**Week 9: Plasticity**

7 groups: 27+ participants

**Summary:** Groups discussed phenotypic plasticity based on Waddington’s classic work (*Evolution* 1953) and Schaum and Collins 2014 paper on evolution in marine algae (*Proc. Of the Royal Society B*).

**1. Compare and contrast the two experiments. In what ways are they similar and different?**

**LSU:**

* Main difference is experiment itself. Waddington used artificial selection to select for particular trait, while Schaum paper enforced a stressful event and let natural selection take its course.
* Probably no mortality in flies, so no fitness disadvantage, while the strong selection event in algae does rely on fitness.
* Waddington paper was trying to demonstrate genetic assimilation via canalization of a trait, question whether it is actually shown.
* Would be interesting to see if flies become canalized for the veinlessness trait if they were heat shocked and then allowed to mate randomly (rather than with just other veinless). Certainly demonstrated canalization which was also observed in some of the Schaum paper.
* Schaum paper demonstrated that algae grown in stable high CO2 environments had higher growth at control levels of CO2. Algae grown in fluctuating environments had greater plasticity and were able to have normal growth rates under normal CO2 conditions demonstrating that a trait that is plastic under high CO2 scenarios can become canalalized if it is continuously exposed to these conditions.

**NEU:**

* Baseline difference was focus of Waddington on a purportedly non-adaptive variant through artificial selection vs. the direct focus on adaptive natural selection.
* While Waddington focused on stable exposure, Schaum focused on fluctuating vs. stable exposure.
* Both experiments highlight broad umbrella of cross-generational plasticity, Waddington paper focused on immediate responses of a stable temperature change as opposed to the effect of a fluctuating exposure.

**FSU:**

* Possible interpretation of waddington’s work is that the variation for that trait was in ancestral populations and that environmentally induced phenotype were actually present in the original wild stock and plastic phenotype was not actually plastic but rather a kind of threshold trait.
* Alleles for veinlessness are expressed after the heat shock exceeded some threshold for expression, then just increased in frequency over multiple generations of artificial selection for cross-veinlessness.

**UC Davis:**

* Schaum uses Ostreococcus which is large pop of marine microbes with short gen times and ample scope of evolution, while Waddington uses drosophila with smaller pop sizes and slower mutation rates.
* Schaum starts with 7 strains that differ in plasticity before the start of the experiment, Waddington uses one
* Schaum exposes both stressors and fluctuating environment, wadington only exposes one stressfull environment against ambient.
* Waddington’s trait not adaptive, Schaum saw adaptiveness
* Waddington did a lot of back crosses to fid genetic architecture which Schaum did not do.
* Waddington did no measure a fitness trait, do not kow whether mutated flies would survive or not. Schaum tested some fitness traits (baldwin’s).
* Waddington gives empirical evidence of a case where non-heritable environmentally induced variation is converted ito heritable variation. Initially this is cryptic genetic variation, will it become adaptive?
* Both have no idea about genetic architecture of the traits.
* Both investigate environmental drivers of phenotypic variation.
* Both show genetic assimilation

**UChicago:**

* Appreciate clear experimental design in waddingtons paper that first aimed to evolve plasticity and then test the extent that it augments evolution. Does seem difficult to be convinced that their metric of plasticity (o2 consumption in 2 environments) was able to resolve whether the phenotypic variation in the FA line was driven by increased genetic variation or plasticity.
* Revisited Botero et al. 2015. Model explored conditions under which plasticity is expected to evolve. Focal parameters of model were time scale of fluctuation and predictability of environmental switch.
* Environmental switch in schaum is not predictable and time scale is long relative to generation time.
* Under such scenarios, Botero predicts reversible plasticity is not favored but rather a diversified bet-hedging or adaptive in which phenotypic variation among individuals is fixed and genetic variation is maintained to facilitate adaptation to sudden and random shift in the environment.
* Hard to be certain this isn’t what happened in the FA line of the Schaum paper, as ultimate result of FA line evolving faster would be increased genetic variation in that line.
* More robust if they could track patterns of genetic variation in each lines to ensure that this metric did not accumulate disproportionately across treatments.

**UCSB:**

* Waddington paper selected arbitrary trait with no ecological relevance or fitness consequences. Schaum picked oxygen evolution rates as example of plastic trait with adaptive value as well as strong selective pressures on fitness related traits that are ecologically relevant.
* Two experiments used different selective pressures: Schaum used stable and fluctuating pCO2 treatments to drive selection rather than the artificial selection of crossveinless phenotype
* Direction of evolved trait differed between two experiments. Waddington demonstrated that genetic assimilation via canalization of phenotypic trait is unidirectional whereas in the case of Schaum et al the evolved trait was in the opposite direction of the evolved response.
* Schaum’s effort to raise 14 generations of variation adapted lines in static pco2 environment in order to rule out maternal effects as the driver of the adaptive pattern. While Waddington demonstrated the crossveinless was clearly heritable, we were not convinced that the increase in frequency of this phenotyp wasn’t tied to maternal effects.
* Acquired characters could have been cryptic genetic variation that manifested as a phenotype due to plasticity and increased in frequency across heat stressed generations via transgenerational effects.

**Rutgers:**

* Discussed how these two papers both investigate environmental drivers of phenotypic variation and in both cases how genetic architecture of trait is unknown.
* In both studies, genetic assimilation was observed.
* Classical paper such as waddingtons compared to newer paper – differences between two studies.
* Constrast between types of traits examined differed between papers (fitness vs. non fitness trait).
* Schaum demonstrates that evolutionary trajectory can be determined by ancestral plasticity. Agreed that in both papers, findings were close to proposed hypotheses.
* Plasticity and amount of plasticity required was addressed and how plasticity allows for flexible pathways which allow shifts in the default.

**2. How does plasticity in ancestral populations determine evolutionary trajectory?**

**LSU:**

* The more plastic the population, the more those populations seemed to evolve. Schaum paper clearly demonstrated that evolutionary trajectory can be determined by the ancestral plasticity.
* Wish there were more discussion on whether the evolutionary trajectory is always going to be beneficial for population.
* Lower growth rates might seem disadvantageous, authors do a nice job of explaining this can provide fitness advantage but want more empirical support.
* Don’t think the direction of evolution can be determined by plasticity and whether those changes will be beneficial or maladaptive.

**NEU:**

* Consider situations where plasticity is cyclical (or appears that way). In some environments, could be beneficial to be increasingly plastic while in others it may be beneficial to canalize around fixed phenotype.
* Discussed situation in which canalization may be a periodic point of evolution but there could be sufficient variation maintained around the canalized slope that could allow for plasticity to re-evolve if the environment changes and plasticity becomes adaptive again (sensu Lande et al. 2009).
* Consider how timing of environmental exposure can affect plasticity vs. canalization. Some traits can be developmentally plastic, but once induced, become fixed in the phenotype even if the environment changes.
* In contrast, some responses like gene expression are much more flexible and responsive to continual fluctuations in the environment. Differences could have important implications for the ultimate fitness and evolutionary trajectory of species.

**UC Davis:**

* More plastic lineages evolved faster than the less plastic ones.
* Why does plasticity in one trait make the population/strain evolve faster in another trait? Apparently two traits are correlated.
* Generally it would depend on strength and direction of selection as well as on the standing genetic variation in a population.
* If there is no underlying variation, a population might not adapt. I.E. adaptive plasticity can be so good it prevents adaptive evolution because the all purpose genotype produces an optimal phenotype in every environment.
* There is potential for adaptation, as long as the change in mean trait value goes into the same direction favored by selection in the new environment but below the adaptive peak.

**UCSB:**

* Results from schaum paper demonstrate that evolutionary trajectory can be determined by ancestral plasticity. Ostreococcus lineages founded from more plastic ancestors evolved more in high pCO2 environments than lineages founded from less plastic ancestors supporting the relationship between plasticity and evolution.
* With many ecological and evolutionary concepts, the adage “it depends” applies here. Plasticity does not always confer an adaptive benefit – in some cases, such as in a fluctuating environment, it benefits the population to maintain a degree of plasticity. In others, such as in a more stable environment, the costs outweigh the benefits of plasticity and the evolutionary trajectory leads in a direction away from the plastic population.
* Even in this scenario, it depends on generation time of focal organism, frequency and duration of environmental fluctuation, etc.

**3. Do empirical results agree or disagree with theoretical arguments?**

**LSU:**

* They agree.
* Past theoretical arguments converged on plasticity hindering a populations’ ability to evolve, more recent theoretical work seems to demonstrate the opposite.
* Plasticity enhances evolution/adaptation to new environments and Schaum paper results agree.

**NEU:**

* Plasticity should counteract true adaptive evolution and only if your plastic response happens to align with directional selection can in improve response rates to environmental stressors.
* Repeatedly refer back to fisher’s geometric model to visualize misaligned plastic potentials with adaptive gradients.
* The role of epigenetics in plasticity provides one particular mechanism of plasticity that requires more explicit study before broader theoretical models can be properly tested.
* Given theoretical predictions around genetic assimilation and plasticity, there are some theoretical scenarios that could only be supported once explicit mechanisms are more properly understood: with epigenetics being the elephant in the room.
* Relying too much on a single mechanistic determinant of plasticity can be a pitfall, and the theoretical value of work observing plastic responses, even in the absence of clear mechanisms is evident by the fact that we collectively read and compared a research article written almost 70 years ago to discuss the many still unsanswerd questions about plasticity.

**FSU:**

* Way authors define and use genetic assimilation seems to be slightly different to use Waddingtons version.
* Some definitions of GA are that it is a process that converts a plastic response into a genetically invariant one. If one considers plasticity itself (slope of reaction norm) as a quantitative phenotypic trait subject to selection and capable of evolving like any other quantitative trait.
* When viewing plasticity as quantitative trait, idea that responses to environmental change are through plasticity or evolution or the idea that plasticity promotes or affects evolution seem odd.
* Larger environmental changes could more easily be bridged by a plastic genotype. When environment is constant, there is no longer selection for plasticity so the reaction norm slope does not evolve or evolves to zero.
* Rate of environmental fluctuation was slow relative to generation time, so some environments were both variable and predictable and these treatments selected for plasticity.
* Results of schaum and Collins consistent with predictions from quantitative genetic theory that treats plasticity itself as a trait.

**UC Davis:**

* As Ghalambor points out: adaptive plasticity that places populations close enough to a new phenotypic optimum for directional selection to act is the only plasticity that predictably enhances fitness and is most likely to facilitate adaptive evolution on ecological time scales in new environments.
* This type of plasticity is likely to be the product of past selection on variation that may have been initially non-adaptive.
* Historically, theory suggested that selection acts on non-heritable phenotypic variation will not produce an evolutionary response is unimportant. (wtf)
* Environmentally induced variation might slow rate of adaptive evolution because it is shielding the genotype from the effects of selection.
* But west-eberhard showed that plasticity can become GA or speed up process of adaptive evolution. For this to work, there needs to be initial phenotypic variation/plasticity and the population needs to be faced with an environmental change following directional selection.
* May be disadvantageous at first to be plastic but the cost is not high relative to selective pressure. In other words, only those that are plastic can survive.
* But later directional selection will favor the new trait and genes coding for it will be under direct selection. Ultimately, selection might cause a variable trait to be fixed in the future. This depends on whether the environment changes to a new state or is fluctuating. Invasion bio is good place to study this.
* How likely is it? Will majority of populations die instead of resisting to new directional selection? Is maintaining phenotypic variation in a constant environment costly?
* As ghalambor points out: adaptations to new environments rarely involve single traits but rather suites of traits that respond to diverse selection pressures. Brings us back to week 5 where we discussed genetic correlations between different life stages of an organism. Might constrain potential for plasticity.

**UCSB:**

* Empirical results agree with more recent theoretical arguments regarding plasticity’s ability to reveal genetic variation at the phenotypic level, allow slection to occur across a greater number of otherwise cryptic genetic variants – plasticity promotes evolutionary innovation or adaptation and schaum paper demonstrates this.
* Previous evolutionary theories regarding plasticity have noted that it may limit adaptive potential. Schaum demonstrated that not all selective pressures result in adaptive responses by plastic populations. Can help synthesize competing theories regarding plasticity’s role in evolution.