**Week 8 – Balancing Selection**

**12 groups – 49+ participants**

**1. What constitutes strong evidence for fluctuating selection, especially if the trait under selection is maintained by many loci with small effects?**

**UGA:**

* Discussion over how expectations play out over distinct life histories – gave example.

**WSU:**

* Presence of variability does not preclude alternative hypotheses of causation. We think you can’t separate phen. Plasticity from underlying genetic structure by looking at phenotype- just correlation at the phenotypic level is not strong evidence for fluctuating selection.
* Using definition of selection, have to have genetic info underlying the traits (census of the multiple loci that we think are driving the pattern. Also important to do this over long time period, not snapshot.

**UMass Amherst:**

* Does fluctuating selection require a temporal component? Yes.
* How do fluctuations in the ocean depart from seasonality? More rooted in large scale climate cycles (el nino) and changes in salinity, tide, environmental conditions.
* Fluctuating selection may contribute to greater diversity which would support higher adaptive capacity in response to changing environments.
* Appreciate isolating fluctuating selection as driver of season adaptive oscillations in drosophila especially since presence of oscillations could reflect a myriad of ecological conditions.

**UCSB:**

* Clear that fluctuating selection was maintaining genetic variation among seasonal SNPs independent of other processes such as pleiotropic balancing selection.
* Evidence for fluctuating selection stronger when this pattern exists for multiple alleles that are not in linkage disequilibrium and when the phenomenon can be observed in multiple populations experiencing cyclical shifts in selection.
* Fluctuating selection may be more likely to maintain polymorphisms at multiple alleles of small effect rather than a few alleles of large effect, as fewer alleles are more likely to exhibit an “all or nothing” pattern that does not maintain variation under fluctuating selective pressures. If so, wonder if evidence of fluctuating selection at small number of alleles requires more investigation than what is present in Bergland paper.
* Fluctuations in direction of selection could simultaneously decrease certain alleles while increasing others. Why do seasonal patterns in bergland paper emerge (more seasonal SNPs in spring, decrease in fall).
* Some alleles should be under greater positive selection during fall and increase in abundance.
* But flies grow faster during warm seasons, so did this allow for beneficial alleles to propagate faster in the spring? Life cycles faster than the frequency of selection are the only cases that lend themselves to fluctuating selection and could be broadly important for ectotherms with rapid life cycles.

**Uchic/GaTech/Auburn:**

* Fluctuating selection pressures are likely prevalent in marine systems and the extent to which a fluctuating selection pressure produces and maintains genetic variation likely driven by the frequency/periodicity of selective regime relative to the species’ generation time.
* Species with shorter generation times amplify strength of divergent selection acting on a trait across generations. Species with generations that exceed periodicity of the fluctuations are likely to evolve a plastic response with regards to the stressor.
* Specific timing of an environmental fluctuation in respect to the life history stage of a species may also be an important consideration. (if sensitive stage occurs in different seasons).
* Identifying the presence of such temporally fluctuating selection difficult because they probably have polygenic basis, so the selective signature of which will be spread across several loci of small effect. Powerfully identifying loci involved in this process within a single population will therefore be difficult.
* Suggest following seasonal fluctuations in genetic variation across multiple “replicate” populations (separate populations exposed to the same fluctuating selective pressures). Allow for a more powerful way to identify small-effect loci that exhibit fine scale temporal fluctuations.

**Cornell:**

* Regarding the Bergland paper, the empirical case is strong. Recognized the interest in estimating the age of these seasonally cycling polymorphisms to address hypotheses about the importance of balancing selection for maintaining polymorphisms, and because it strengthens the balancing selection inference relative to alternative mechanisms.
* However, some thought that balanced polymorphisms needn’t be interspecific in age to be interesting and important for patterns of diversity.
* Adaptation to new environment might entail temporal fluctuations not experienced before, such that adaptation is via fluctuation of relatively new variants.
* Question whether old alleles should be a necessary criterion for demonstrating fluctuating selection.
* Short generation time of drosophila made it an excellent model for cycling adaptation to seasonal variation. What types of variation is periodic and regular enough to generate this dynamic for longer lived organisms? El-nino maybe, but these aren’t as symmetrical.
* How irregular can environmental flux be and still maintain diversity by fluctuating selection? Partially addressed in second paper, describing conditions for stable balanced polymorphisms in a polygenic model with reversal of dominance and diminishing returns of fitness.
* Curious about reversal of dominance beause it is crucial for model, but unfamiliar. Other papers have shown beneficial reversal of dominance for survival to adulthood in fresh vs. saline water. Dominance depends on environment, is an attribute of the favored allele in each environment. Need easier ways to screen for dominance!

**Laval:**

* We first discussed what we came up with from the readings of the two proposed papers. Wittman et al. showed that stable polymorphism at many loci is possible if currently favored alleles are sufficiently dominant (segregation lift), and Bergland paper revealed that typically revealed that typically variable selection contributes to repeatable adaptive oscillations at balanced polymorphisms.
* Showed that seasonal SNPs are enriched among functional genetic regions and present their association with variable phenotypes (starvation tolerance and disease recovery) so there is evidence of fluctuating selection.
* In marine environments, fluctuations are not necessarily representative of seasonality but correspond more to large scale changes like climate cycles. Even assuming seasonality in marine environment to be able to see evidence of Fluctuating selection the generation time should be shorter than the season length. So evidence of FS will be more plausible for organisms with rapid life cycles. Another point is that FS has to be stronger than stabilizing selection to persist.
* Finally, in marine environment, genetic drift is minimized (because of gene flow and generally high Ne) so natural selection is more efficient and more detectable (phenotypically talking) even with many loci of small effect involved.

**Rutgers:**

* Evidence is convincing to us (repeatable allele frequency variation by season, the time vs. space comparison, the links to fitness, plus the natural experiment with frost event).
* Many seem accepting of genomic evidence for fluctuating selection now, but we were relatively skeptical earlier about genomic evidence for local adaptation. Are they that different?
* Set up paper as if theory was established and all they needed was empirical support. Except Wittmann paper makes it clear that theory actually isn’t well developed. Bergland paper actually provided evidence for new theory.
* Severe limits in our ability to detect fluctuating selection that acts on many loci with small effects. If effects are small, the frequency changes will be small and/or identity of alleles changing frequency will change through time. Makes detection more difficult.
* Discussed segregation lift and mechanisms that could produce temporal changes in dominance. Thought of traits where plasticity is driven by gene expression, including cases in which one allele might be expressed in one environment but the other expressed in the other environment.

**MIT/WHOI:**

* Seems like actual phenotypic changes are needed to demonstrate strong evidence for fluctuating selection. Also seems like Bergland paper combined multiple lines of evidence to build convincing argument. Opportunistic experiment before and after frost event helped a lot with making it convincing.

**Virtual group:**

* This is the big question.
* Fundamentally, it is a question of detecting local adaptation to seasons
* Many loci of small effect, then signal may not be consistent through time, which makes things difficult. But if signal is consistent through time and across populations, the presence of fluctuating selection is fairly compelling.
* How might one experimentally reproduce the signal of seasonal selection?
* For marine organisms, especially planktonic species with rapid life cycles, there should be abundant seasons fluctuating selection
* Doing this in the lab might help parse down which environmental factors are the primary component to selection
* But also should figure out how widespread that mechanism is as contributor of genetic variation.
* Necessary to consider what types of organisms and fluctuations may be influenced by this – seasonality works with short lived species – what about el-nino? Upwelling? Etc.

**NEU:**

* Finding a simple allele frequency shift that correlates with some environmental variable is likely not sufficient evidence for selection. However, could be strengthened if found over several repeat measures (many seasons) or if the allele frequency shift is observed in different measurements of a particular environmental variable.
* For example, observing allele shifts correlated with season that are also correlated with latitudinal cline provides stronger evidence that these shifts may be the result of selection on temperature related traits.
* Linking genetic variation and allele frequency data with phenotypic variation could also bolster support of selection over drift. Correlations might be hard to find in highly polygenic traits.

**2. What are the benefits/consequences of fluctuating selection for long term changes in the environment?**

**WSU:**

* Maintaining variation is always good for pre-adaptation for future conditions, esp. under climate change.
* Maintenance of variation necessary but perhaps not sufficient if conditions are different from what has been experienced evolutionarily.
* Haven’t read much about seasonal maintenance of diversity.
* May also be relationships with generation time scales and time scales of fluctuation – are these papers relevant to marine organisms with seasonal reproductive events and/or generation times that span multiple seasons?

**UCSB:**

* Fluctuating selection during long-term changes in the environment maintains heterozygosity and increases standing genetic variation.
* Benefit of standing variation in a system where fluctuating selection occurs is unclear. On flip side, fluctuating selection has to be stronger than stabilizing selection may be capable of canalizing phenotypes that are adaptive under future conditions.
* Scale at which fluctuating selection is occurring relative to the scale at which long term changes in the environment are happening is a crucial consideration.
* Population subject adapted to annual fluctuating selection may not be able to sufficiently respond to an increase in the amplitude of monthly changes.

**Uchic/GaTech/Auburn:**

* Bergland paper presents comprehensive analytical framework for examining genome wide patterns of seasonal adaptation that may be useful for future empirical studies, although there were some elements that could be improved.
* To minimize variation, collection protocols should be standardized (same microhabitat, same timing).
* Like the comparison of seasonal SNPs with SNPs from diverged populations to test association with standing genetic variation, however, we felt this comparison would have been more meaningful if they had reported amount of overlap in seasonal SNPs and ancestral SNPs, and given more info on the environmental conditions and seasonality in the ancestral pops.
* Temporal variable selective pressures likely maintain variation within ecologically relevant traits. The standing variation provides raw fuel for adaptive response during a directional shift in the environment.
* Important that as environment shifts, previously adaptive variation for conditions that are becoming increasingly rare diminishes. Therefore, as long as variability continues during the directional shift, anomalous reversions back to previous conditions may induce sharp population declines.

**Cornell:**

* Argument that fluctuating environments are conducive to these mechanisms maintaining higher standing diversity, improving the odds of successfully weathering rapid environmental change.
* These ideas seem consistent with segregation lift models.

**Laval:**

* Preserving diversity baseline, fluctuating selection appears to be an advantage to keep stable polymorphism to keep pace with environmental change. FS and sweepstake reproductive success (i.e., context of overlapped generations or not).
* Evidence of FS should be more pronounced for discrete generations than overlapping generations.
* When there is balancing selection at a large number of loci genetic load is a potential concern but in the case of segregation lift with diminishing-returns epistasis, however, genetic load does not appear to play important role.
* Advantage/disadvantage of FS in invasive species. FS can play a role in invasive species expansion in a case of multi-invading events over time.

**Rutgers:**

* Biggest benefit we saw was the maintenance of polymorphisms in a population upon which selection could later act directionally. Summer fly pops look “southern” and so pops may be pre-adapted to more southern climates.
* Effects wouldn’t even have to be as well-balanced as in the fly example (old alleles) but could also be useful when they transiently prolong the survival of an allele.
* By increasing standing genetic variation, fluctuating selection can increase adaptive potential.

**MIT/WHOI:**

* Fluctuating selection is mostly beneficial. Requires species to balance decreased extinction risk with a decreased level of absolute adaptation or “optimality”.
* Consequences will rarely be realized because environment always fluctuates.
* Takes standing genetic variation that is likely to be beneficial for many species in the face of long-term changes in the environment.

**Virtual group:**

* Most important consequence is maintenance of genetic variation for traits under selection. I feel like there is a fair amount of hand waving about “temporal balancing selection” maintaining diversity without much elaboration.
* However, fluctuating selection on many different time scales is likely an important driver in this. Should increase adaptive potential and population resilience.

**NEU:**

* Benefit or consequence of fluctuating selection would in part depend on a few factors including the strength of selection, the magnitude of change in selection over a single fluctuation, the relative difference in selection strength among different events within a single fluctuation, and the relative length of an environmental fluctuation to the generation time of a species.
* In fly example, seasonal variation seems strong enough to see shifts in allele frequency between seasons, but not too strong as to drive a particular allele to fixation (or too weak to allow it to drift to fixation).
* Fact that several generations occur within each season may allow sufficient time for population wide shifts in allele frequency to occur (even if selection is not that strong). In this case, fluctuating selection may help maintain a larger amount of genetic variation and possibly contribute to increasing the adaptive capacity of a species if the environmental variables that are fluctuating are also those that are expected to undergo long term changes.