Methods for Modeling Adaptive Evolution

In the lab portion, we will explore various approaches for modeling adaptive evolution and some of the implications of the assumptions of these approaches. For the lab, we will be working with a simple, theoretical model based on Boots and Haraguchi 1999.

Boots, M. and Y. Haraguchi. 1999. The evolution of costly resistance in host-parasite systems. Am. Nat. 153: 359-370.

The Modeling Question

The basic ecological model describes strains of host that may differ in their susceptibility to a directly transmitted pathogen. The question is how the evolution of host susceptibility is impacted by different forms of costs of resistance. Some model assumptions (among many) are that the disease is lethal and only susceptibles reproduce. Ultimately, the model assumes a tradeoff between reproduction and resistance. The basic ecological model is:

$$\begin{aligned} \frac{dx}{dt} &= rx - q(x+y)x - Bxy \\ \frac{dy}{dt} &= Bxy - gy \end{aligned} \qquad (1)$$

Where x is the density of susceptibles, y is the density of infecteds, r is the intrinsic rate of increase of the healthy strains, q is the intraspecific competition coefficient, B is the rate at which the pathogen is transmitted (i.e., susceptibility or resistance), g is the death rate of infected individuals.

The goal of Boots and Haraguchi 1999 is to look at how the evolution of susceptibility (i.e., the B parameter) is affected by different types of tradeoffs. In particular, they consider a linear tradeoff, $r = a * B + b$, and a convex/concave tradeoff, $r = \frac{1}{a(B-b)} + c$.

Warnings and Caveats

Boots and Haraguchi use an Adaptive Dynamics approach to explore how susceptibility evolves under these various tradeoffs. We will apply a number of different approaches to the problem to see how and when they differ. I have had to necessarily simplify the analyses we will do somewhat so that we can fit them into the time allowed and so they will be (hopefully!) understandable given everyone's differing backgrounds. In other words, there may be some hidden assumptions in our analyses, and I want to caveat this lab because anyone who wants to use these techniques will need to do more research on them beyond this brief introduction. That said, I think you will get a good feel for some of the advantages and disadvantages of the various approaches.

Game Plan
We have developed code for the linear tradeoff for four different approaches. The code is developed in both Matlab and r. Special thanks to my graduate student, Dylan George, for translating the Matlab code into R and to Stu Fields for updating it. The plan is to explore these four approaches for the linear tradeoff. You can then modify the code to look at other types of tradeoffs (e.g., convex and concave), other models, or however you want. I put this code together just for this lab (i.e., not for my research), so there are likely to be many ways that you could improve it. If you want to think about how to improve the code, that would be useful too.

Evolutionary Consequences of Linear Tradeoffs
Let's get started. Your mission is to first understand the code that we've written and how it relates to the four approaches that I've described: Lande's Deterministic Approach, Adaptive Dynamics, Lande's Deterministic Approach with Ecology, and Adaptive Dynamics with Ecology.

1) Boots and Haraguchi used an Adaptive Dynamics approach, but we'll start with Lande's Deterministic Approach. The code is in the file "Lande". In terms of understanding the approaches, you should understand where the equations come from and you may want to play around with the sigma parameter (additive genetic variance) and possibly the time scale.

2) Compare the results from Lande's Approach to the Adaptive Dynamics approach. The Adaptive Dynamics approach is coded in the file "AdaptiveDynamics". The main difference is the addition of mutational stochasticity. How does the addition of mutational stochasticity impact the results? Again, try to understand how the code is working, where the mutational stochasticity is implemented and play around with the initial conditions, mutation size and time scale.

3) Next, look at how making ecology explicit might change the outcome. This basically means relaxing the assumption that the populations are at the ecological equilibrium all of the time and allows some interaction between the ecological and evolutionary time scales. The deterministic approach with ecology explicit is coded in the file "LandeEcology". Again, understand how the equations are working and then play around with the mutation rate. As you increase the sigma parameter, you are increasing the amount of interaction between ecological and evolutionary processes. How does this change the results? (This was the approach used in the Darwinian Extinction example).

4) Finally, we want to look at adding ecology explicitly to the Adaptive Dynamics approach. Essentially, this means that we consider both mutational and demographic stochasticity (like the plague example). First, we should look at how an ecological model with demographic stochasticity is coded (no evolution at all). Open and run the file "EcologySim". This is a stochastic version of the ecological model (1) coded using a Gillespie algorithm. Try to understand how the code is working and where the demographic stochasticity comes in. If you want to compare to a deterministic model, you can run "LandeEcology" with sigma set to zero.

5) Both demographic and mutational stochasticity are implemented in the code in "AdaptiveDynamicsEcology". Can you see the skeleton of the ecological simulation? How is mutational stochasticity implemented here? How are the results the same or different from the results using Adaptive Dynamics assumptions or deterministic models with ecology explicit? Why do the results look this way for this model? How important is the assumption in Adaptive Dynamics that the ecological system is at equilibrium? How important is the assumption of no stochasticity in the deterministic models with and without ecological dynamics?

Biologically Interesting Things to Play With

I did not provide code to plot the tradeoff, but you may want to do this because it can sometimes help you think about the biological implications of what is going on.

Linear Tradeoff

1) Play around with q and think about the relationship between q and the value of B ultimately reached.

2) How does adjusting the strength of the tradeoff affect the evolutionary trajectories?

Other Tradeoffs

I suggest that you work with the approaches without explicit ecology to explore the impact of these other tradeoffs because the models with ecology explicit (particularly the stochastic approach) are difficult to work with as the mutation parameters need to be tuned to see interesting results.

3) The linear tradeoff has a slow approach to the ESS. It is technically an ESS that is neutrally stable. You may want to play around with other tradeoffs to see other evolutionary behaviors. The convex tradeoff is an ESS that is convergent stable. One consequence of this is that the convex tradeoff example should move more quickly to the ESS than the linear tradeoff. Try the following parameter values for the convex tradeoff [q=.05; g=1; a=-2; b=-2; c=2.5]. The concave tradeoff does not have an ESS. It acts as an evolutionary repeller. The evolutionary trajectory depends on initial conditions. Try the following parameter values for the concave tradeoff [q=.05; g=0.05; a=-2; b=2.2; c=0.01].

4) q and the cost parameters have somewhat similar effects for the concave/convex tradeoffs. You may want to confirm this for yourself.

5) In the concave tradeoff, the value of g determines whether or not there are two evolutionary trajectories depending on initial conditions or if there is just one. Play around with this.