

## 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). 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  $\text{Var}(x(1 - x/K)) = V$ , 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

- 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>.