trivial \((\xi^{0,0})\): \(R, C = 0\)

Resource only \((\xi^{+,0})\): \(R = K(T)\) and \(C = 0\)

Coexistence \((\xi^{+,+})\), \(R = \frac{m(T) \cdot R_0}{(1 - \delta) I_{max}(T) - m(T)}\) and

\[C = \left( 1 - \frac{R}{K(T)} \right) \left( \frac{r(T) \cdot (1 - \delta)}{m(T)} \right) R\]
Figure A1. Changes in resilience across temperature for the chemostat model (top panel) and the logistic growth model (bottom panel). Resilience is given on the vertical axis and temperature on the horizontal axis.
a) $R_0 = 0.7$

b) $R_0 = 0.8$

c) $R_0 = 0.9$
Figure A2. The dynamics of the consumer and resource when the resource’s dynamics are given by the logistic model with temperature sensitive parameters $r$ and $K$ (Equation 7-8). Stable equilibrium branches are shown as solid lines and unstable branches as dashed lines. The exchange of stability between equilibrium branches ($\xi^i$) occurs at transcritical bifurcations. The coexistence equilibrium ($\xi^3$) loses stability (and regains) stability at Hopf bifurcation points which generate limit cycles (with amplitudes shown by the shaded regions). Each panel shows a different $R_o$ ranging from $R_o = 0.7$ (top panel) to $R_o = 0.9$ (bottom panel). Parameters are: $b_{max} = 1, d_1 = 0.01, d_2 = 0.1, d_3 = 0.05, \gamma = 0.5, \beta = 150, m_a = 0.01, m_b = 0.1, m_c = 0.05, e = 0.5, \delta_T = 0, T_{opt} = 25$. 
Figure A3. Dynamics of the consumer-resource model with logistic resource dynamics where the optimum for resource growth is shifted to colder (a; $\Delta T = -22$) and warmer (b; $\Delta T = +11$) temperatures. These two scenarios represent situations where consumers exist only within a range of temperatures that generate declines (increases) in resource equilibrium abundance. Panel a shows a scenario where metabolic meltdown would be extremely important. All parameters are as in Figure 5.
Conclusion

Together, this dissertation represents an advance in our understanding of what scenarios might allow populations to undergo evolutionary rescue, and adapt to persist in the face of climate change. I took a multiscale approach, from looking at the effect of environmental change on individuals, to landscapes of individuals. This allowed me to show (1) that the way that environmental change effects individual vital rates in our predictive models makes a significant difference in the ability of the population as a whole to survive environmental change, (2) that the spatial landscape plays a significant and at times complex role in the ability of populations to survive environmental change, and lastly (3) that when species are interacting, it is vital to look at the effect of environmental change on each individually in order to see how the indirect effects of temperature on species interactions play out in a climate change scenario.

The importance of each chapter must be taken together when we consider how species will respond to climate change and attempt to make predictions. Each chapter on its own elucidates important factors that aren’t currently taken into account sufficiently in predictive models, and thus together they have the potential to significantly improve our ability to prioritize what populations may need more or less support and management as their environment changes. Although future work need not take each component into a framework simultaneously, I suggest that they acknowledge the potential role of each component in their results.
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