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.

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Driving adaptation by stabilising selection is additive genetic variance or VA. Theory predicts that increased 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.

So here we’ve seen a paradox: populations need VA to make the move towards an optimum (gesture to orange arrow), but inherently being variable around an optimum (hovering blue line) means populations are maladapted to a degree.

In other words, there is a trade-off between adaptability and adaptedness. The nature of this trade-off depends on how variance is maintained in populations, and the genetic architectures underpinning important traits in those populations.

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. Ignoring drift for now, which results in random fixations or losses of alleles, quantitative genetic models aim to simulate this balance based on one of two assumptions.

Gaussian models assume weak selection relative to mutation rates, resulting in higher levels of standing genetic variation.

House-of-Cards models on the other hand assume strong selection and relatively low mutation rates, leading to lower standing variation. However, genetic aspects of the traits themselves can also influence the propagation and maintenance of variation in populations.

Quantitative genetics aims to tease apart nature from nurture: the genetic (point) and environmental effects (point) contributing to a phenotype. To do this, we can define a trait’s genetic architecture, which consists of the genetic characteristics defining G in this equation.

The genetic architecture of a trait defines its characteristics – the number of genes affecting it, their locations within the genome, and their strength of allelic effects (POINT TO EACH ON FIGURE). Here I explore the effect of allelic effect distributions on equilibrium variance after adaptation.

Now with a firmer view on how adaptation is driven in quantitative traits, we can reform our question:

Is there a specific 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 a phenotypic optimum for 100,000 generations.

Populations had eight traits with equal effects on fitness, which I combined to a ‘mega-trait’ for simplicity. I explored a ‘parameter space’, where I varied six parameters: pleiotropy rate, mutational correlations between traits, additive effect size variance, recombination rate, mutation rate, and selection strength. The idea is to sample combinations of parameters across the entire hyperspace (gesture to cube) in order to efficiently sample the entire range of parameters.

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 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 size variance on the other hand…

Additive effect size variance was strongly correlated with the chance to get to the optimum: 36.12% of models with low effect size variance reached the adapted space, versus 2.29% of medium-variance populations, and 0.19% of large effect, high-variance populations. However, additive effect size had considerably different effects on Gaussian versus House-of-Cards models.

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. Bear in mind only one model reached the adapted space in high variance Gaussian models, and only three in medium variance House-of-Cards models.

Variance followed a similar pattern.

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 purged, without large numbers of new mutations coming in to swamp the population.

So now that I knew Gaussian models responded differently to increasing mutational variance than House-of-Cards models, I wanted to find what was mediating this difference. 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.

From this, we can say that House-of-Cards models deal with deleterious alleles differently to Gaussian models. The strong selection – low mutation combo leads to 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.

For example, here Xs represent populations, with the size of the X representing the mutational variance in that population. The ability to hover around the optimum closely, maintaining adaptedness, is greater even with high mutational variance in House-of-Cards models.

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

In environments where spatial or temporal change is rare, House-of-Cards models should be favoured: the increased stability and favours stronger adherence to the optimum over time, and so in the trade-off between adaptability and adaptedness, adaptedness is favoured.

In heterogeneous environments, Gaussian models should be favoured: increased mutation rates allow for a broader exploration of the phenotype space, and over time those explorations might become adaptive – as seen here, with the future optima, shown in orange, being closer to current levels of variation. 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.

There’s a lot of potential for this methodology and clearly a lot more to understand in terms of how mutation-selection-drift equilibria interact with genetic architecture to influence adaptation. Increased parameterisation of the models would help gain more insight in this regard: population size to assess the effects of drift, fitness differences among traits for more realistic insights into covariance structures and correlated selection, the number of loci contributing to the trait, and the positions of those loci along the chromosome to name a few. With enough refinement it should be possible to predict genetic architectures of natural populations by matching experimental data with a model in our hypercube sample.