notes on Levins 1966

On Levins (1966)

evolutionary population genetics models ("Robust and Non-robust Theorems")

Don't get too hung up on these; understand the main points if you have time, but this is **not** the main reason I'm asking you to read this paper! The first time through the paper, focus on the **results** from this section (i.e. (a) first paragraph of the section; (b) first para. on p. 425 (results of Model 1); (c) last *full* paragraph on p. 425 ("These two models differ ..."); (d) last paragraph on p. 426 (carrying over to p. 427); here "environmental uncertainty" means *temporal* variation while "certain but diverse environments" mean *spatial* variation.

- There is a fundamental difference between **spatial** averaging of fitness (which leads to an arithmetic average of the fitness of all phenotypes) and **temporal** averaging of fitness (which leads to a geometric average). (See e.g. Frank (2011).) As an example, consider a phenotype that has a 50% probability of fitness of $W_A = 2$ and a 50% probability of fitness of $W_B = 0$, depending whether it occupies environment A or B (which each have a frequency of 50%).
  - If we distribute N individuals randomly across a spatial landscape, $N/2$ of them will have fitness of 2, $N/2$ will have 0, the total population will have a fitness of 1 (N offspring from N individuals).
  - Not suppose that the environment A and B occur in sequence. The total fitness over two years is $\sqrt{W_A W_B}$=0. This idea generalizes considerably; as long as there is any non-zero probability of a fitness of zero, the expected long-term average fitness is zero — it doesn't matter whether the alternation of environments is deterministic or stochastic. This is why Levins says that the average fitness is $pW_1 + (1-p)W_2$ for spatial heterogeneity and $W_1^p W_2^{1-p}$ for temporal heterogeneity (and equivalently that the best strategy maximizes the log of this expression, $p \log W_1 + (1-p) \log W_2$).
- Model 1 is hard to understand without reading Levins (1962) first: I think the key insight is that when the 'fitness set' (i.e. the region in the plane that represents the full set of **feasible** (physically possible) phenotypes) is concave, the fitness of the population can fall anywhere on the **convex** set that circumscribes (??) the

fitness set (this is called F', in contrast with the fitness set F). The biological meaning here is that this convex extensions represents **polymorphic** evolution strategies, i.e. genotypes that give rise to a mixture of phenotypes.

- p. 427: "As an example of a non-robust theorem": I believe that this assumes that K is a **temporally variable** parameter. The geometric mean of a random variable is a *decreasing function* of its variance. If $\mathrm{Var}(x(1-x/K)) = V$, then multiplying by r will make the overall variance in the rate of growth r^2V, so a larger r will make the variance larger $\rightarrow$ the geometric mean smaller (this is very rough; in particular, r will also affect the variance of x, so we haven't really proved anything). This paradox *might* be resolved by reparameterizing the model as $dx/dt = x(r - \alpha x)$ (Mallet 2012) ...

references

Frank, S. A. 2011. "Natural Selection. I. Variable Environments and Uncertain Returns on Investment*." *Journal of Evolutionary Biology* 24 (11): 2299–2309. https://doi.org/https://doi.org/10.1111/j.1420-9101.2011.02378.x.

Levins, R. 1966. "The Strategy of Model Building in Population Biology." *American Scientist* 54: 421–31. https://www.jstor.org/stable/27836590.

Levins, Richard. 1962. "Theory of Fitness in a Heterogeneous Environment. I. The Fitness Set and Adaptive Function." *The American Naturalist* 96 (891): 361–73. https://doi.org/10.1086/282245.

Mallet, James. 2012. "The Struggle for Existence. How the Notion of Carrying Capacity, K, Obscures the Links Between Demography, Darwinian Evolution and Speciation." *Evolutionary Ecology Research*. https://dash.harvard.edu/handle/1/30212075.