Summer Internship Project
Report

Modelling the Evolution of ARTs Using a Trait-Based Adaptive Dynamics Approach

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Summer Internship 2025

CERTIFICATE

This is to certify that that **C L Srinivas** has completed his summer internship, spanning a duration of 10 weeks **(from** 22^{nd} **May 2025 to** 1^{st} **August 2025)** under **Dr.Colin T Kremer**, University of Connecticut, Storrs.

Signature of project guide

Acknowledgment

I would like to express my heartfelt gratitude to all those who have supported and guided me throughout the journey of completing this project report. I thank the Indo-US Science and Technology Forum (IUSSTF) and the Khorana Program for Scholars for funding this summer internship. I extend my sincere gratitude to all the IUSSTF staff, UConn administration and UConn Center for International Students and Scholars whose prompt responses and support facilitated a smooth travel and internship experience for me.

I want to thank my project guide, Dr.Colin T Kremer, for his valuable insights and guidance. His expertise and encouragement have been instrumental in the completion of this project.

I would also like to extend my appreciation to my friends, seniors and fellow lab mates who have been a constant source of assistance. Their kindness and willingness to share their knowledge and experience ensured that I had a great time in the lab!

Last but not the least, I would like to acknowledge the collective support of my family, especially my brother, whose support and encouragement have been pivotal in ensuring the successful completion of this project.

Thank You
C L Srinivas

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Modelling Alternative Reproductive Strategies as Evolutionarily Stable Strategies Using Game Theory and Adaptive Dynamics

C L Srinivas

July 25, 2025

Abstract

This report contains a detailed summary of the evolutionary game theory, trait based framework, adaptive dynamics and theoretical evolution literature read and studied by me during the course of the internship. I also worked to extend my master's project; a theoretical model for the evolution of alternative reproductive tactics in *Oecanthus henryi*, by adapting the previous discrete game model into a continuous trait based evolutionary game framework. Most of the literature read and summarized here helped me directly in modeling the evolution of baffling behavior in *O.henryi* using a continuous trait based approach. The first two papers discuss the parallels between trait based adaptive dynamics and evolutionary game theory and present a framework for analysis of the stability properties of evolutionary fixed points using the second order derivatives of invasion fitness with respect to resident strategy and the invading mutant strategy. It introduces the concept of Pairwise Invasibility Plots (PIPs) and a graphical classification of them based on the properties of the evolutionary fixed point (termed evolutionarily singular strategy or singular strategy). The third, book chapter presents a comprehensive review of the different flavors and applications of trait based frameworks, its advantages and caveats. The fourth paper on the temperature response of fitness in ectotherms provides a mathematical framework to partition the fitness effect of temperature into its different life history components using the Euler-Lotka equation. This method can be used to model the fitness affect of baffling propensity through its effects on the life history components of *O.henryi* males. The book chapter "Selection on One Locus" elucidates a simple method for updating allele frequencies in an evolving population where fitness is a function of a single gene with two alleles. This method can be used to update the frequency of traits in the model for the evolution of baffling as an alternative reproductive tactic. Finally, I briefly describe my model, the functions used, assumptions involved and some preliminary analysis.

1 INTRODUCTION

This summer internship report documents the literature reviewed, knowledge gained and skills applied in furthering my model for the evolution of alternative reproductive tactics in tree crickets (*O.henryi*). My previous modeling and analysis attempts targeted at this problem were largely based on the discrete, action-response game described in Hurd 1995. The analysis greatly resembled those done for classical economic games involving cost-benefit considerations (refer here). There were a couple of drawbacks to such an approach. Firstly, the discrete nature of the game could not accurately represent the scope of the actual strategy space available in the real world. Secondly, this approach did not lend itself to model evolution of traits which requires analysis on large timescales based on population level attributes like average lifetime fitness as opposed nightly payoffs. During the initial parts of my internship, I read key papers outlining the connections between evolutionary game theory and trait based adaptive frameworks. This provided an understanding of how to model evolutionary systems using functional trait based models. The crux of which is that the fitness functions are functions of the functional trait value and sometimes (depending on the system) of the frequency of players with a particular trait value. Section 2 encapsulates the summary of all the papers read. The mathematical framework presented in Amarasekare and Savage 2012 was ultimately used to model the effect of baffling (the trait of interest in my model) on the lifetime fitness of calling males. The fitness function derived for my model resembles that obtained by Amarasekare and Savage 2012. The different individual components in the fitness function, viz. the instantaneous birth rate and mortality rate were modeled based on hypothetical functions constructed based on empirically observed data and regressions performed on experimental data points. Non-linear averaging was performed for a component function of the instantaneous birth rate in order to calculate the mean population fitness. Further analysis was done (is being done!) using this mean population fitness.

2 READING

2.1 EVOLUTIONARY GAME THEORY AND ADAPTIVE DYNAMICS OF CONTINUOUS TRAITS (MCGILL AND BROWN 2007)

This review paper primarily concerns itself with the modeling of biological evolution using evolutionarily continuous games where strategies are represented by heritable phenotypic traits. As opposed to classical games, in evolutionary games, the players are allowed to replicate themselves in the next iteration. The magnitude of this replication is a function of the payoff obtained by the player in the previous iteration. Hence, here the notion of payoff is used to represent "fitness" in an evolutionary context. This fitness (or payoff) is a function of the strategy employed by the player, i.e. its "trait value" and the strategy(s) employed by the rest of the population (the co-players), i.e. the trait values of the remaining population of players. The trait dependent nature of the fitness function and the heritability of this trait gives rise to **adaptive dynamics**. The most basic definition of fitness in an evolutionary context is the per capita growth rate, i.e;

$$W(u, U, N) = \frac{1}{N}\frac{dN}{dt} \tag{1}$$

Here, $W(u, U, N)$ denotes the fitness of a player employing strategy u against a population of players all of whom use U at a population size of N. The tri-variate fitness function invites analysis of the changes in fitness as a result of changes in u, U, N and all possible combinations of these variables. The condition for what is popularly considered as an Evolutionarily Stable Strategy (ESS) (by Maynard Smith and Price) can be written as follows;

$$W(u, U^*) < W(U^*, U^*) \tag{2}$$

We can infer from 2, that the strategy U^* is resistant to invasion by any rare mutant u. This ESS strategy U^* can be computed by finding a maxima of the fitness function W such that $u = U = U^*$;

$$\frac{\partial}{\partial u} W(u, U^*) = 0 \tag{3}$$

$$\frac{\partial^2}{\partial u^2} W(u, U^*) < 0 \tag{4}$$

However, invasion resistance (property guaranteed by condition 2) only means that any population starting at U^* can resist invasion by rare mutants, it does not shed any light as to the fate of the system if initialized at say $U^* + \delta$. The following inequality gives the condition for this kind of stability to perturbation/different initial starting point, called **"convergence stability"**.

$$\frac{\partial^2}{\partial u^2} W(u, U) + \frac{\partial^2}{\partial u \partial U} W(u, U) < 0 \tag{5}$$

Note that condition 5 and 4 do not imply/restrict each other. Hence, we can have all 4 possible combinations of convergent stable and invasion resistant fixed points, i.e. convergent stable and invasion resistant (evolutionary end points, ESS), convergent stable but not invasion resistant (evolutionary attractors), invasion resistant but not convergent stable (evolutionary repellers) or non convergent stable and not invasion resistant. Most interesting of these possibilities, are a class of points that are both a fitness minima and convergence stable (evolutionary attractors) called **"branching point"**. As the term suggests, populations branch at these points into two separate species or populations with distinct traits. Figure 1 shows a branching point in action. Branching points are evolutionary attractors at long distances but repellers for populations nearby. Hence, once the population is in the neighborhood of a branching point, it may split into two populations that evolve to occupy distinct nearby fitness peaks.

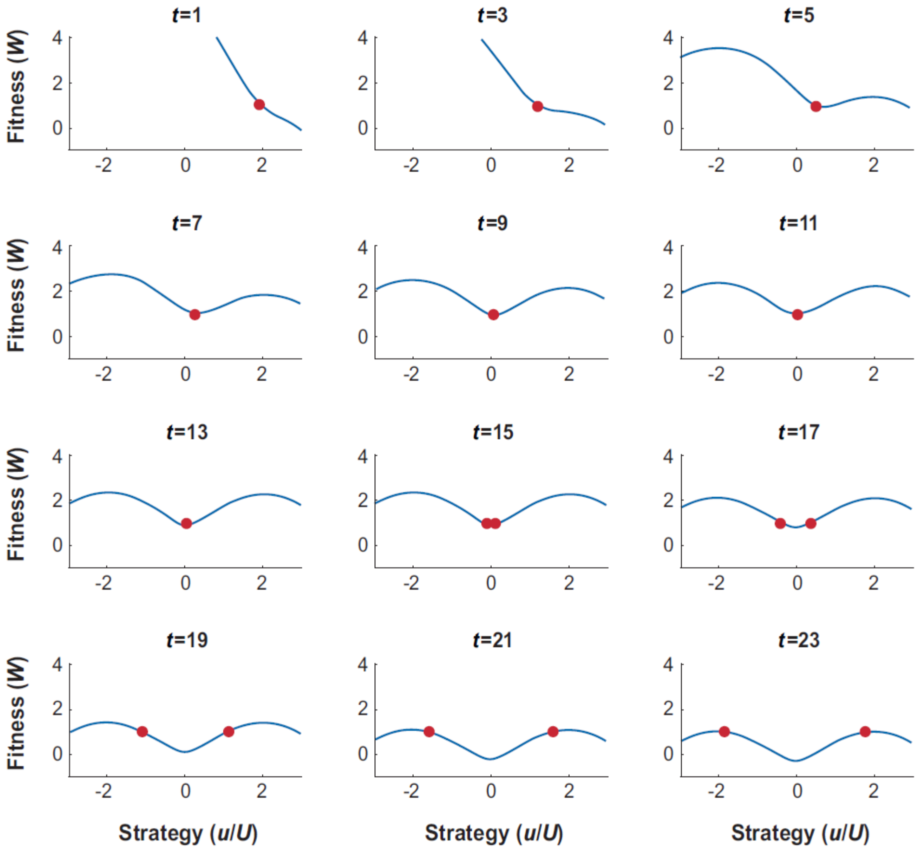


Figure 1: A branching point in action (McGill and Brown 2007).

The fate of the system after passing through a branching point maybe one of the following:

1. After branching, each population moves to a local ESS
2. One or both of the populations moves to another branching point leading to subsequent branchings that can lead to an adaptive radiation.
3. One population moves towards an ESS while the other populations becomes extinct
4. Both populations become extinct

Are such branching points realistic? A major criticism of the concept of such evolutionary branching points has been the assumption of asexual reproduction. In sexually reproducing organisms, recombination and hybridization can cause the initially diverging sub-populations to intermix and lead to offspring with intermediate trait values. This process of homogenization of trait value between the two sub-populations will eventually lead to the population being stuck at the fitness minima hence preventing branching. However, it is conceivable that under certain circumstances, such kind of branching may occur even in sexually reproducing organisms, that is if;

1. There is **assortative mating** based on the trait of interest such that individuals choose to mate with partners who share a similar trait value as themselves. This can lead to inbreeding within the two sub-populations and cause them to move apart from each other even more which further enhances the assortative mating. This cycle eventually leads to separation of the population into two distinct groups.
2. There is a perceivable **marker trait** that is used for sexual selection and is linked to the trait of interest (Eg:- like a green beard effect with respect to altruism). Then assortative mating can occur based on the marker trait.
3. There is spatial separation between the individuals of the two sub-populations as a result of their different trait values. For example difference in trait value may cause certain individuals to occupy slightly different habitats, host plants etc. This spatial separation can cause assortative mating as a consequence of proximity.

Hitherto, we have discussed only monomorphic ESS, as suggested by our analysis of branching points, there maybe a coalition of two or more strategies that are resistant to further invasion by mutants. We can characterize such scenarios by performing a straightforward extension of the notation used for single strategy ESS. The population dynamics can be written as;

$$\frac{1}{N_i}\frac{dN_i}{dt} = W(u, U_1, U_2, ..., U_n, N_1, N_2, ...N_n) \tag{6}$$
$$= W(u, \mathbf{U}, \mathbf{N})$$

for $u = U_i$, where $\mathbf{U}$ and $\mathbf{N}$ are n length vectors representing the resident strategies and their corresponding population sizes. The conditions for an invasion resistant coalition $\mathbf{U^*}$ is given by an extension of the conditions 3 and 4;

$$\frac{\partial}{\partial u}W(u, \mathbf{U}, \mathbf{N}) = 0 \tag{7}$$

$$\text{for } u = U_i \text{ for each } i$$

$$\frac{\partial^2}{\partial u^2}W(u, \mathbf{U}, \mathbf{N}) < 0 \tag{8}$$

$$\text{for } u = U_i \text{ for each } i$$

$$W(u, \mathbf{U^*}, \mathbf{N^*}) \leq W(U_i, \mathbf{U}, \mathbf{N}) = 0$$

The first order condition for convergence stability of $\mathbf{U^*}$ remains the same as condition 3, however, the second order condition becomes quite difficult and untractable for coalition size of more than 3. The idea is still the same that, $\mathbf{U^*}$ is convergent stable if the system returns to $\mathbf{U^*}$ after perturbation strategies S by an amount δ_i where $S \subseteq \mathbf{U^*}$, $|S| = m$, $i \in \{1, 2, ..., m\}$.

Note that till now, we have ignored the effect of population size N on the strategy dynamics. The rationale for this is based on the assumption that population dynamics and evolutionary processes occur on different timescales (the latter occurring on very large timescales). This means that we can assume evolution to be happening when the population has achieved its equilibrium size N^*. But, in cases of rapid evolution under extreme selection pressure or in cases where there are no equilibrium points with respect to population size, this assumption does not hold. For example, in case of seasonally varying populations, the population size may exhibit a cyclic nature. In order to analytical solve such systems, we look at the long term fitness of a particular strategy using Lyapunov exponents, which are log geometric means of fitness;

$$\begin{aligned} &W_{longterm}(u, U, N) && (9)\\ &= [log|W(u, U_1, N_1)W(u, U_2, N_2)...W(u, U_T, N_T)|]^{\frac{1}{T}}\\ &= \frac{1}{T\Sigma_i log|W(u, U_i, N_i)|} \end{aligned}$$

U^* is a an ESS under non-equilibrium dynamics if;

$$W_{longterm}(U^*, U^*) > W_{longterm}(u, U^*)$$

$$\forall u \text{ or for all nearby } u$$

i.e if U^* is a global or local maxima. Convergence stability in non-equilibrium systems remains poorly understood. Lastly, we can use the idea of Lyapunov exponents to consider the concept of long term fitness in a stochastic and fluctuating environment which represents the reality of life more accurately;

$$W_{stochastic}(u, U, \varepsilon) = E_\varepsilon\{logW(u, U, \varepsilon)\} \tag{10}$$
$$= \frac{1}{T\Sigma_t logW(u, U, e_t)}$$

where E_ε denotes taking the expectation with respect to the probability distribution ε and e_t denotes the state of the environment at time t. Convergence stability in these contexts remains largely unsolved.

Furthermore, trait based adaptive dynamics can also be used to study coevolution of multiple species as a special case of the multi-trait model. For a two species model we have;

$$\begin{aligned} &W_1(u,U,V,N,M) \\ &\& \\ &W_2(v,U,V,N,M) \end{aligned} \tag{11}$$

The fitness functions subscripted by their species ID can take very different forms when looking at an asymmetric coevolution model as in a prey-predator system for example.

2.2 Evolutionarily Singular Strategies and the Adaptive Growth and Branching of the Evolutionary Tree (Geritz et al. 1998)

This paper describes a mathematical model for the long term phenotypic evolution of a single heritable continuous trait. The authors generalize the concept of an ESS into what they call an evolutionarily singular strategy. They further describe the various kinds of singular strategies based on 4 distinct, independent properties, *v.i.z* ESS stability (resistance to invasion by rare mutants), convergence stability, ability to invade other populations when initially rare itself and the possibility of protected dimorphisms occurring in the neighborhood of the singular strategy. The model assumes an asexually reproducing organism such that parent and offspring trait value are same. Mutations are rare and random. Evolution proceeds in small but discrete steps. Fitness is defined as the long term exponential growth rate of a phenotype in a given environment. E_x denotes the environment in a monomorphic population with trait value x. $r(x, E_x)$ denotes the population s long term exponential growth rate. At the demographic attractor we have;

$$r(x, E_x) = 0 \tag{1}$$

Now, consider a mutant with strategy y emerging in this population. As long as the mutant is rare, its effect on the environment is negligible, thus we have;

$$s_x(y) = r(y, E_x) \tag{2}$$

If the mutations are sufficiently small so that x and y are close enough, then we can write the following approximation for the mutant's fitness;

$$s_x(y) = s_x(x) + D(x)(y - x) \tag{3}$$

where $D(x)$, the local fitness gradient is defined as,

$$D(x) = \left[\frac{\partial s_x(y)}{\partial y}\right]_{y=x} \tag{4}$$

Note that $s_x(x) = r(x, E_x) = 0$ by definition. Hence, the mutant's fitness is determined only by the sign of the local fitness gradient and $(y - x)$. If the local fitness gradient is positive, then mutants with a larger trait value can invade, and if the local fitness gradient is negative then mutants with a lesser trait value can invade. Thus the population evolves until it reaches a point where the local fitness gradient is zero. This is called an **"evolutionarily singular strategy"**. A Pairwise Invasibility Plots (PIP) allows the graphical analysis of the evolution of a monomorphic population, Figure 2 shows an example of a PIP.

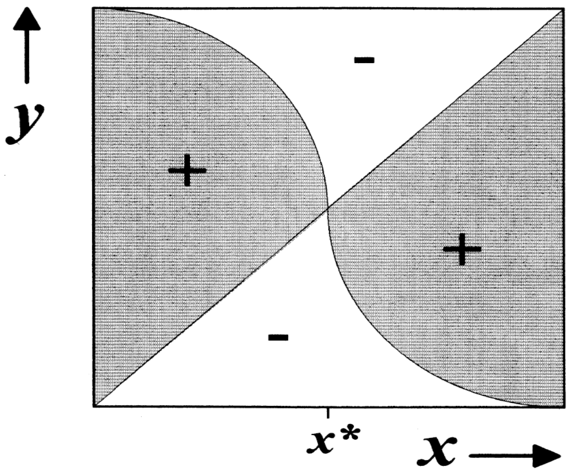


Figure 2: An example of a pairwise invasibility plot. The x axis represents the resident strategy and the y axis represents the mutant's strategy. Thus, for each point (x, y) we may ask the question "Does the mutant invade?". For the points along the principal diagonal i.e $y = x$ by definition the invasion rate $s_x(y) = r(y, E_x) = 0$. If $s_x(y) > 0$, then the answer is yes. If the answer is yes, then we mark it with a "+" sign and it the answer is no, then we mark the point with a "-" sign. Thus the PIP shows the sign of the invasion rate $s_x(y)$ as a function of x and y. The intersection of the diagonal with another line where $s_x(y) = 0$ corresponds to the evolutionarily singular strategy (Geritz et al. 1998).

Close to a singular strategy there are only 8 possible generic configurations of the pairwise invasibility plot near the evolutionarily singular strategy which can be algebraically categorized based on the second order derivative of $s_x(y)$ (Figure 3). Each of these configurations represents a different evolutionary situation that can be interpreted in terms of the ESS stability, convergence, ability of the singular strategy to invade another population if initially rare itself and the possibility of protected dimorphisms in the neighborhood of the singular strategy.

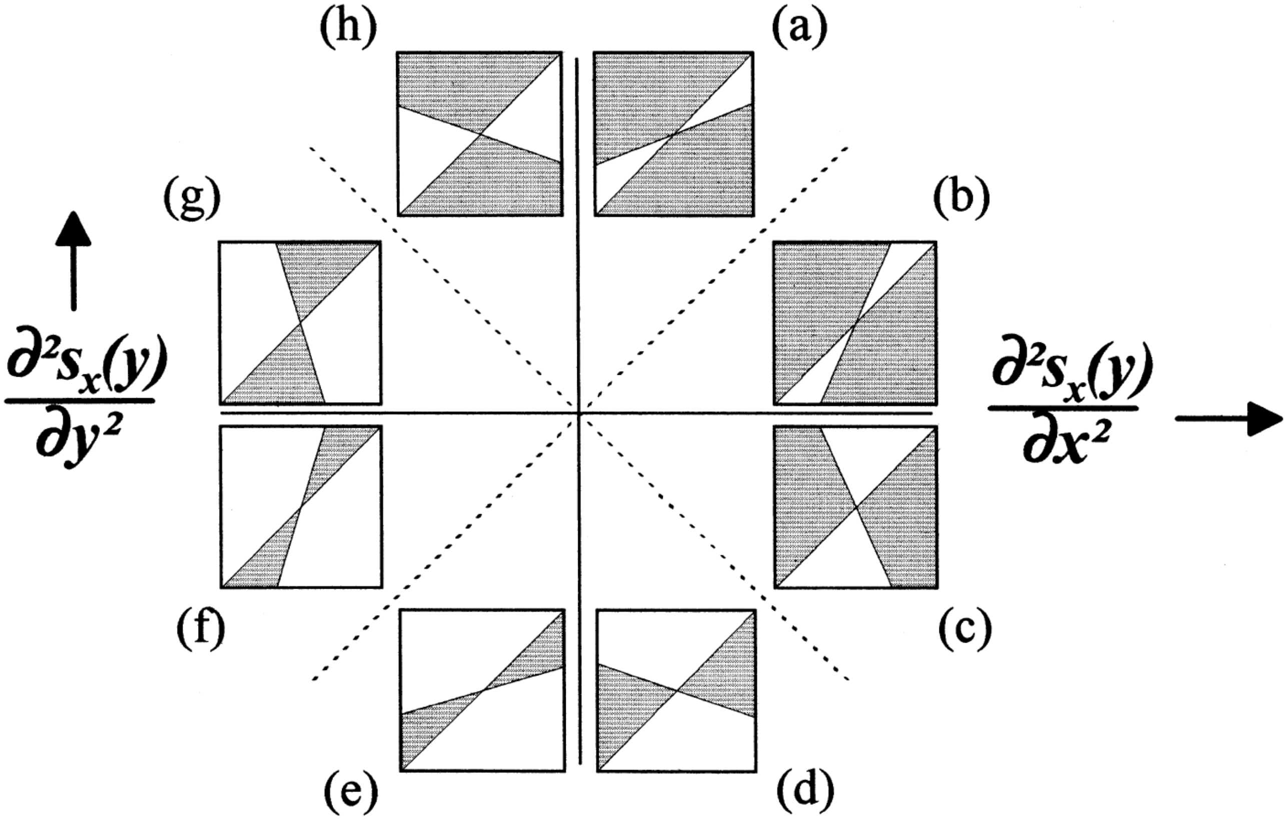


Figure 3: A diagrammatic representation of the different possible local configurations of the PIP near the evolutionary singular strategy (Geritz et al. 1998).

Table 1: Properties and their mathematical conditions

Property	**Condition**
ESS Stability	$\frac{\partial^2 s_x(y)}{\partial y^2} < 0$
Convergence Stability	$\frac{\partial^2 s_x(y)}{\partial x^2} > \frac{\partial^2 s_x(y)}{\partial y^2}$
Ability to Invade	$\left[\frac{\partial^2 s_x(y)}{\partial x^2}\right]_{y=x^*} > 0$
Possibility of Nearby Dimorphism	$\frac{\partial^2 s_x(y)}{\partial x^2} + \frac{\partial^2 s_x(y)}{\partial y^2} > 0$

Each of these possibilities can be described by a combination of inequalities of the second order derivatives of $s_x(y)$ (Table 1)

A singular strategy that is both ESS stable and convergence stable is termed **"continuously stable strategy" (CSS)**. Note that mutually invasible pairs of strategies in the neighborhood of a CSS will eventually evolve into a monomorphic population as mutants closet to the singular strategy continuously invade. However, mutually invasible pairs in the neighborhood of an ESS stable but not convergent stable strategy will move apart further as mutants farther from the singular strategy continuously invade (refer Figure 4).

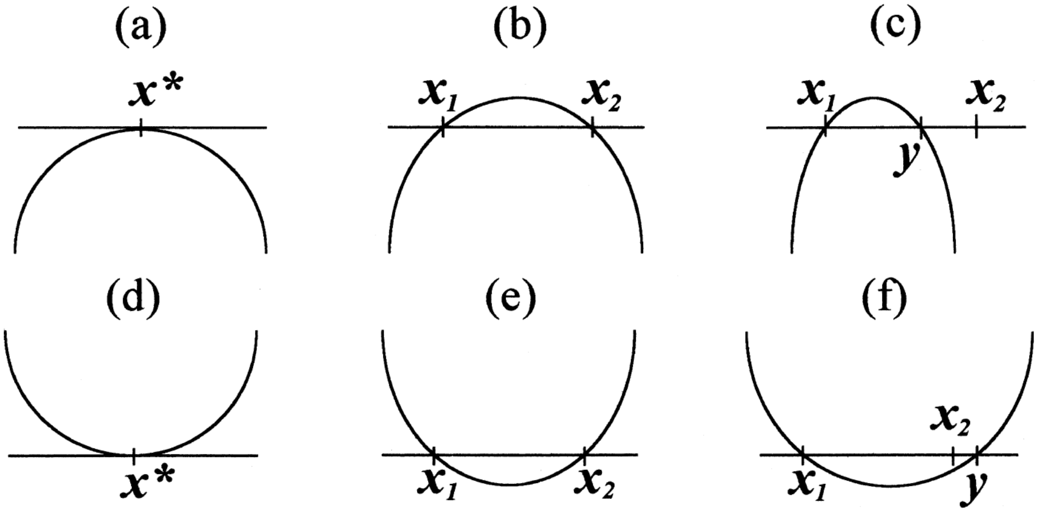


Figure 4: (a)-(c) Depicts the invasion profile of a mutant for two mutually invasible strategies x_1 and x_2 in the neighborhood of a CSS x^*. (d)-(f) Depicts the invasion profile of a mutant for two mutually invasible strategies x_1 and x_2 in the neighborhood of a convergent stable but not ESS stable singular strategy x^* (Geritz et al. 1998).

We can generalize this formalism to a population with arbitrarily many phenotypes. Let $E_{x_1,x_2,...,x_n}$ denote the environment on a population with strategies $x_1, x_2..., x_n$ at its demographic attractor. Then;

$$r(x_i, E_{x_1,x_2,...,x_n}) = 0 \tag{5}$$

$\forall x_i$ where $r(x_i, E_{x_1,x_2,...,x_n})$ denotes the long term exponential growth rate of the $x_{i^{th}}$ phenotype. The invasion rate of a rare mutant y in this population is therefore;

$$s_{x_1,x_2,...,x_n}(y) = r(y, E_{x_1,x_2,...,x_n}) \tag{6}$$

With small mutations the local fitness gradient with respect to the $x_{i^{th}}$ strategy is,

$$D_i(x_1, x_2, ...x_n) = \left[\frac{\partial s_{x_1,x_2,...,x_n}(y)}{\partial y}\right]_{y=x_i} \tag{7}$$

Combination of strategies for which $D_i(x_1, x_2, ...x_n)$ is zero lie on an n-1 dimensional manifold that we call an x_i isocline. Along this isocline, there is no directional selection in the x_i strategy. The point of intersection of all isoclines, $(x_1^*, x_2^*, ..., x_n^*)$ is an **evolutionarily stable coalition**. A singular coalition is evolutionarily stable if and only if all its constituent strategies are ESS, that is;

$$\left[\frac{\partial^2 s_{x_1,x_2,...x_n}(y)}{\partial y^2}\right]_{y=x_i^*,x_j=x_j^*\forall j} < 0 \tag{8}$$

Mutual invasibility of a mutant and the resident strategy is possible near a singular coalition under the following condition;

$$\left[\frac{\partial^2 s_{x_1,x_2,...,x_n}(y)}{\partial x_i^2}\right]_{y=x_i^*,x_j=x_j^*\forall j} < -\left[\frac{\partial^2 s_{x_1,x_2,...,x_n}(y)}{\partial y^2}\right]_{y=x_i^*,x_j=x_j^*\forall j} \tag{9}$$

Note that mutual invasibility has no long term significance if the singular strategy is ESS. A singular coalition that is both convergent stable and ESS is the long term endpoint of the the evolutionary process. A convergent stable singular coalition lacking ESS stability can lead to branching if there are mutually invasible strategies in the neighborhood.

As a specific example to demonstrate evolutionary dynamics and branching in a monomorphic population, let us consider Levene's (1953) 'soft selection' model with continuous strategies. Consider a population of an organism with discrete, non-overlapping generations with strategies $x_1, x_2, ...x_n$ residing in a homogeneous environment with m different patches. Each patch has a carrying capacity of K_i, $i \in \{1, 2, ..., m\}$. The total population size in each generation is constant, i.e.

$$\sum_{i=1}^{n} N_i = \sum_{j=1}^{m} K_j \tag{10}$$

where N_i denotes the total number of individuals using strategy x_i across all patches. In each generation, the offspring disperse into the different patches with the number of juveniles entering a patch being proportional to the frequency of that strategy amongst the dispersing offspring. Under the assumption that all individuals have equal fecundity irrespective of strategy or patch, the number of juveniles landing on a particular patch is proportional to N_i. Within a patch, juveniles first undergo a period of frequency independent selection after which they experience a non-selective contest, during which the available space in the patch is portioned off randomly among the survivors. The fraction of space allocated to individuals using strategy x_i in the j^{th} patch is;

$$f_j(x_i)N_i / \sum_{h=1}^{n} f_j(x_h)N_h \tag{11}$$

where $f_j(x_i)$ is the pre-competitive survival probability of an individual using strategy x_i in patch j. Thus the total number of x_i users in the next generation (summed over all patches) is;

$$N'_i = \sum_{j=1}^{m} \left(\frac{K_j f_j(x_i) N_i}{\sum_{h=1}^{n} f_j(x_h) N_h} \right) \tag{12}$$

At equilibrium, $N'_i = N_i \ \forall \ i$. Consider a rare mutant strategy y invades this population at equilibrium. A first order approximation for the number of mutants in successive years is;

$$N'_{mut} = \sum_{j=1}^{m} \left(\frac{K_j f_j(y) N_{mut}}{\sum_{h=1}^{n} f_j(x_h) \hat{N}_h} \right) \tag{13}$$

where $\hat{N}_h$ denotes the equilibrium number of x_h strategy users. Thus the mutant's exponential growth rate can be written as;

$$\begin{aligned} s_{x_1,\ldots,x_n}(y) = & \\ & log \frac{N'_{mut}}{N_{mut}} \\ & = log \sum_{j=1}^{m} \left(K_j f_j(y) / \sum_{h=1}^{n} f_j(x_h) \hat{N}_h \right) \end{aligned} \tag{14}$$

Let us consider a simple case with exactly three patches each with the same carrying capacity i.e. $K_1 = K_2 = K_3$. We use the following bell curve to represent the pre-competitive survival probabilities of the different strategies;

$$f_j(x) = \alpha \exp \left(-\frac{(x - \mu_j)^2}{2\sigma^2} \right) \tag{15}$$

where $\mu_1 = -d, \mu_2 = 0$ and $\mu_3 = d$ for some value of d. Based on the above assumptions, there is a unique evolutionarily singular strategy at $x^* = 0$ that is convergence and ESS stable, that can invaded other populations if initially rare and in the neighborhood of which protected dimorphisms are possible. The properties of the singular strategy vary as a function of d/σ. This property is depicted in the Figure (5).

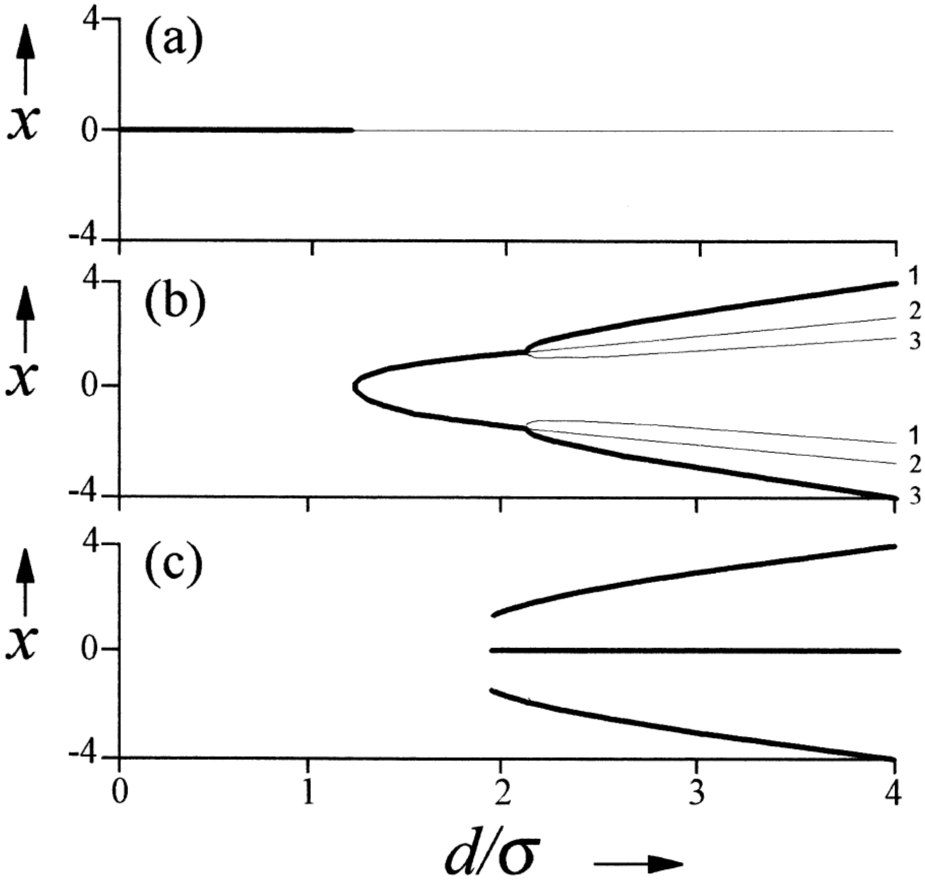


Figure 5: A diagram showing the bifurcation plot with d/σ as the bifurcation parameter for (a) the monomorphic singular strategy, (b) Dimorphic singular coalition and (c) Trimorphic singular coalition. Thick lines correspond to ESS stability and thin lines correspond to a lack of ESS stability (Geritz et al. 1998).

2.3 Trait Based Ecology and Eco-Evolutionary Theory (Klausmeier, Kremer, and Koffel 2020)

This book chapter provides a comprehensive overview of trait based frameworks and their applications to eco-evolutionary studies. It discusses the benefits and assumptions involved in trait based approaches and how different approaches are related to each other. Traits are defined as measurable properties of living organisms; *functional traits* are those that affect the performance or fitness of an organisms. For the major part, trait based approaches are focused on functional traits and the assumption that organisms and populations can be viewed merely as entities possessing a certain value of this "trait" of interest. This allows modelers to represent individuals and populations using trait values and trait value averages. *Optimality theory* tries to explain the evolution of trait values based on the concept of an "optimal" trait value given a constant environment. The drawback to this approach is that it assumes the fitness of a particular trait depends only on the external, constant factors and does not account for the traits/strategies used by other individuals in the population, AKA *frequency dependence.* Game theory was a designed to analyze such scenarios initially in economics, and was later imported to evolutionary biology. In this framework, the fitness of a particular strategy depends on the strategic composition of the rest of the population as well. The notion of an optimal strategy is replaced by that of an evolutionary stable strategy, a strategy that cannot be improved upon once universally adopted. Amongst many trait based approaches that emerged in the late 19^{th} century, two independent groups– one American (Brown and Vincent 1987) and European (Metz et al.1996) proposed a trait based theoretical framework that allows for the emergence of community structure, termed *adaptive dynamics.* It combines ideas from evolutionary game theory and community ecology. These frameworks hinge on the fact that payoffs can be identified as Darwinian fitness which is described as the per capita growth rate in community ecological models.

Community assembly theory is a purely ecological framework where different species are repeatedly introduced into a local community from a finite or infinite regional species pool. The different outcomes of such a process include; (a) an un-invasible community, (b) recurrent assembly cycle continues or (c) Community assembly continues indefinitely along different trajectories. Even though community assembly theory has a lot in common with the adaptive dynamics framework, the two literatures have remained largely separate.

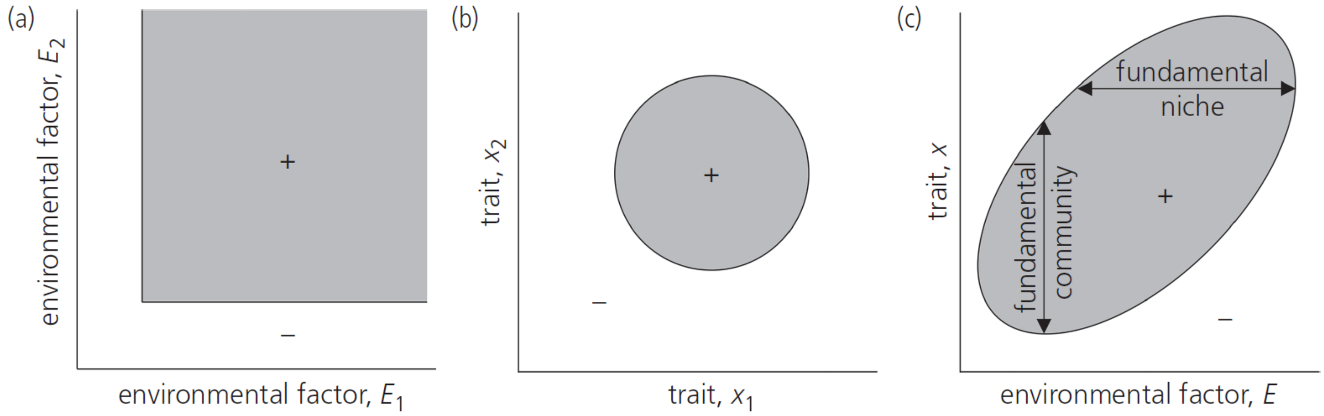


Figure 6: Zero Invasion Plots (a) two environmental factors, (b) two traits (c) one environmental factor and one trait. Shaded region indicates positive fitness.

Figure 6 depicts Zero Invasion Plots for a density independent system where per capita growth rate is described by

$$\frac{dN_i}{dt} = r_i N_i$$

where $r_i(\bar{x}_i, \bar{E},)$ depends on the trait and the state of the environment. Figure 6(b) shows a hypothetical scenario where, in a fixed environment, positive growth occurs only in certain combinations of both traits. For a given trait value, a horizontal slice through the shaded region in Figure 6(c) give the fundamental niche. And a vertical slice through a fixed environment factor value gives the fundamental community; species with trait values outside the fundamental community range cannot persist. The simplest density dependent model might be the Lotka-Volterra model which can be written as;

$$\begin{cases} \frac{dN_1}{dt} = (r_1 - \alpha_{11}N_1 - \alpha_{12}N_2)N_1 = g_1 N_1 \\ \frac{dN_2}{dt} = (r_2 - \alpha_{21}N_1 - \alpha_{22}N_2)N_2 = g_2 N2 \end{cases} \tag{1}$$

where N_1, N_2 are the populations of two species, r_i are maximum growth rates α_{ii} and α_{ij} are intra and inter specific competition coefficients respectively. The possible outcomes of such a system are; (a) species 1 out-competes species 2, (b) species 2 out-competes species 1, (c) species 1 and species 2 coexist, (d) species 1 or species 2 excludes the other based on initial conditions or (e) species 1 and species 2 neutrally coexist.

Invasion analysis is a powerful tool to analyze the stability of multi-species or multi-strategy population. The idea is to ask whether a particular population when introduced in sufficiently low numbers (invader) into a monomorphic population of another (the resident) has a positive per capita growth rate or not. A positive per-capita growth rate implies that invasion is possible. The invader population/strategy is assumed to be rare enough such that it faces no density dependent inhibition of growth and that it does not affect the surrounding environmental state. This density independent growth rate of the invader is termed its *invasion fitness*,$g_{inv}(E_{res})$. The advantage of invasion analysis is that it is easier than trying to solve for the coexistence attractor and characterize its stability.

The following are four steps to set up a trait based model.

1. Identify groups of population that are functionally similar and place them into a *guild*. For example, predators and prey species might form two separate guilds. Let ς denote the number of guilds.

2. Let $\exists$ N_G populations in guild G, indexed by subscripts. Any terms that signify interaction between populations or between populations and the environment must be replaced by a sum over all populations.

3. Make model parameters functions of traits. Thus the model consists of a set of differential equations of the form;
$$\frac{dN_{G,i}}{dt} = g_G(x_{G,i}, \vec{E}(\vec{N}, \vec{x}))N_{G,i}$$
where $\vec{x} = (\vec{x_1}, \vec{x_2}, ..., \vec{x_\varsigma})$, $\vec{x_G} = (x_{G,1}, x_{G,2}, ..., x_{G,N_G})$, $\vec{N} = (\vec{N_1}, \vec{N_2}, ...\vec{N_\varsigma})$ and $\vec{N_G} = (N_{G,1}, N_{G,2}, ..., N_{G,N_G})$.

4. The final step in setting up a trait based model is to define the source of variation. In adaptive dynamics, this is assumed to be small infrequent mutations.

The analysis of such trait based models is covered in section 2.2. Other insights come from studying how the properties of Evolutionarily Singular Communities (ESC) change as a function of environmental parameters. An efficient way to compute bifurcation diagrams using an environmental factor z as the bifurcation parameter is given by Klausmeier and Kremer 2017. Figure 8 shows the bifurcation diagram for an ESC as function of a bifurcation parameter z.

Apart from stable fixed points, in recent years there has been discovery of multiple other possible outcomes of eco-evolutionary processes such as *limit cycles, evolutionary suicide, branching-extinction evolutionary cycles* and *alternative evolutionary stable states.* In systems that fall into limit cycles, population densities and traits both fluctuate over time in a periodic fashion. Evolutionary suicide or more generally "Tragedy of the Commons" (TOC) occurs when adaptive evolution leads to progressive decrease in gross population abundance culminating in extinction. Branching-extinction cycles occur when one of the two sub-populations at a branching point goes extinct and the extant population falls back into the branching point causing this cycle to repeat itself indefinitely. Alternative stable states can occur in the form of alternate ESS/ESCs where the initial conditions will determine which stable state is achieved.

There are other trait based frameworks, each of which differ from the other on the basis of the degree to which biological details are abstracted, the level of biological organization at which variances involved are manifested, the source of new phenotypes and the heritability in the trait variations. Despite these differences, they can reach similar conclusions about long term outcome of community assembly/evolution as depicted in Figure 7. We can try to understand how these different frameworks lead to similar outcomes by considering the oligomorphic dynamics framework (Sasaki and Dieckmann 2011). The framework tracks the three moments of the population, the zeroth moment which is the population size, the first moment which is the mean trait and the second moment which is the trait variance. These are given by the following expressions respectively;

$$N_i = \int n_i(x)dx$$

$$\bar{x}_i = \frac{\int x.n_i(x)dx}{N_i}$$

$$V_i = \frac{\int (x - \bar{x}_i)^2 n_i(x)dx}{N_i}$$

In the absence of immigration and mutation, the dynamics of each population is given by;

$$\begin{aligned}\frac{dN_i}{dt} &= \int g(x)n_i(x)dx \\ &\approx g(\bar{x}_i)N_i + \frac{1}{2}V_i\frac{\partial^2 g(x)}{\partial x^2}\bigg|_{x=\bar{x}_i}\end{aligned} \tag{2}$$

$$\begin{aligned}\frac{d\bar{x}_i}{dt} &= \frac{1}{N_i}\int x.g(x)n_i(x)dx - \frac{\bar{x}_i}{N_i}\int g(x)n_i(x)dx \\ &\approx V_i\frac{\partial g(x)}{\partial x}\bigg|_{x=\bar{x}_i}\end{aligned} \tag{3}$$

$$\begin{aligned}\frac{dV_i}{dt} &= \frac{1}{N_i}\int (x - \bar{x}_i)g(x)n_i(x)dx \\ &- \frac{V_i}{N_i}\int g(x)n_i(x)dx \\ &\approx V_i^2\frac{\partial^2 g(x)}{\partial x^2}\bigg|_{x=\bar{x}_i}\end{aligned} \tag{4}$$

Assuming small trait variance, each extant species at equilibrium is characterized by $g(\bar{x}_i) = 0$ (Equation 3) and

$\frac{\partial g}{\partial x} = 0$ (Equation 4) $--$ the same conditions for an evolutionary equilibrium in adaptive dynamics (section 2.2). The condition for convergence stability matches the linear stability of Equation 4 and Equation **??** shows that the trait variance $V_i \to 0$ if $\frac{\partial^2 g}{\partial x^2} < 0$ $--$ the same condition for evolutionary stability as in adaptive dynamics.

There are scenarios where one can expect these different frameworks to generate distinct outcomes:

1. In case of the presence of multiple local ESS but not a global ESS.
2. In case ecological quantitative genetics or oligomorphic dynamics models are not initialized with sufficient number of species.
3. In case of the the absence of fixed points, the details of the emergence of new strategies will determine the non-equilibrium dynamics.
4. In case of high immigration or mutation rates.

Hitherto we saw the analysis of trait based systems under the simplistic assumption of spatial and temporal homogeneity. However, the factors that affect an invading mutant's fitness (like external environment, resident population composition etc.) may fluctuate over time. In order to deal with such systems, we need to calculate the time-averaged invasion rates $\bar{g}_{inv}$. All the methods discussed in section 2.2 can then be applied to $\bar{g}_{inv}$. In the case of an unstructured population facing periodic forcing, we can define $\bar{g}_{inv}(x_0; \vec{E}(t))$ as;

$$\bar{g}_{inv} = \frac{1}{\tau} \int_0^\tau g_{inv} \left(x_0; \vec{E}(t) \right) dt \tag{5}$$

note that;

$$\frac{\partial \bar{g}_{inv}}{\partial x_0} = \frac{1}{\tau} \int \frac{\partial g_{inv}}{\partial x_0} \tag{6}$$

In the case of structured populations undergoing fluctuating environments, one needs to calculate Floquet exponents or more generally the Lyapunov exponents.

Spatially non-homogeneous systems are modeled as a collection of discrete patches and their collective dynamics are modeled using Leslie matrices;

$$\frac{d\vec{N}_i}{dt} = \left(G \left(x_i; E(\vec{x}, \vec{N}) \right) + D(x_i) \right) \vec{N}_i \tag{7}$$

where $\vec{N}_i$ is a vector of the abundances of the population i in different patches, G is a diagonal matrix governing within patch dynamics and D is a matrix encoding dispersal among patches. Alternatively, similar modeling can be done across continuous space using reaction-diffusion systems which can be represented using differential equations of the form;

$$\frac{\partial N_i}{\partial t} = g \left(z, x_i; E \left(\vec{x}(z), \vec{N}(z) \right) \right) N_i + d(x_i) \frac{\partial^2 N_i}{\partial z^2} \tag{8}$$

where z denotes the spatial dimension, g determines the local dynamics and the last term allows for dispersal.

In conclusion one of the biggest advantages to trait based approaches is that (a) they can be integrated a number of theoretical frameworks, (b) they allow us to analyze complex interactions in a simplistic functional way without dealing with the mechanistic complexities of genetics and inheritance and (c) they allow us to make quantitative predictions which can be empirically tested/verified.

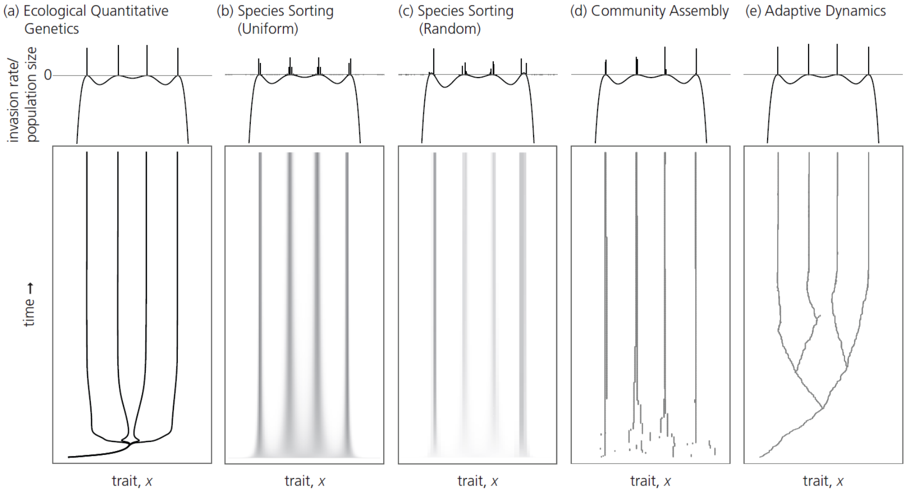


Figure 7: The evolution of a trait based Lotka-Volterra model under 5 different frameworks (Klausmeier, Kremer, and Koffel 2020).

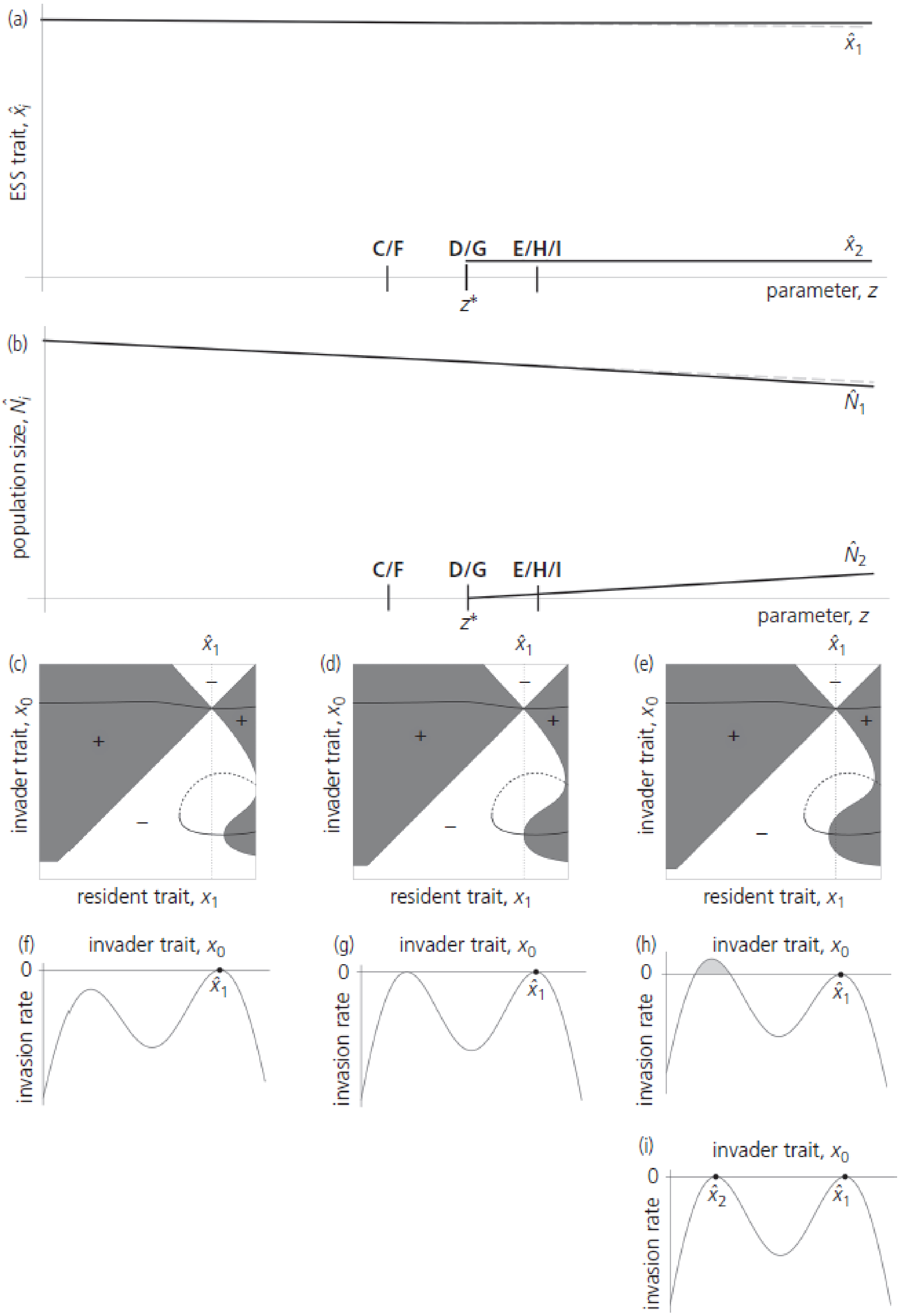


Figure 8: A bifurcation diagram showing equilibrium traits (a), population size (b), PIPs (c-e) and invasion profiles (f-i) (Klausmeier, Kremer, and Koffel 2020)

2.4 A FRAMEWORK FOR ELUCIDATING THE TEMPERATURE DEPENDENCE OF FITNESS (AMARASEKARE AND SAVAGE 2012)

This paper presents a mathematical framework to partition the temperature dependent fitness response of ectotherms into components of fecundity, development and mortality. Such a partitioning is crucial to understand the temperature dependent responses and extinction risks of ectothermic organisms, especially for those organism whose optimum temperature T_{opt} is closer to the maximum viable temperature T_{max}. This is because small increments in global temperatures will adversely affect well adapted species of the former type. Age structured population dynamics provide a way to investigate the temperature dependence of r_m as a function of the temperature response of underlying life-history traits. Let $B(t)$ be the instantaneous birth rate of the population.l_x be the fraction of individuals that survive until age x (survivorship) and b_x be the age specific fecundity of the individual; then we can write;

$$B(t) = \int_0^t B(t-x) l_x b_x dx \tag{1}$$

Substituting $B(t) = Qe^{r_m t}$ as a candidate solution, where r_m is the growth rate of the population, in 1 we have;

$$\begin{aligned} Qe^{rt} &= \int_0^t Qe^{r_m(t-x)} l_x b_x dx \qquad (2) \\ \implies 1 &= \int_0^t e^{-r_m x} l_x b_x dx \end{aligned}$$

Assuming α is the age of first reproduction, the expected reproductive success of a newborn is given by;

$$\int_\alpha^\infty e^{-r_m x} l_x b_x dx = 1 \tag{3}$$

Consider the common case where fecundity declines with age; that is,

$$b_x = \begin{cases} 0 & \text{for } x < \alpha \\ b_{\alpha_{peak}} f(x - \alpha_{peak}) & \text{for } x \geq \alpha \end{cases} \tag{4}$$

where α_{peak} is the age at which fecundity is maximum. The function $f(x-\alpha)$ is unimodal and by definition has a peak at $f(0)$. The survivorship function follows an exponential decay after reaching age of reproduction such that;

$$l_x = l_\alpha e^{-d(x-\alpha)} \tag{5}$$

where d is the age independent instantaneous adult mortality rate. Then equation 3 becomes;

$$\begin{aligned} & b_{\alpha_{peak}} l_\alpha e^{d\alpha} \qquad (6) \\ & \times \int_\alpha^\infty f(x - \alpha_{peak}).e^{-(d+r_m)x} dx \\ & = 1 \end{aligned}$$

substituting $y = x - \alpha_{peak}$,

$$\begin{aligned} & b_{\alpha_{peak}} l_\alpha e^{-d(\alpha_{peak}-\alpha)}.e^{-r_m \alpha_{peak}} \qquad (7) \\ & \times \int_{\alpha-\alpha_{peak}}^\infty f(y).e^{-(d+r_m)y} dy = 1 \end{aligned}$$

Since the function $f(y)$ is sharply peaked at $f(0) = 1$, we will approximate the above integral by approximating the value of $f(y)$ near the peak and performing integration over the remaining exponential term, giving us;

$$b_{\alpha_{peak}} l_\alpha e^{-r_m \alpha} - (d + r_m) \approx 0 \tag{8}$$

We can use $l_\alpha = \exp - \int_0^\alpha d(x)dx = e^{-\bar{d}\alpha}$ where $\bar{d}$ is the average juvenile mortality rate. Then equation 8 becomes;

$$b_{\alpha_{peak}} e^{-(\bar{d}+r_m)\alpha} - (d + r_m) \approx 0 \tag{9}$$

Implementing explicit temperature dependence of $b_{\alpha_{peak}}, d, \bar{d}$ and α we have;

$$\begin{aligned} & b_{\alpha_{peak}}(T) e^{-[\bar{d}(T)+r_m(T)]\alpha(T)} \qquad (10) \\ & -(d(T) + rm(T)) \approx 0 \end{aligned}$$

Solving equation 10 for an analytical expression of $r_m(T)$ we get;

$$\begin{aligned} r_m(T) = -d(T) + & \frac{1}{\alpha(T)} \qquad (11) \\ & \times W\left\{ b_{\alpha_{peak}}(T)\alpha(T) e^{(d(T)-\bar{d}(T))\alpha(T)} \right\} \end{aligned}$$

where W is the principal branch of the Lambert W function or the product logarithm. Incorporating a Gaussian function for fecundity and exponential (Boltzmann-Arrhenius) function for development and mortality we have;

$$\begin{aligned} r_m(T) = -d_{T_R} e^{A_d TD} + & \frac{1}{\alpha_{T_R} e^{A_\alpha TD}} \\ & \times W\left(\bar{b}_{T_R} \alpha_{T_R} e^{A_\alpha TD - \frac{(T-T_{opt_{\bar{b}}})^2}{2s^2}} \right. \\ & \left. + \alpha_{T_R} e^{A_\alpha TD} \left[d_{T_R} e^{A_d TD} - \bar{d}_{T_R} e^{A_{\bar{d}} TD} \right] \right) \\ & \qquad (12) \end{aligned}$$

Where $TD = [\frac{1}{T_R} - \frac{1}{T}]$, d_{T_R} is the mortality rate at a reference temperature, A_d is the Arrhenius constant, $\frac{1}{\alpha_{T_R}}$ is the development rate at reference temperature T_R, $b_{\bar{T}_R}$ is the per capita fecundity at reference temperature $T_{opt_{\bar{b}}}$, s is the standard deviation of the Gaussian function describing fecundity and $d_{\bar{T}_R}$ is the juvenile mortality rate at the reference temperature T_R.

The first term of equation 12 is the negative effect of temperature response due to adult mortality. The second term which is positive for all temperature values combines the exponential, Gaussian and Gompertz-like functions arising out of the temperature response of development (exponential), fecundity (Gaussian) and the interaction between fecundity and development (Gompertz-like). Hence the sign of $r_m(T)$ is decided by which of the two terms dominate. This is depicted in figure 9. Figure 11 depicts the effect of temperature dependent development rate on the symmetry of $r_m(T)$.

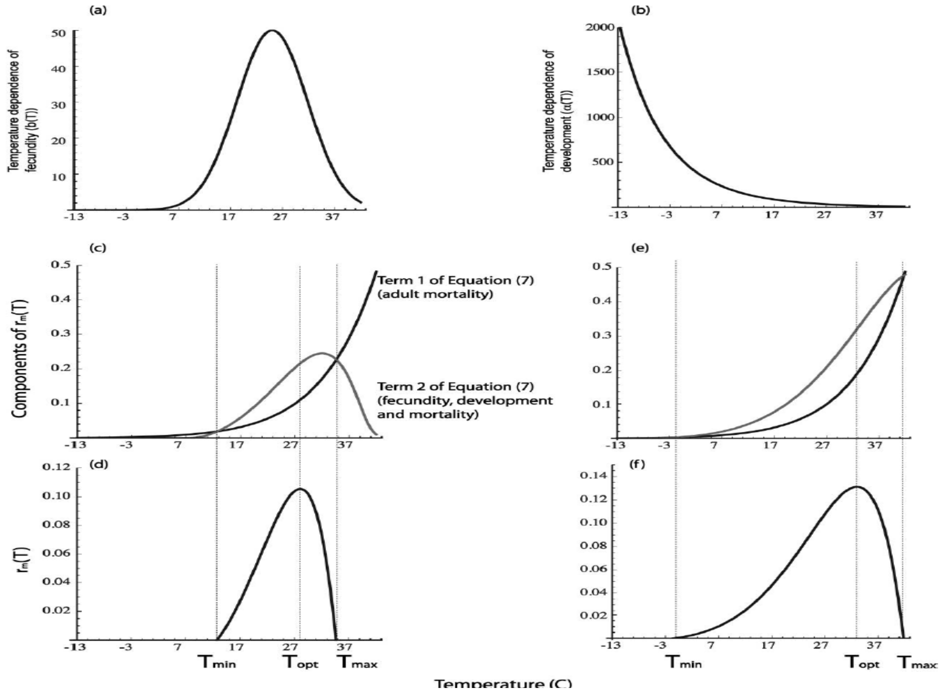
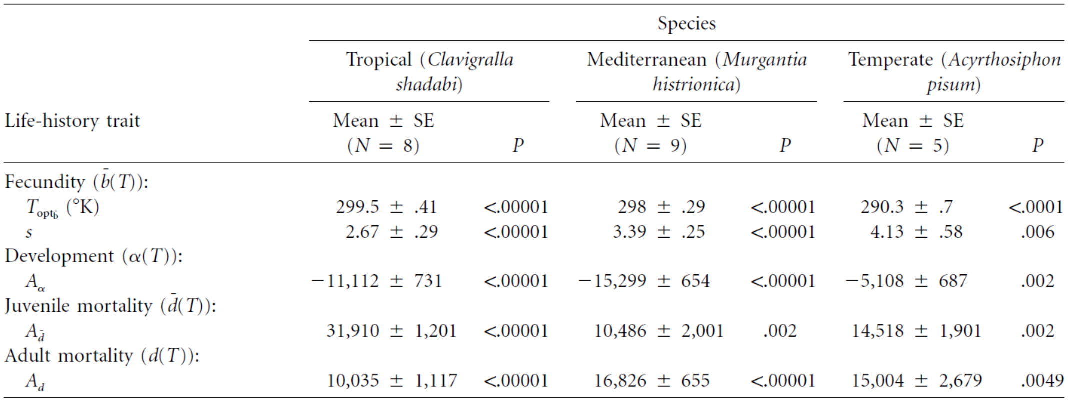


Figure 9: Grey line depicts the negative term of equation 12 and the black line depicts the first, positive term. In the case of (c) and (d) $s = 2.5$ and in (e) and (f) $s = 4.8$ (Amarasekare and Savage 2012).



Life-history trait	Species Tropical (*Clavigralla shadabi*) Mean ± SE ($N = 8$)	P	Mediterranean (*Murgantia histrionica*) Mean ± SE ($N = 9$)	P	Temperate (*Acyrthosiphon pisum*) Mean ± SE ($N = 5$)	P
Fecundity ($\bar{b}(T)$):						
T_{opt_b} (°K)	299.5 ± .41	<.00001	298 ± .29	<.00001	290.3 ± .7	<.0001
s	2.67 ± .29	<.00001	3.39 ± .25	<.00001	4.13 ± .58	.006
Development ($\alpha(T)$):						
A_α	−11,112 ± 731	<.00001	−15,299 ± 654	<.00001	−5,108 ± 687	.002
Juvenile mortality ($\bar{d}(T)$):						
$A_{\bar{d}}$	31,910 ± 1,201	<.00001	10,486 ± 2,001	.002	14,518 ± 1,901	.002
Adult mortality ($d(T)$):						
A_d	10,035 ± 1,117	<.00001	16,826 ± 655	<.00001	15,004 ± 2,679	.0049

Figure 10: Table depicting the measured parameter values of the temperature response for a tropical, mediterranean and temperate hemipteran. N indicates sample size (number of temperatures in which these values were measured)(Amarasekare and Savage 2012).

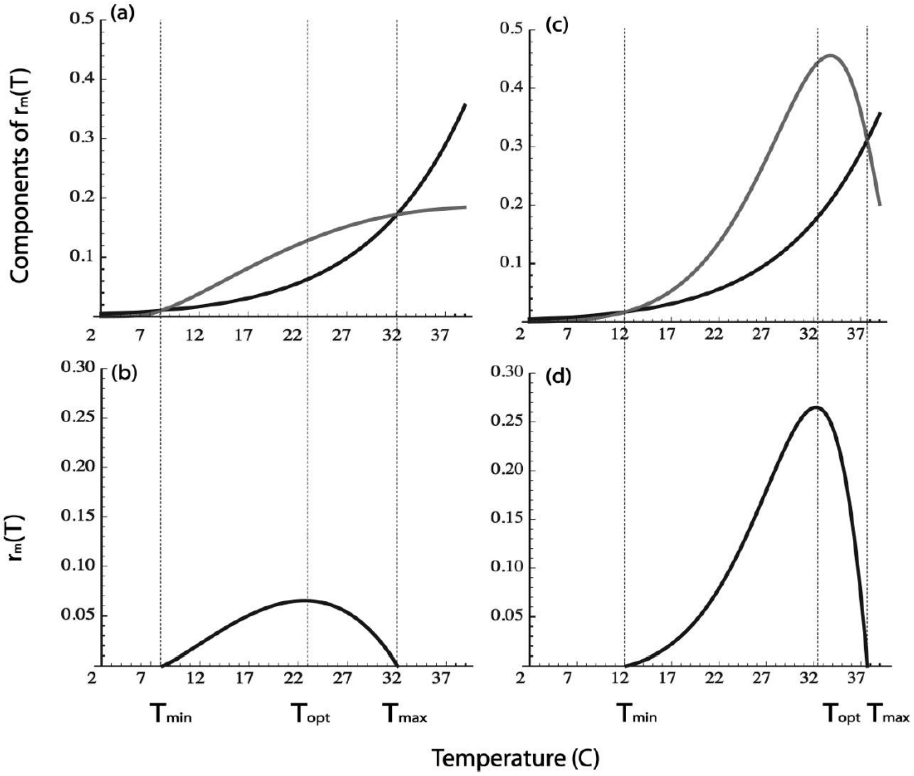


Figure 11: Figure depicting how temperature response to development (A_α) affects the symmetry of $r_m(T)$ (Amarasekare and Savage 2012).

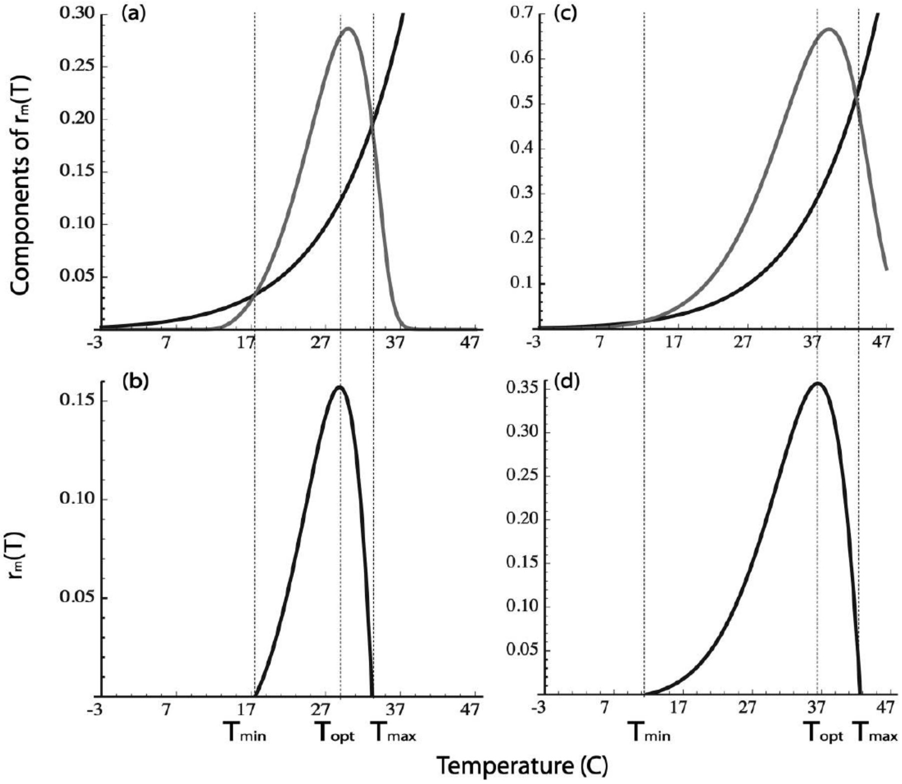


Figure 12: Figure depicts how s, the width of temperature response of fitness affects $r_m(T)$ (Amarasekare and Savage 2012).

A wider temperature response for reproduction causes T_{opt} to move closer to T_{max} whereas a narrower response decreases the left skew (figure 12). Figure 13 shows data points in comparison with the predicted $r_m(T)$ for temperate, tropical and Mediterranean hemipteran species (10). In conclusion, partitioning of the temperature response of fitness into its different components highlights how differential effects of temperature on life-history traits such as fecundity, development, and survivorship can affect overall fitness.

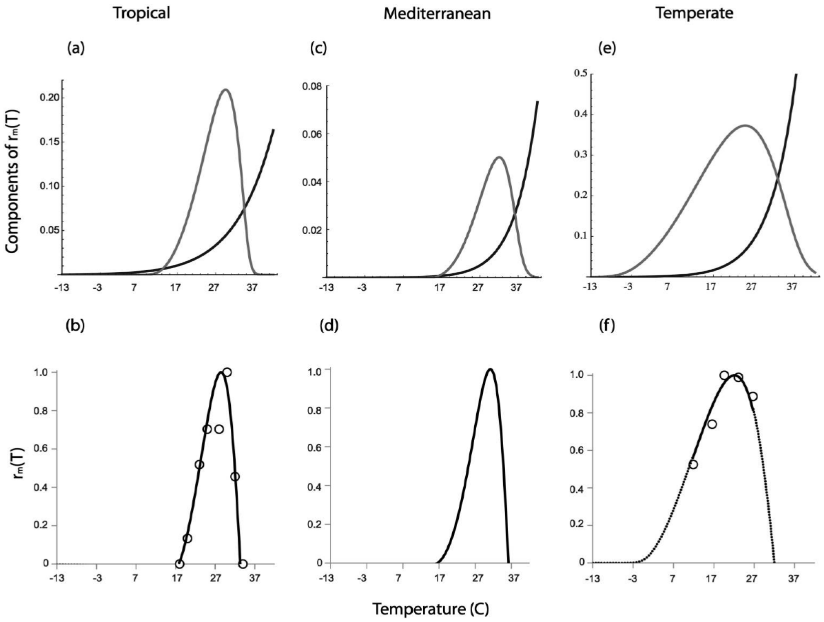


Figure 13: Data points overlayed on top of predicted $r_m(T)$ functions for a Tropical, Mediterranean and a Temperate hemipteran species (Amarasekare and Savage 2012).

2.5 SELECTION ON ONE LOCUS (RICE 2004)

My interest in this chapter from the book "Evolutionary Theory: Mathematical and Conceptual Foundations" by Sean H Rice was to understand the way allele frequencies were updated after every generation in a fitness dependent manner. **Absolute fitness** is the expected number of surviving offspring produced by a parent with a particular genotype. **Relative fitness** is just absolute fitness scaled in some way. Let us consider a system with 2 alleles at a single locus, namely A_1, and A_2. Let w_{ij} denote the average fitness of the genotype A_iA_j. Let the frequency of allele A_1 be p. Then we have,

$$N_{t+1} = p^2N_tw_{11} + 2p(1-p)N_tw_{12} + (1-p)^2N_tw_{22} \tag{1}$$

Rewriting this as;

$$N_{t+1} = \bar{w}N_t$$

where:

$$\bar{w} = p^2w_{11} + 2p(1-p)w_{12} + (1-p)^2w_{22} \tag{2}$$

The term $\bar{w}$ is called the **mean population fitness**, which is just the sum of the fitness values of each genotype in the population scaled by their respective frequencies. This mean population fitness can be related to the instantaneous per capita growth rate used in continuous growth as follows;

$$\begin{aligned} N_t &= N_oe^{rt} \\ \implies N_{t+1} &= N_te^r \\ \implies N_t\bar{w} &= N_te^r \\ \implies r &= \ln(\bar{w}) \end{aligned} \tag{3}$$

To know how the mean population fitness changes with change in p, we can differentiate equation 2,

$$\begin{aligned} \frac{d\bar{w}}{dp} &= 2pw_{11} + 2w_{12} - 4pw_{12} - 2w_{22} + 2pw_{22} \\ &= 2\left[pw_{11} + (1-p)w_{12}\right] - 2\left[pw_{12} + (1-p)w_{22}\right] \end{aligned} \tag{4}$$

Note that here we assume that the values w_{ij} are themselves not functions of p, that is, **we assume frequency independent fitness**. We can also calculate the fitness of an allele as the sum of the fitness of the genotypes in which the allele is present weighted by the respective probabilities of the allele being found in that genotype. We will use w_i^* to denote the fitness of allele A_i. Thus we have;

$$\begin{aligned} w_1^* &= pw_{11} + (1-p)w_{12} \\ w_2^* &= pw_{12} + (1-p)w_{22} \end{aligned} \tag{5}$$

Thus, $\bar{w}$ becomes,

$$\bar{w} = pw_1^* + (1-p)w_2^* \tag{6}$$

From equation 4 and equation 5 we have;

$$\frac{d\bar{w}}{dp} = 2(w_1^* - w_2^*) \tag{7}$$

Let n_i be the actual number of A_i alleles in generation t and n_T is the total number of alleles. Then;

$$p_{t+1} = \frac{n_1 w_1^*}{n_T \bar{w}} = \frac{p_t w_1^*}{\bar{w}} \tag{8}$$

Thus, we can scale fitness values any way we want as any scaling factor applied to all fitness values appears in both the numerator and denominator and thus cancels out.

3 MODELING

Here I further develop and extend the model I had previously worked on during the first year of my master's thesis (refer here). During the course of this summer, I have tried to adapt my existing discrete game theoretic model into a continuous trait based evolutionary model. The following are the major simplifying assumptions involved in this approach;

1. There exists a trait that controls the baffling threshold. We will refer to this trait henceforth using 'x'. Baffling threshold refers to the loudness below which a male will choose to baffle and above which a male does not choose to baffle.
2. x is sex limited and female imprinted, so that the value of x in male offspring is determined solely by the father's trait value.
3. The active acoustic volumes of signaling males does not overlap, that is, males are significantly scarcely distributed in the environment such that their calls do not influence one another.
4. All males are uniform with respect to body size OR females don't show preference based on male body size.
5. All females have identical lifetime fecundity ϕ. ϕ may be a function of the environmental resource availability $\mathcal{R}$, i.e. $\phi(\mathcal{R})$. Lifetime fecundity is defined as the total number of eggs laid by a female during her lifetime.
6. 50% of all offspring are males and 50% are females.
7. Females have a fixed, uniform mortality rate.
8. Instantaneous adult mortality rate of males is influenced by their history of calling/baffling.
9. All juveniles have identical development times.
10. Male fecundity is not affected by age. Male fecundity is defined as the rate of sperm transfer.
11. The environmental resource concentration is constant and the energy status of males inhabiting this environment follows a normal distribution such that

    $$z \in N(\bar{z}, \sigma)$$

    where σ denotes the standard deviation of the distribution.

The total number of births in a population at any time t denoted by $B(t)$ is given by

$$B(t) = \int_0^t B(t-a)l(a)b(p(x)) \quad da \tag{1}$$

where $p(x)$ denotes the baffling propensity, $l(a)$ denotes the age dependent survivorship and b denotes the instantaneous birth rate (analogous to age independent male fecundity). Plugging a candidate solution $B(t) = Qe^{rt}$ in equation 1 we have,

$$1 = \int_0^t e^{-ra}l(a)b(p(x)) \quad da \tag{2}$$

Using equation 2, we can express the lifetime fecundity of a newborn male as;

$$1 = \int_\alpha^\infty e^{-ra}l(a)b(p(x)) \quad da \tag{3}$$

where α is the age of first reproduction. Substituting $l(a) = l_\alpha e^{-d(p(x))(a-\alpha)}$ in equation 3, we have;

$$\begin{aligned} l_\alpha b(p(x)) \int_\alpha^\infty e^{-ra}.e^{-d(p(x))(a-\alpha)} \quad da &= 1 \\ \implies l_\alpha b(p(x)) \int_\alpha^\infty e^{-a(r+d(p(x)))}.e^{\alpha d} \quad da &= 1 \\ \implies l_\alpha b(p(x)) e^{\alpha d} \left[-\frac{1}{r+d(p(x))} e^{-a(r+d(p(x)))} \right]_\alpha^\infty & \\ \implies l_\alpha b(p(x)) e^{\alpha d} \left(\frac{e^{-\alpha(r+d(p(x)))}}{r+d(p(x))} \right) &= 1 \\ \implies l_\alpha b(p(x)) e^{\alpha d(p(x))}.e^{-\alpha(r+d(p(x)))} &= r + d(p(x)) \end{aligned} \tag{4}$$

Substituting $l_\alpha = e^{-\bar{d}\alpha}$ in equation 4, where $\bar{d}$ is the juvenile mortality rate, we have;

$$\begin{aligned} b(p(x))e^{-\bar{d}\alpha}.e^{-\alpha r} - (r + d(p(x))) &= 0 \\ b(p(x))e^{-\alpha(\bar{d}+r)} - (r + d(p(x))) &= 0 \end{aligned} \tag{5}$$

Considering the explicit dependence of r on $p(x)$ we can write;

$$r(p(x)) = b(p(x))e^{-\alpha\bar{d}}e^{-\alpha r(p(x))} - d(p(x))$$

Substituting $y = r(p(x))$, we have;

$$y = -d(p(x)) + b(p(x))e^{-\alpha\bar{d}.e^{-\alpha y}} \tag{6}$$

Using the general solution for $p(x) = a + be^{cp(x)}$ given by $p(x) = a - \frac{1}{c}W(-bce^{2c})$ and equation 5, we have;

$$\begin{aligned} y &= -d(p(x)) + \frac{1}{\alpha}W\left(b(p(x))e^{-\alpha\bar{d}}\alpha e^{d(p(x))\alpha}\right) \\ \implies r(p(x)) &= -d(p(x)) + \frac{1}{\alpha}W\left(b(p(x))e^{-\alpha\bar{d}}\alpha e^{d(p(x))\alpha}\right) \\ \implies r(p(x)) &= -d(p(x)) + \frac{1}{\alpha}W\left(\alpha b(p(x))e^{\alpha(d(p(x))-\bar{d})}\right) \end{aligned} \tag{7}$$

Equation 7 gives an expression to calculate the fitness of a male where $d(p(x))$ describes how the instantaneous mortality rate of a male increases as baffling propensity increases, W is the principal branch of the Lambert W Function and $b(p(x))$ is the instantaneous egg fertilization rate (analogous to instantaneous birth rate) as a function of baffling propensity $p(x)$ and the intrinsic energy status z. The function $b(p(x))$ is constructed as follows;

$$\begin{aligned} b(p(x)) = &\ \textit{active acoustic volume} \\ &\times \textit{female density per unit area} \\ &\times \textit{rate of attraction of females} \\ &\times \textit{mating duration per female} \\ &\times \textit{effective sperms transferred per unit time} \end{aligned} \tag{8}$$

Here, effective sperms transferred denotes the number of eggs fertilized by the sperms transferred. Since the number of sperms are much much greater than the number of eggs fertilized, we have to somehow scale down the number of actual sperms transferred to get an idea of how many eggs are fertilized by those many sperms. The functions used to approximate these quantities are provided in table 2. The function for audience is based on the spherical spreading of sound in 2 dimensions, function for attraction is hypothesized based on qualitative observation of female phonotaxis rate to playback sounds of different loudness (Deb, Modak, and Balakrishnan 2020), function for Spermatophore Attachment Duration (SPAD) was obtained by performing regression on supplementary data from Deb, Modak, and Balakrishnan 2020 and the function for Effective Sperm Transfer Function is adapted and modified from the same paper. The graphical plots of these functions is depicted in figure 14. Substituting 8 in equation 7 and assuming a simple linear function $d(p(x)) = m.p(x)$ we can get an expression for $r(p(x))$ (refer figure 15). Notice that $r(p(x)) < 0$ even when the instantaneous birth rate $b(p(x))$ and the instantaneous death rate $d(p(x))$ are equal. This is not the case though when a juvenile phase is not considered, i.e. $\alpha = 0$. It is important to note that figure 14 and 15 depict functions computed on the average intrinsic energy state of a population of males $\bar{z}$. It is not necessarily the same as the average of each of those functions computed for every individual in the population. The later, in fact, gives the true **mean population growth rate**. However, since the later endeavor entails the use of not so simple mathematics to convolute these functions, one may be tempted to check if the former is a good enough approximation for the later. Figure 16 depicts the average of these functions within 95% CI overlayed with the same functions computed on $\bar{z}$. As we can see, for small variation in z and a comparatively larger variation in Attraction, this approximation holds well.
For greater robustness we can obtain an expression for *average attraction* by convoluting the attraction function with the normal distribution for $z \in N(\bar{z}, \sigma)$. What results is a rather large expression;

$$\text{average attraction} = \frac{1}{\sigma\sqrt{\frac{s^2+2\sigma^2}{\sigma^2 s^2}}} \exp\left(-\left(\frac{s^2+2\sigma^2}{2\sigma^2 s^2}\right)\left(\frac{\bar{z}^2 s^2 + 2\sigma^2(X - 12p_x)^2}{2\sigma^2 + s^2} - \left(\frac{\bar{z}s^2 + 2\sigma^2(X - 12p_x)}{2\sigma^2 + s^2}\right)^2\right)\right) \tag{9}$$

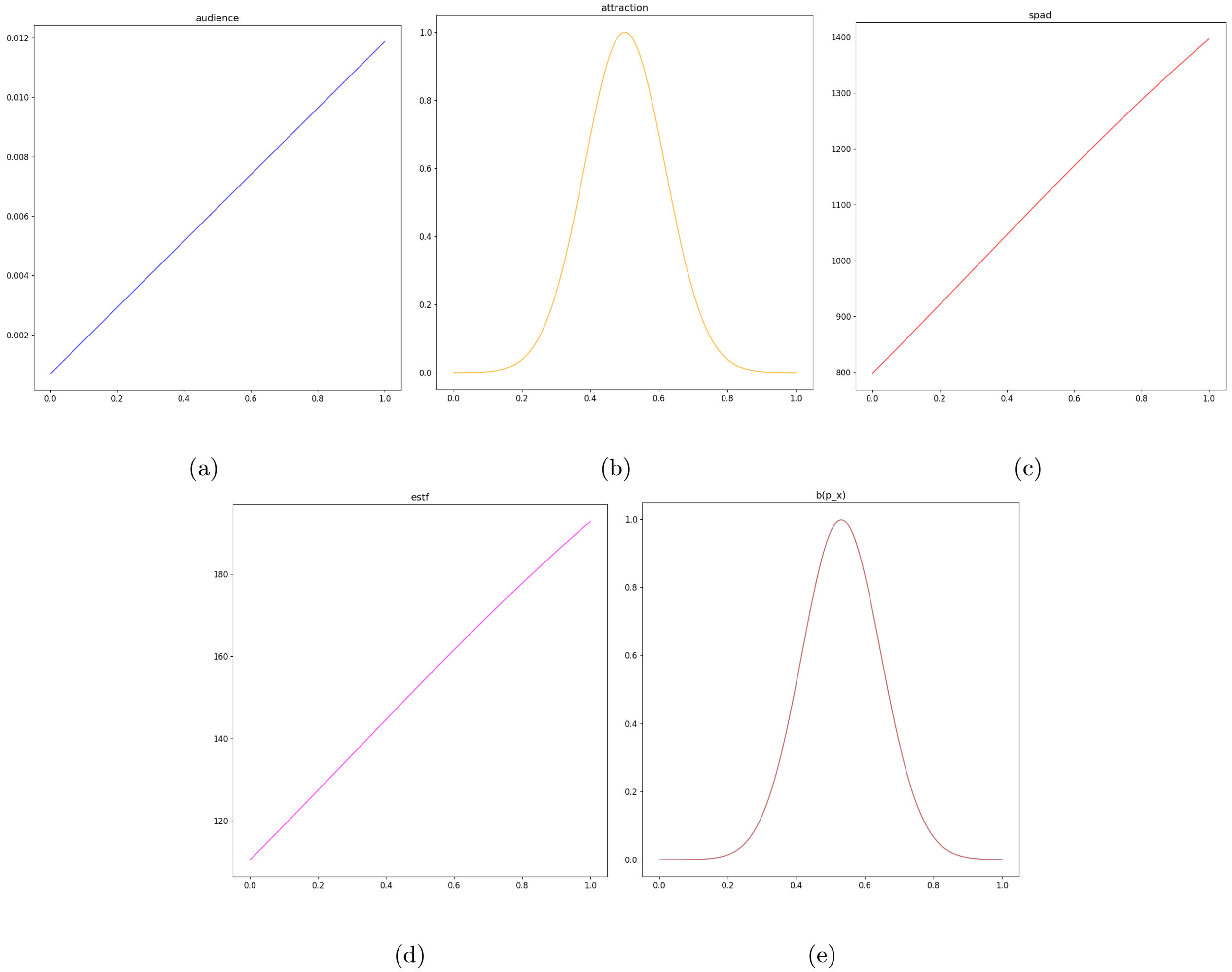
Using equation 9, we can see that $\overline{r(p(x), z)}$ is better approximated by $r(p(x), \bar{z}, \sigma)$ when $\sigma \leq 1$ (figure 17). Now, in an evolutionary context, often what is more useful than the absolute rate of growth is the relative fitness of one phenotype with respect to another. We can therefore consider the relative fitness of a mutant with trait value y in a resident population of x users as;

$$s_x(y) = r(p(y)) - r(p(x)) \tag{10}$$

Thus $s_x(y)$ also gives the invasion rate of a mutant y in a resident population of x users. We can construct Pairwise Invasibility Plots (PIPs) using $s_x(y)$ for different values of x_0 and $\bar{z}$ (figure 18).

Table 2: Functions and their expressions. z is the intrinsic energy status, k, a_0, x_0, σ and c_0 are model parameters that can be tuned using empirical data.

Function	**Expression**
Audience	$\frac{k\left(\pi 2^{\frac{z-45}{3}} + p(x)\pi 2^{\frac{z+12-45}{3}}\right)}{10000}$
Attraction	$e^{\frac{(x_0 - z - 12p(x))^2}{s^2}}$
SPAD	$\frac{1974}{1 + e^{-(0.105832(z+12p(x)) - 5.67869)}}$
ESTF	$\frac{\left(-0.0018(\frac{spad}{60})^2 + 12.468(\frac{spad}{60})\right)}{c_0}$



(a) (b) (c)

(d) (e)

Figure 14: (a)-(e) Audience, Attraction, Spad, Estf and $b(p(x))$. Parameters used: - $z = 50$, $k = 0.7$, $x_0 = 56$, $\sigma = 2$ $a_0 = 1$, $c_0 = 1.5$

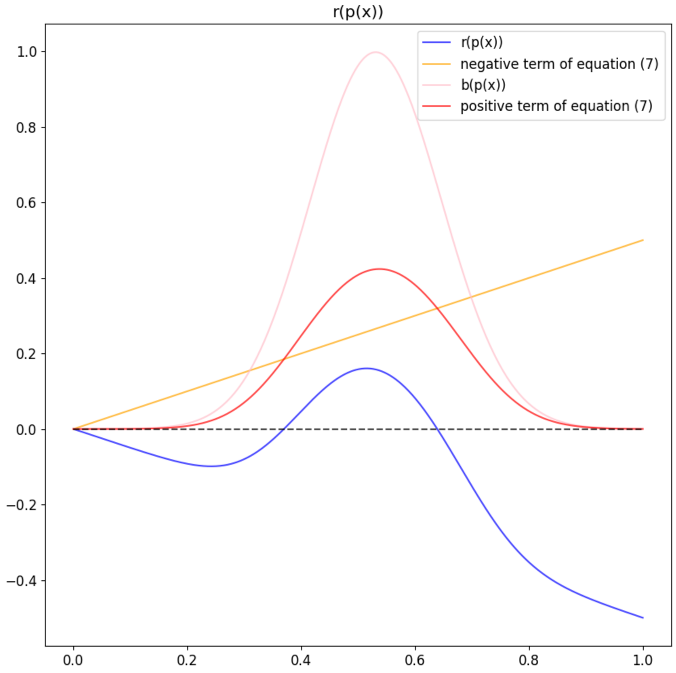


Figure 15: Plot of $r(p(x))$ along with its negative and positive components and $b(p(x))$. Parameters used: - $m = 0.5$, $\alpha = 1$ and $\bar{d} = 0.7$ (other parameters same as in figure 14)

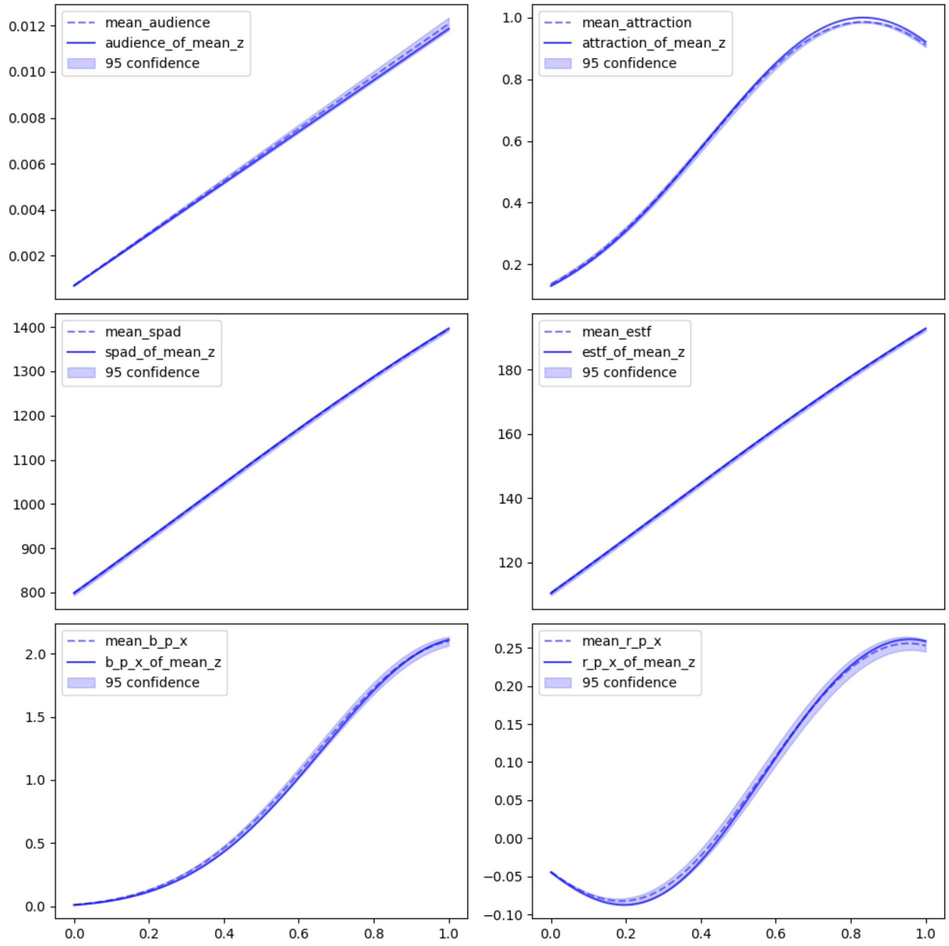


Figure 16: Plots showing the value of $\overline{f(z)}$ with 95% CI and $f(\bar{z})$. Standard deviation in z, $\sigma = 0.8$, standard deviation in Attraction $s = 7$

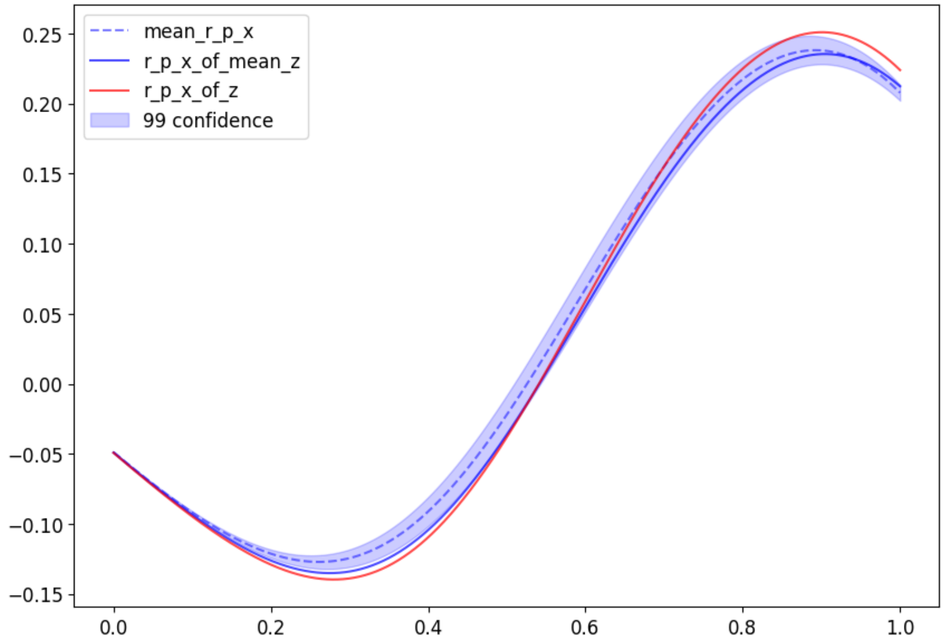
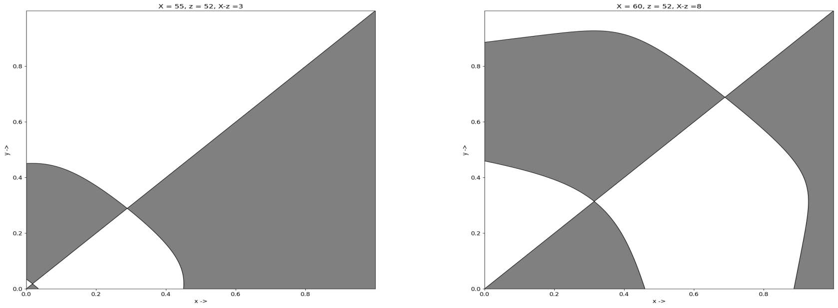
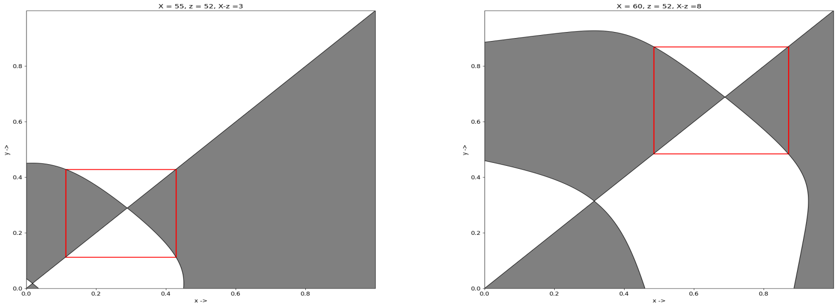


Figure 17: Plot showing the better approximated function $r(p(x), \bar{z}, \sigma)$ (blue) using equation 9 alongside the earlier approximation $r(p(x), \bar{z})$ (red) and $\overline{r(p(x), z)}$ (dotted line). Values of σ and s are 1 and 5 respectively.



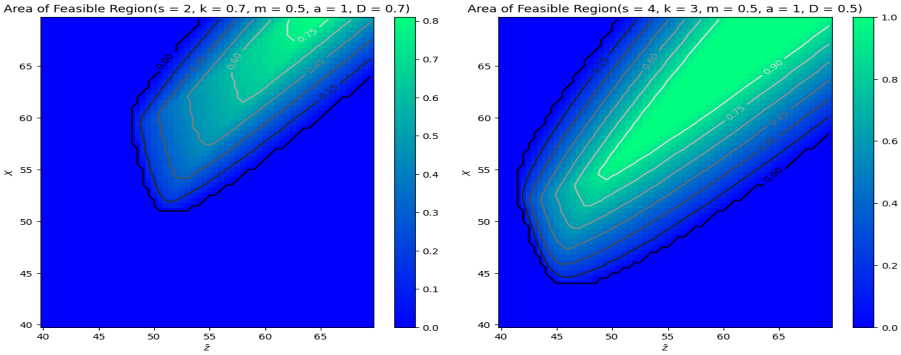
(a) $x_0 = 55,\ \bar{z} = 52$ (b) $x_0 = 60, \bar{z} = 52$



(c) $x_0 = 55,\ \bar{z} = 52$ (d) $x_0 = 60, \bar{z} = 52$

Figure 18: Figure depicting Pairwise Invasibility Plots for different values of x_0 and $\bar{z}$. Figures (c) and (d) depict the feasible region within figures (a) and (d).

Note that we have to be careful when interpreting these PIPs since not for all parameter values $r(p(x))$ is non-negative. A negative value of $r(p(x))$ would mean that the population is headed towards extinction in the long term and hence is not viable. Thus, it is important to analyze the PIP within the **"feasible region"** of trait values for a given parameter combination to ensure that all the populations/trait values considered have a non-negative intrinsic growth rate. Additionally, we can also look at the size of this feasible range as a function of the different parameter values (figure 19).



(a) (b)

Figure 19: Figure depicting color maps of feasible region range as a function of x_0 (corresponding to X) and $\bar{z}$. The color maps change as we change the other model parameter like k, m, s etc.

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