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### Preamble ###

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1, Welcome and welcome to the 2019 American Society of Naturalists symposium. Thank you all for attending, thank you to the speakers for discussing their recent work, and thank you to the American Society of Naturalists for hosting this symposium.

[[::: *Causes and consequences of temporally fluctuating selection in the wild.* :::]]

2, We will be discussing the causes and consequences of fluctuating selection. This is, of course, a large topic that is central to our understanding of the forces that affect diversity at all levels of biological organization. During this symposium, we will focus on work that addresses the three basic questions about the nature and dynamics of **rapid adaptation in response to fluctuating selection**:

* What are the **theoretical dynamics** of rapid adaptation in response to fluctuating selection pressures?
* What are the **environmental drivers** of adaptation in response to fluctuating selection?
* What are the **ecological and genetic consequences** of rapid adaptation in response to fluctuating selection?

3, I would like to take a few minutes during this talk to situate these questions with a bit of background on their development.

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### Introduction ###

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1. How organisms cope and populations adapt to fluctuating selection pressures is central to our understanding of phenotypic diversity across the tree of life.

[[[:: obligate montage of diversity ::]]

2. It has long been appreciated that fluctuating selection can promote phenotypic diversity. Much of this work was pioneered by early ecological geneticists and still forms the motivation for the research that many of us are engaged in.

[[[:: Picture of E.B. Ford's book against a screen-shot of SSE2019 session titles ::]]]

2a. What do we know about the relationship between fluctuating selection and diversity? On the one hand, we know that fluctuating selection can promote the adaptive evolution of phenotypic plasticity. Plasticity is expected to arise when individuals (or genotypes) experience a diversity of environments, or when environmental change is predictable.

[[[:: cartoon of reaction norm; for cartoon figures in this slide, make into 4x4 grid time & space, plasticity and adaptation::]]]

2b. On the other hand, fluctuating selection can drive rapid genetic adaptation when certain genotypes perform better at some times or places but not others. This is local adaptation or adaptive tracking, and it occurs across spatial landscapes and through time. Local adaptation is generally thought to occur when individuals experience only a subset of possible environmental conditions or, perhaps, when environmental change is unpredictable or sufficiently slow.

[[[:: cartoon of allele frequency change through time & space ::]]]

2c. Of course, these two outcomes - plasticity and local adaptation - form ends of a spectrum, and there is a wide grey area: Variation exists in plasticity and this variation may itself be subject to local adaptation.

3. Our symposium today focuses on recent work examining the causes and consequences of fluctuating selection as it specifically relates to rapid adaptation. Much of the research in this symposium focuses on temporal dynamics, which of course lay at the heart of evolutionary thinking.

4. To advance our understanding of the role of rapid adaptation to fluctuating selection pressures, speakers today will be discussing their recent theoretical and empirical work examining the :

• the stability and signatures of polymorphisms underlying adaptation to fluctuating selection

• the environmental drivers and adaptive response to fluctuating selection

• the ecological consequences of fluctuating selection

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### Theoretical background ###

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1. Much of the theoretical work examining adaptive dynamics to temporally varying selection pressures stems from an interest in evaluating the role of fluctuating selection in maintaining genetic variation.

[[[:: some sort of nucleotide diversity slide ::]]]

2. Starting in the 1950’s, the abundance of polymorphism in natural populations was first being realized and with that observation came the basic goal of population genetics to determine the forces that generate, maintain, and deplete that variation. Likely spurred by the observations of ecological geneticists, many early models of polymorphism examined the role of selection in maintaining diversity.

[[[:: AmNat title pages ::]]]

3. Two classic papers, one by Howard Levene and the other by John Maynard-Smith and Suresh Jayakar, set the stage for this work by examining what was later dubbed ‘marginal overdominance’. These models established that polymorphism can be maintained in (a) spatially and (b) temporally varying environments if the fitness of the heterozygotes exceeded that of the homozygotes, averaged across environmental regimes. For spatially varying selection, Levene established that the harmonic mean of the heterozygote must exceed the homozygotes, whereas for temporally varying selection, the geometric mean of the heterozygotes much exceed that of homozygotes.

[[[:: slides of fitness rxn norm; delta-q ~ q ::]]]

3a. However, at least for an additive model, the harmonic mean is always less than or equal to the geometric mean (Pritchett-Ewing 1980), and so spatially varying selection was generally thought to be more efficient at maintaining genetic variation than temporally varying selection pressures.

4. In addition, other conditions of these models which examined spatially and temporally varying selection generally argued that temporally varying selection was inefficient at maintaining genetic variation. These models incorporated random vs. periodic fluctuations, positive and negative autocorrelations in the environment, and so on. In these simple, but increasingly complex models, many authors concluded that temporal fluctuations are not only inefficient at maintaining diversity, in some cases they may actually cause diversity to be lost more quickly than at a neutral locus.

5. These models, in addition to more recent ones, therefore suggest that adaptive evolution to temporally fluctuating selection pressures could possibly drive high rates of adaptive substitution, at least under some circumstances.

[[[:: figure from Desai & Dean papers? Also, quote from Hoekstra 1975, “It is concluded that this relevance is probably rather limited with regard to the creation of protected polymorphism, but that the influence of cyclical selection on transient polymorphisms might be more significant” ::]]]

5a. Of course, the parameter space of models examining adaptive evolution in response to fluctuating selection is vast (Gillespie 1991), and so we might choose to take conclusions about the role of temporal fluctuations in maintaining fitness related diversity with some skepticism. Indeed, much work over the last several decades has extended the conditions under which temporal fluctuations can indeed promote the long-term persistence of diversity. Two of our invited speakers today will discuss their recent work examining this important topic.

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### Environmental drivers ###

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1, The way in which the environment changes through time is predicted to have a major role on in shaping the dynamics of rapid adaptation. As we discussed earlier, the speed of fluctuations, patterns of autocorrelation, and their predictability have a major role in shaping whether, for instance, plasticity evolves, or whether polymorphism remains protected through balancing selection.

1a, As empiricists and naturalists, it is also interesting to explore the interactions between organisms and their environment.

1b, And, such lines of inquiry have important implications for predictive models of adaptive dynamics and species distributions as a consequence of future climate change; antibiotic resistance, disease dynamics, and ecosystem processes.

2, Broadly, we can classify drivers of rapid adaptation into general categories such as those stemming from biotic or abiotic factors. Aspects of **weather and climate**, perhaps; or **predation and resource availability**.

2a, We also realize that in some cases, environmental change (whether biotic or abiotic) imposes uni-directional selective effects: Adaptive change, for instance, of a bird following frost has little to do with when the next frost will arrive.

[[[:: Bumpus slide ::]]

2b, Broadly, and to generalize, much of the work examining adaptation across spatial landscapes or across seasons falls into this category: temperature, rainfall, humidity as prox dist. For such work, a major challenge remains to identify specific factors, or suites of highly co-linear factors that shape diversity

* **within species,** [[[:: example 1 ::]]]
* And at **specific regions** of the genome [[[:: example 1 ::]]]

2c, In other cases, the adaptive dynamics of a focal species may interact with the selective factor to form feedback loops, typically envisioned as negative frequency dependent processes. Arguably, much of this work has focused on biotic interactions: **host-parasite interactions**, for instance; **predator-prey dynamics;** or even **niche-construction**.

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### Ecological consequences ###

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1. Fluctuating selection can drive rapid adaptation with ecological consequences. Selection and adaptation can affect ecology by altering trait values/distributions that affect ecological interactions (direct effect), and by affecting mean absolute fitness and thus the absolute number of organisms (indirect effect).

1a. We know that rapid adaptation can affect population dynamics and species interactions in lab experiments/mesocosms, however, less is known about how this plays out in nature, and specifically about fluctuating vs. directional selection (though biotic interactions often cause the latter, e.g., predator-prey dynamics).

[[show results from classic mesocosm experiment; and/or NFDS on stripe in Timema coupled with Tim’s results on community consequences]]

1b. Less is known about the ecosystem consequences of fluctuating selection (or selection/adaptation in general), however, evidence that intraspecific genetic variation (individual genotypes and diversity levels) can affect ecosystem processes suggests that fluctuating selection (which will affect the genetic composition of a focal species) can have effects at the ecosystem level.

[[example from Andrew’s book on ecosystem eco-evo]]

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### Challenges ###

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1, One clear pattern stemming from the combined evidence of the fossil and contemporary record is that the magnitude of evolutionary change is larger at shorter time-scales. One interpretation of this observation is that fluctuating selection is common, but that the direction of selection changes frequently enough that there may even appear to be stasis across longer time scales.

1a, Of course these adaptive dynamics occurring over short time-scales have major consequences across many levels of biological organization, ranging from the level of diversity within the genome, to ecological interactions, and current and future ecosystem goods and services.

2, The central challenge of studying the manifold effects of rapid adaptive evolution to fluctuating selection pressures is simply observing it.

2a, One excellent option for some systems could be seed banks or museum collections, and certainly these resources have provided valuable insight into these basic problems.

2b, Otherwise, it is reasonable to focus on organisms with rapid generation times. Often small and possibly un-charismatic, these species may nonetheless harbor large population sizes making adaptive dynamics more deterministic.

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### Open questions ###

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1. Under what conditions do we expect fluctuating selection to drive adaptive tracking, or to promote highly plastic alleles going to fixation? Do empirical data support existing models?

2. Are biotic or abiotic interactions more likely to drive adaptation in response to fluctuating selection?

3. Is the genetic architecture of adaptive responses to temporally fluctuating selection fundamentally different than that of spatially varying selection?

4. At what scale, i.e., seasonal, annual, decadal, etc., is temporal variation in selection most prevalent/consequential?

5. How/to what extent are the ecological consequences (for populations, communities or ecosystems) of fluctuating selection different from the ecological consequences of directional selection?

6. Does (when does) fluctuating selection contribute in a non-trivial way to the maintenance of genetic variation or more generally towards levels of genetic diversity observed in natural populations?

[even in best case circumstance, need multiple time points and this means that collections have to be made and stored; challenging from the perspective of a phd student, etc etc]

[1 slide]

4. "Temporally fluctuating selection pressures can drive rapid adaptation, however our understanding of the dynamics of this adaptive process in the wild is limited. Our field needs to promote work examining how fluctuating selection promotes the maintenance of functional genetic diversity, shape ecological interactions, and modifies ecosystem goods and services. Our symposium seeks to address these basic questions from three perspectives."

Sample limitation

[3, On average, prey species are one to two orders of magnitude smaller than their predators. Because size scales with generation time, lower tropic levels will tend to have multiple generations per generation of a higher tropic level. Population size is inversely related to body size, and thus census population size tends to be much larger for smaller, lower food chain organisms. These basic inequalities will likely lead to top-down adaptive cascades because the rate of adaptive evolution (in real-time and as determined by population size and generation time) will increase with at lower levels of the food chain.

work of Howard Levene on multiple niche polymorphism

Multiple niche polymorphism

1. Much of our formal thinking about adaptive evolution in response to fluctuating selection come from classic work examining so-called ‘marginal overdominance’.

2. Marginal overdominance

2. This work articulated the view that alternate genotypes can be stably maintained in a population under certain ecological circumstances, and has been influential in our understanding of both genetic diversity and species diversity.

[[[:: Levene’s paper shot ::]]]

* Levene’s spatial model requires that the harmonic mean fitness of heterozygotes is greater than the harmonic mean of the homozygotes
* Haldane adn Jayakar requires that the geometric mean fitness of the hets is greater than that of homozygotes
* Because the harmonic mean is always less than or equal to the geometric mean (Pritchett-Ewing 1980), spatially varying selection was generally thought to be more efficient at maintaining genetic variation than temporally varying selection pressures.

2, Over the last several decades, three basic theory based questions in stemmed from this classic work  
 1. First, under what ecological & genetic conditions do locally adapted, “specialist” genotype arise?

2. Second, are alternate genotypes stable in the sense that they are maintained at intermediate frequencies for long periods of time?

3. Third, what are the molecular signatures of polymorphisms underlying local adaptation through time and space?

3, As discussed previously, our understanding

3, Stability, autocorrelations,

3a; Gillespie quote p142 on the complexity of models

[I think the point to make here is about the stability of polymorphism; classic theory suggests X, newer models suggest Y]

[Tie into Mieke & Jason's talks]

[we teach that response to selection is slow; Gillespie, etc]

[~2-3 slides]

3. I want to take a moment to discuss some of the historical aspects of research into the temporal dynamics of fluctuating selection. To do this, I first want to introduce the concept of grain size. Grain size is central to the

2c. When we study the evolutionary response to fluctuating selection, we often compartmentalize the role of plasticity and local adaptation as they relate to either temporal or spatial fluctuations in selection pressures. At least in the case of studies that examine free-living organisms, we often study local adaptation in response to spatial variation and plasticity in response to temporal variation.

2c. This bias stems from both pragmatic

[[[:: uses slide from #2 ::]]]

3. This bias reflects the assumptions that we have to make in order to empirically study these processes. [grrr - have to tie this into grain size; #3.X needs work. Somehow we have to tie this into the time-scale problem]

3a. First, most species have range sizes much larger than the average dispersal distance of an individual. In this situation, which we refer to as a coarse grained environment, genotypes only exist in a subset of possible environments. Differential selection on alleles that confer fitness benefits in one environment but not another are sorted out across spatial landscapes. The time-scale of this sorting is unclear, but it is often assumed to be quite long, leading to the steady accumulation of differentiation of conditionally beneficial polymorphisms. Indeed, decades of work on a variety of organisms, using both phenotypic and genetic data, have confirmed theoretical models that spatial variation in selection pressures drives local adaptation.

[[[:: some sort of figure ::]]]

3b. Work examining the biological responses to temporally varying selection, on the other hand, have typically focused on plasticity. Indeed, much of our understanding of physiology and behavior is rooted in understanding plastic changes in relationship to [...yuk].

4. [Trying to get to the thesis: "Temporally fluctuating selection pressures can drive rapid adaptation, however our understanding of the dynamics of this adaptive process in the wild is limited. Our field needs to promote work examining how fluctuating selection promotes the maintenance of functional genetic diversity, shape ecological interactions, and modifies ecosystem goods and services. Our symposium seeks to address these basic questions from three perspectives."]