The allure of adaptation comes from the power of Darwin’s theory to explain natural diversity both within and between populations. Indeed, much of evolutionary study is focused on natural selection and its role in shaping the forms of diversity around us. For instance, Darwin’s finches and the specificity of their beak shape to conform to their diet provide a classic example of natural selection leading to adaptation.

As intuitive as it is to focus on the ability of populations to adapt to new situations, populations are seldom perfectly adapted. Trait values are rarely optimal, populations decline, and extinctions are commonplace. It seems unlikely that populations would ever be able to perfectly match their phenotypic optimum.

This idea leads us to maladaptation, the pattern where populations maintain a stable phenotype some distance away from a phenotypic optimum. For example, here a population hovers around a phenotype described by two polygenic traits, with selection keeping it from drifting too far away, but new mutation, and genetic drift keeping the population from being precisely at the optimum.

This behaviour seems common in nature: a 2007 literature review by Estes and Arnold found 64% of the studied populations were maladapted to some degree.

Despite this, maladaptation is rarely studied. Over 4600 papers featuring the keyword ‘adaptation’ were published in Nature research journals in 2019. The keyword ‘maladaptation’ was mentioned in just 45.

The prevalence of maladaptation in nature raises interesting questions into the essence of evolution: what does it take to be adapted? Quantitative genetics aims to solve these kinds of questions.

Quantitative genetic models attempt to explain adaptation to phenotypic optima using stabilising selection on polygenic traits, where intermediate trait values lead to peak fitness.

Stabilising selection models can be used to determine how heritable variation, known as additive genetic variance or VA, drives adaptation. Increasing VA allows for more rapid responses to selection, because the larger the range of phenotypes in the population, the higher the chance of one of them become adaptive after an event spurs on a selective pressure.

During adaptation, VA is expected to decline, as populations become more similar as more and more individuals reach the optimum phenotype.

This dichotomy leads to the adaptability versus adaptedness trade-off – populations which maintain high variance over time will be able to adapt to environmental change quickly, but they perhaps won’t be able to maintain their position very close to the new optimum because of the variability which arises within the population. The balance of variability is dependent on three evolutionary forces: genetic drift, stabilising selection, and mutation.

VA is maintained in populations by a balance between incoming mutation introducing new variation, and the forces of drift and selection which drive allele fixations or losses.

The effects of each of these processes are further altered by genetic architectures – the number of loci affecting the trait, the size of mutational effects and their variance – mutational variance, pleiotropy, linkage, etcetera. Together, these genetic factors might define where in phenotype space equilibria lie, and hence, outline the limitations to adaptedness that populations might face. For example, introducing more mutational variance through highly variable mutations at a high rate might enhance adaptability through more raw genetic material for selection to act on, but this may be costly for adaptedness, as most of these mutations will be deleterious when hovering around an optimum, driving populations away.

Is there a particular genetic architecture or balance of evolutionary forces that facilitate movement towards a phenotypic optimum, and being able to hover around it over time?

To investigate this I used a simulation approach using the forward genetics software SLiM. I simulated (or rather SLiMulated) populations hovering around an optimum for 100,000 generations.

Populations had eight traits with equal effects on fitness, which I combined to a ‘mega-trait’ for simplicity.

I ran a total of 128,000 simulations with 100 replicates of 1280 parameter combinations. To explore the data, I first investigated how common adaptation was.

In my simulations I found a strong distinction between adapted and maladapted populations: a visible ‘dead zone’ where populations weren’t represented. I split populations that fell on either side of the dead zone into ‘adapted’ populations and ‘maladapted’ populations.

Within null models with no selection treatment at all, populations very rarely reached the optimum – 0.5% of the time. Gaussian and House-of-Cards models reached the optimum a similar amount – 15.23 and 16.1%, respectively.

But what caused these populations to break away from their maladapted cousins? For that, I investigated the effects of my genetic parameters on adaptation.

I found pleiotropy, mutational correlation, and recombination rate each had very little effect on whether populations appeared in the adapted zone.

Additive effect variance was strongly correlated with the chance to get to the optimum: 36.12% of models with low effect size variance reached the optimum, versus 2.29% of medium-variance populations, and 0.19% of large effect, high-variance populations.

Changes in mutational variance affect the two models differently – under House-of-Cards, where mutation is weak and selection is strong, populations tend to be more robust to increases in mutational variance, whereas under Gaussian models, populations are more susceptible to increases, with distance to the optimum tracking the mutational input closely.

One way to visualise this is via the movement of molecules with temperature – Gaussian models are hot, erratically moving around with increasing mutational variability, whereas House of Cards models are cold, responding to a lesser degree to mutational variability, since strong selection allows for deleterious mutations to be efficiently purge, without large numbers of new mutations coming in to swamp the population.

While this confirms that some aspect of genetic architecture plays a role, we still don’t know if this is reflected on a population genetics level. Are alleles mediating this effect? To test this I looked at the distributions of allelic effects underpinning each model.

Here, I found distributions of allelic effects mirrored the impact of each model and mutational variance treatment on distance to the optimum. Once again, House-of-Cards mutations were more robust to change in allelic distributions than Gaussian models when increasing mutational variance.

The relative protection from large mutational effects that House-of-Cards models enjoy comes down to the mutation rate populations from being swamped by deleterious alleles. When this is paired with strong selection, this results in an efficient removal of deleterious alleles that drag populations away from the optimum. Under Gaussian models, selection is less able to reign in these effects, so fluctuations away from the optimum are more likely as more and more mutations pile up.

Where does this matter though? These findings have implications for the environments under which different mutation-selection balances could flourish.

In homogeneous environments, where environmental change is rare both spatially and temporally, House-of-Cards models should be favoured: the increased stability and favours stronger adherence to the optimum over time, and so in the balance between adaptability and adaptedness, adaptedness is favoured.

In heterogeneous environments, as long as the change in environment is predictable, Gaussian models should be favoured: increased mutation rates allow for a broader exploration of the phenotype space, and given the environment changes rapidly, those explorations will become adaptive quickly. In a spatial sense, this could also allow for adaptive radiations into spatially variable niches, depending on the heterogeneity of the environment. For example, plants with a highly mutable trait for preferred levels of sunlight might find that high mutation is preferred in an environment where canopy cover is patchy, whereas it could be detrimental in either densely or sparsely covered areas.

Obviously, I’ve only really looked at the tip of the iceberg here, and there is a lot of future potential for this kind of simulation work. Introducing variation in the strength of drift via changes in population size would be an interesting venture into how the dynamics of these models shift with changing efficiency of selection. More complex differences between traits would enable a more complex look into variance-covariance structures, called **G** matrices, for more realistic insights into limitations on selection multi-trait phenotypes. In addition, increased parameterisation of the hyperspace with the number of loci impacting traits, chromosomal effects, and increased ranges of recombination and pleiotropy could give further insights into genetic architecture limitations on adaptation.

Finally, the most exciting prospect is the use of mathematical emulators to predict responses given the population of samples we have collected, and using that to fit experimental data to model architectures. If we do our job correctly, we should be able to roughly predict the genetic architectures and mutation-selection-drift balances underpinning the evolution of complex traits.

Snippets

This is particularly apparent in polygenic characters, where the many alleles and loci contributing to a trait form a continuous distribution of trait effects and phenotypes. In this scenario, many mutations contribute to the trait of interest, leading to an increased importance on the relative strength of selection and mutation rate.

How stabilising selection controls the maintenance of VA in populations following adaptation depends on how mutation, selection and drift are balanced.

This may occur for several reasons: the strength of selection may be too weak, the environment may change too quickly for the population to keep up, or the new mutations entering the population each generation may be too variable and common to enable closeness to the optimum. A 2007 literature review by Estes and Arnold found that 64% of studied populations were maladapted to some degree.

Both models have trouble accurately predicting levels of genetic variation found in natural populations, but perhaps a part of this is in the assumption that these natural populations are perfectly adapted. Given the prevalence of maladaptation, providing more genetic variation than expected when a population is at a local optimum.

Comparing these models (Gaus HoC) is important for adaptation because it outlines the limitations populations might have adapting to new environments given their genetic architectures.