Principles of Ecology, Evolution, and Conservation Biology Study Guide

EECB 703 Fall 2017

DISCUSSION 1: Behavioral Ecology and Biodiversity

Group A Discussion Notes 9/5

Developmental Perspective

There are many physiological aspects of an organism that influence its behavior and thus the developmental perspective should not be ignored when seeking to understand behavioral ecology and evolution. The most basic of developmental concepts is that hormones influence behavior. For instance, it has been well documented that testosterone is linked to aggression. It is important to understand the regulation of brain chemistry and to recognize that any deviations in behavior could be a result of a hormonal imbalance. One of the more complicated aspects of including a developmental perspective is that natal experiences modify the way we interact with our environment, including an organism's later behavior and reproductive success. That being said, it is also important to remember that behavior can also influence hormone concentrations, so that learned behavior or socialization are critical to creating positive or negative hormonal feedback loops. Indeed, Dr. Pravosudov pointed out that as behavior has a degree of plasticity, it can act as a buffer that limits genetic evolution. On the other hand, some behaviors that are genetically linked can be favored by natural selection and thus increase in a population over time, particularly if they lead to reproductive success, reducing predation, or even increased foraging efficiency.

Reproductive behavior and altruism are two topics that reoccured in our readings as well as in Dr. Pravosudov's presentation this week. For instance, parents are selected to invest in their offspring, even though that is costly and certainly can reduce the parent's ability to produce more offspring. Likewise the offspring is selected to manipulate parents to provide more investment than parents are selected to give. Trivers (1974) explained this conflict as a result of the offspring being more related to itself than to any of its siblings, while the parents are theoretically equally related to all of their offspring.

It is also important to consider stage-specific parent-offspring conflict when evaluating certain behaviors. The costs and benefits to a behavior change as the offspring develops and become more independent, causing the parent to re-evaluate parental investment while the offspring may resort to behavioral tactics to promote continued parental care. Evaluating the costs and benefits in terms offspring survival rates, lifetime fertility of the parents, degree of relatedness, as well as the tradeoffs between the two, can help predict behavioral shifts. It can also help explain phenomena such as altruism and how altruistic acts differ between relatives and non-relatives, as well as between offspring and parents. Similarly, understanding the origins of habitat preferences and how they might vary across individuals can help biologists understand things such as causes of genetic variation across a landscape, or help them predict colonization rates after disturbances, or how habitat loss might affect populations.

Children, Parents, and Our Understanding of a Baby Crying for its Mother

The crying of an infant for its mother can be looked at through the lens of a conflict, one that is occurring between the biology of the parent and the biology of the offspring. Some infant behavior, particularly excessive crying or throwing a tantrum, can be explained by the weaning-conflict. Although the parent generally initiates the first feeding event for the offspring, as the child develops the parent will begin to resist feeding events. The child will learn to initiate the parental investment through behaviors such as crying. The benefit to cost ratio of parental investment declines in value over time as the offspring increases in size (and thus cost of feeding). However, the offspring is selected to act in such a way as to manipulate the investment of the parent. Trivers (1974) suggested that offspring will resort to regression or means of psychologically manipulating a parent to continue investing in care until the benefit to cost ratio reaches ½ or smaller. This is calculated using degrees of relatedness between the parent, offspring, and future siblings. It is also possible that the crying may be an attempt to extract care and investment from a negligent mother in preparation for potentially being abandoned later, or in order to strengthen bonds with the parent as the child becomes more independent. So, a baby crying for its mother has evolutionary roots, and may demonstrate advanced psychology in infants when it is used for manipulation or in response to lacking care. In either case, behavior is a dynamic exchange that occurs between two or more actors, with situational levels of costs and benefits.

Zahavi and Perspective on Communication Between the Sexes

Sexual selection imposes a costly character that acts as an honest signal of genetic quality. In theory the genetic quality of mate with a handicap will be higher than those of the randomly chosen mate. Although this handicap must be recognizable to a potential mate, so that extreme traits represent easy to understand signals of quality. The degree of sexually selected handicap is of course limited by levels of predation. Communication can shift due to changes in habitat, so that cryptic colorations may be preferred in some area. In general there are longer courtship for species with less extreme signals of mate quality as mating quality is then more difficult to determine. Without sexually selected traits, communication of quality between sexes is less accurate and more time consuming.

Tinbergen's 4 Questions and Studying Behavior

Tinbergen famously declared there are four fundamentally different types of problem raised in terms of biology, which he called 'survival value', 'ontogeny', 'evolution', and 'causation'. These questions are often considered the four 'major problems of biology'. They are useful because they offer a sophisticated and multi-dimensional understanding about any feature of an organism. Bateson (2013) suggested that these problems can be expressed as four questions: what is it for? How did it develop during the lifetime of the individual? How did it evolve over the history of the species? And, how does it work?". Although these questions should be considered together in order to gain a deeper understanding of a particular trait, considering them individually is indeed possible and can even make research more manageable. As answering one question does not answer another, Tinbergen's four questions can still generate independent pieces of information.

A good resource for understanding these questions can be found here.

Measuring Diversity

Biological diversity can be simply thought of as the number of different species on Earth, although biologists will often include communities of organisms and the habitats when assessing levels of diversity. However, diversity is not limited to comparing between species, it can also be applied to within a species, particularly if looking for genetic diversity. Diversity is rooted in variety and can be applied to a myriad of topics including genetics, habitats, and species. Measuring diversity has many issues. The first one being even just defining what is the most important aspect of diversity, for instance there is some debate around if we should be more concerned about the total number of species or the number of viable populations present.

A few basic metrics of community analysis are species richness and evenness. However, species richness is a simple count of the number of species present and does not consider the abundances of the species present. There are several diversity indexes that look at both species richness and evenness, specifically these indexes take into account the rarity and commonness of species within the community being analyzed. Two of the most commonly used to measure a community are Shannon-Wiener index (H') and the Simpson index (D). The Shannon index assumes all species are represented in a sample and that they are randomly sampled. This could be problematic if not all species are included or if there was biased sampling. Meanwhile, the Simpson index gives more weight to dominant species, so that rare species don't change the output very much. This might under-estimate diversity in areas with few dominant species and many rare species. Which index you choose for your study can depend on the characteristics of your unique community.

In addition, diversity indexes can be applied across different spatial scales. In 1972 R. Whittaker introduced the terms alpha, beta, and gamma diversity to define the spatial components of measuring diversity. Alpha diversity relates to the local diversity, while beta diversity measures the differences in species composition among sites, and finally gamma diversity is the diversity of the entire region. As diversity can be measured at different temporal and spatial scales, there are also issues surrounding the dimensions of a study and how to quantify diversity at that scale. This further complicates comparing the results of different studies and can lead to a generic oversimplification if the scales are not considered along with the results. Diversity can be measured by species density (total number of species in a given area) and evenness (the distribution of individuals between species), and can encompass both small scales as well as the turnover of species at larger scales.

Latitudinal Gradient in Diversity

In biology the latitudinal diversity gradient (LDG) refers to an increase in biodiversity at the equator and a dwindling of species richness that occurs as you move toward the poles. Although the LDG has been generally accepted, the mechanisms for why this gradient exists is still widely debated. Perhaps this relates to BOTH our general ignorance and the fact that we have a lot more work to do and that there are a the plurality of causes affecting the origins of diversity. For instance our general understanding of species diversity is biased towards specific, well studied taxonomic groups, regions and ecosystems.There is a historical bias towards basing the LDG on studies of vertebrates and vascular plants, particularly those found in the northern hemisphere. Consider that invertebrates are the most diverse and numerous taxa found on our planet and have been far less researched than vertebrates.

There is also the issue of scale when considering the LDG. For instance, although regional species diversity does follow the LDG, this pattern becomes less clear when considering just molecular diversity. Additionally, although overall species in the kingdom Plantae tend to follow the trend of being more diverse in the tropics, if you consider just bryophytes then the trend is actually reversed.

There are several hypotheses to support why we have seen a general trend of more diversity in the tropics. Two of these concepts are explainer here: **Hypothesis #1:** There are high rates of speciation in the tropics. This relates to the idea that available energy will limit the species richness of an ecosystem (consider that the with a net primary productivity results in a higher number of individuals that can be supported). **Hypothesis #2:** The tropics has low extinction rates. This may be due to the historic location of the tropics providing a milder climate and that the tropics represent a large biome (in that large, resource-rich areas can support more species).

These hypotheses often fail to consider empirical data from unique groups, or are not accurate across all spatial scales. Additionally, they don't clearly explain an underlying mechanism about the origins of the pattern. For example, hypotheses relating to biotic mechanisms, such as the idea that there is more predation in the tropics that reduces competition and increases specialization, fails to explain why there is more competition there than other places. In spatial/area centered hypotheses, which suggest that the tropics are the largest biome and therefore have the highest diversity just because of size, are oversimplified and don't account for habitat variation in the tropics around the world. (Willig, Kaufman, & Stevens, 2003)

Specific Lineage and the LDG

Mammalian diversity has been shown to be highest in the tropics and decrease toward the poles. A combination of hypotheses explains this; total energy input to the system from solar radiation falls as latitude increases, which leads to overall less primary productivity, which would support fewer individuals (and therefore perhaps less genetic variation within species that could lead to speciation), and potentially increase extinction rates toward the poles due to lack of resources. Basically, if it is hard to survive, only species that are truly well-suited to their harsh environments will persist. This is in relation to water availability and cold especially, which physically limit biological functions and are generally less limiting in the tropics. The historical/evolutionary hypotheses might also play a significant role. Over the history of the earth, more landmass has been concentrated at the tropics than at the poles, and the tropics have not experienced major limiting events such as glaciations in a very long time. So, the tropics have had longer for processes like soil development to mature, as well as more time for existing species to evolve and diverge than have higher latitude species moving into younger environments.

Unified Neutral Theory of Biodiversity

It's a false dichotomy because the scale and precision they attempt to describe are different. For instance, the neutral theory seeks to explain the species distribution of species rich communities while the niche theory is based around species-limited communities. Furthermore, as suggested by Wennekes' 2012 article “The neutral-niche debate: a philosophical perspective”, Niche theory says species can co-exist because they are fundamentally different, and tends to do best describing smaller scales; it focuses on a 'realism' perspective where every assumption is strictly true and testable at any scale. Niche theory is a stabilizing process. In contrast, the neutral theory says that species around the same trophic level are functionally the same, and that diversity is governed more by random speciation/extinction/immigration/emigration. This is a more instrumental point of view and tends to explain large patterns well. It is also recognize that it is a destabilizing theory, it adds stochasticity to biodiversity, and both stabilizing and destabilizing processes are required to explain patterns of local and regional biodiversity.

Reading Notes:
Trivers, R. L. (1974). Parent-offspring conflict.

- This paper presents Triver's theory of parent-offspring relationships based on inclusive fitness and allowing for the offspring to be considered an active participant in the dynamics of relationship (as opposed to the idea at the time that offspring where passive vessels for parental care).
- Parent-offspring conflict for parental-care, including the weaning-conflict, can be viewed from a mathematical view-point of both participants, including from benefits, costs, and degrees of relatedness. Based on these mathematical formulas, offspring can be expected to behave in such a way as to change the behavior of the parent to induce further care under certain parameters.

Zahavi, A. (1975). Mate selection—a selection for a handicap.

- Zahavi proposes a mechanism for sexual selection that can be summarized as the handicap principle. The handicap is a costly or deleterious character which reduces survival, so that high quality genes can survive possessing a handicap, and thus creating a reliable signal. These honest signals of health or fitness must be costly to the signaler, as organisms might otherwise develop signals that could deceive each other.

Davis, J. M., & Stamps, J. A. (2004). The effect of natal experience on habitat preferences.

-

Group B Discussion Notes 9/5

Behavioral Ecology

1. Ignoring Development

   Development, or Ontogeny, is one of Tinbergen's Four Questions. It can be a difficult aspect of behavior to study because it concerns the development of a behavior throughout the early years of an organism or even how a behavior changes throughout its lifespan. The difficulty in its study means that it has been ignored in some areas of behavior. The benefit of fully understanding the development of behavior is that it would allow for a better understanding of the target behavior as a whole.
2. Trivers Parent Offspring Conflict

   A baby crying for its mother is a form of communication between the offspring and the parent. Crying normally signals to the parent that the offspring requires care or attention. For example, this may mean that the offspring is hungry and wishes to be fed. However, as the offspring develops, it may evolve methods of manipulation in order to glean more resources from the parent (e.g. crying for food/care when it does not truly require it). Parent-offspring conflict states that there is a certain amount of resources that a parent is required/wants to give to its offspring in order for that offspring to fully develop, increasing the parent's inclusive fitness, while also taking into account its future inclusive fitness and the fitness of its future offspring. The offspring wants to extract as much parental care as possible in order to make themselves more successful in the long term.

The disagreement between the amount of resources shared results in conflict. When you see a baby crying for its mother, you must wonder if the infant is actually hungry or in need of attention or is just trying to secure more care from the parent to increase its own success.

3. Zahavi - Selection for a Handicap
   Handicap display is a basic form of communication that plays a role in sexual selection. For example, in a species of sexually dimorphic birds, males tend to display more ornaments than females. These ornaments can include bright colored plumage, long tails, etc. Living with such an ornament is a handicap to the individual as these ornaments decrease fitness by causing the individuals to be more easily spotted by predators, expend resources growing/maintaining costly structures, etc. Thus, males that have such a handicap and yet survive to court a female are communicating to the female via their handicap their overall quality: only higher quality males would be able to survive while displaying handicaps. Individuals with a shorter period of courtship/breeding cycle normally have large obvious signals which allow the females to make a quick, easy selection of a breeding partner.
4. Tinbergen's Four Questions
   Tinbergen's four questions allow behavioral ecologists to categorize and study the different aspects of behavior. The questions are divided into two separate but related themes. The first two questions focus on the proximate causes of behavior. The first, Mechanism, answers how a behavior is constructed. For example, a study may find the molecular signalling pathway that leads to a certain behavior in dogs. The second, Ontogeny, or Development, is how a behavior changes throughout the early stages of an organism or throughout its lifespan. The second theme involves the ultimate causes of behavior. The first, Adaptive Value, simply answers how the behavior increases an organism's inclusive fitness. The last of the four, phylogeny, is a study of how the behavior evolved over time.
   When studying behavior, it is important to consider ALL the questions together. The phylogeny may affect the understanding of the mechanism etc. Using all four questions allows for a more well-rounded better understanding of the behavior as a whole.
   (will elaborate more)

Diversity and Neutral Models

1. What is diversity?

One of the simplest ways to define 'diversity' is simply to calculate the total number of different species that occur in a defined place. In practice, however, diversity can be approached in many different ways, hence the number of diversity indices used in ecology. Most indices take into account the richness and evenness of a species: the number of individual species present and how the populations of the present species are spread across a given habitat. Two common indices that use both richness and evenness measures are the Simpson index (and its variations) along with Shannon index (and its variations). Measuring diversity is challenging due to the large number of relationships present in the biosphere. How one chooses to measure diversity depends on the scale. Comparing the relationships between two large ecosystems vs comparing several small niche habitats require different, and sometimes unique, diversity indices to accurately describe the present relationships. The difficulty is standardizing these indices in order for comparisons to be easily drawn between studies.

2. What do the catalog of latitudinal gradient hypotheses reflect?

The latitudinal gradient hypothesis states that diversity is at its highest near the equator and slowly declines as it reaches the poles. There is still much debate on the mechanism(s) behind this so-called diversity gradient. The conclusion of this hypothesis shows both the ignorance of current global biodiversity knowledge, the need for further study, and the conclusion that there are many causes affecting diversity. The latitudinal gradient hypothesis focuses on a few closely studied groups of organisms in coming to its diversity conclusions. These are just a mere fraction of the diversity and thus such a small sample size should not be used to make assumptions in regards to the possible diversity gradients of other groups. Future directions would require a more inclusive examination of how diversity fluctuates in multiple phylums. The bias of focusing on a few well-studied groups suggest that the earlier conclusions may not be as simplistic as first imagined.

3. Defend a hypothesis explaining global patterns of diversity with respect to a specific lineage of organisms.

Smith et al. collected genetic data from 210 New World avian species with the goal of better explaining avian patterns of diversity relating to the Latitudinal Diversity Gradient hypothesis (LDG). This pattern is seen by many to be a ubiquitous trend seen in many other lineages. The results of this investigation did indeed support the LDG hypothesis. Tropical avian species were older and more diverse. Tropical species were found to be more stable and established in a diverse array of habitat niches. Avian species that are native to higher latitudes are less diverse and much younger. There also appears to have been a loss of diversity due to unstable environments in the temperate region (e.g. glaciation). Unstable environmental conditions in temperate regions vs stable tropical habitats are often given as evidence supporting the LDG hypothesis for other lineages besides the New World Avian species targeted by this study.

4. Explain why the debate over the acceptance of niche theory or neutral theory is a false dichotomy.

The debate between the niche theory and neutral theory is a false dichotomy due to the basic nature of each approach. Niche theory approaches evaluating diversity in a more traditional to science approach. That is a detailed analysis of the many visible measurable interactions between organisms etc. Neutral theory does not rely on details but in fact sets all members of the community as equals and is meant to be predictive. It has been described as more of a starting place and is not meant to apply to every system. Both of these approaches are not infallible or all encompassing and thus the persecution of one over the other is a false dichotomy.

- Can be summarized into a debate between using a realistic approach to measure diversity vs using a instrumentalist approach.
- Both views have their benefit as they analyze the diversity in different ways
- This does not make one method superior to the other but both can be valued together

(Useful article: http://onlinelibrary.wiley.com/doi/10.1890/0012-9658(2006)87%5B1399:COTNAN%5D2.0.CO;2/full)
Another article: https://link.springer.com/article/10.1007/s10441-012-9144-6

DISCUSSION 2: Diseases and Niche Dynamics

Group A Discussion Notes 9/12

Gabriela Rios-Sotelo, Nathan Cook, Aramee Diethelm, Micaela Enger, Adriana Parra, Tim Caldwell

This is outline form for now so we can follow more easily without much there but we can change it as we add to the discussion and it fills out more

I. **Diseases of wild populations**

  A. Articles

    1. Keesing et al. 2006

    2. Young et al. 2014

  B. Questions

1. The Dilution Effect is an appealing hypothesis, but it is also a highly controversial topic in the fields of disease ecology and epidemiology. What are some critical characteristics of hosts, parasites and vectors that would be key for a dilution effect to occur in a disease system?

As explained by Keesing et al., 2006, variations in species diversity could lead to either a dilution or amplification effect, depending on the complexity of interaction networks of hosts, parasites and vectors. In other words, there is a negative relationship between host disease risk and host diversity thus, a high host diversity "dilutes" disease risk. In general, it could be argued that if the level of complexity of the network involved in the transmission of the disease is low, species diversity could lead to a dilution effect. From our discussion in class we determined some characteristics that would be key for a dilution effect. For example, if the transmission of the disease is based on a specialist interactions between a pathogen and host, or a vector and a host, high biodiversity could lead to encounter reduction, transmission reduction, or susceptible host regulation, among other mechanisms.

Schmidt and Ostfeld (2001) modeled host disease risk in various possible communities with high and low species richness to examine the evidence of the dilution effect in a Lyme disease system. They stated some characteristics they believed to be general across diseases and vectors for the dilution effect to be seen. The vector must be a generalist, parasitizing more than one host. Parasitized hosts must vary in reservoir competence, the probability that they will infect a feeding vector. Vectors must acquire the pathogen mainly through blood meals.

Schmidt, K. A. and Ostfeld, R. S. (2001), BIODIVERSITY AND THE DILUTION EFFECT IN DISEASE ECOLOGY. Ecology, 82: 609–619.
doi:10.1890/0012-9658(2001)082[0609:BATDEI]2.0.CO;2

Other resources:
http://www.caryinstitute.org/science-program/research-projects/biodiversity-community-ecology-and-dilution-effect/dilution-effect

https://parasiteecology.wordpress.com/2013/12/04/the-dilution-effect-numbers-densities-and-prevalences/

2. Imagine a scenario in which high biodiversity could lead to an outcome that is opposite to the Dilution Effect (i.e., an amplification effect) and describe the conditions when this might occur.

We thought of several single conditions that could lead to amplitude effect vs dilution. For increased biodiversity there needs to be more species so we mostly looked at the effects the added species would have on the local community.

There would be a amplitude effect if the additional species:
- Are hosts for the vector and have high reservoir competence
- Increases susceptibility to disease (compete for resources, remove resources, make other species weaker)
- Are parasites or vectors themselves
- Affect hosts such that they encounter vectors more often (have to group together for defence)

Wood and Lafferty (2013) argue that the relationship between biodiversity and disease risk is dependent on scale and complexity. Lafferty and Wood (2013) also speak to the complexity of disease systems. They argue that the complexity of the system has both dilution and amplification effect, however with greater amplification at large scales and across different land-use types. Both articles cited are reviews of back and forth with Ostfeld and Keesing arguing for or against dilution effect.

One idea exemplified (Lafferty and Wood 2013) is that of what constitutes high biodiversity. Higher biodiversity could be any number of additional species from plants that have no direct role in an animal disease cycle, or vice versa. However plant diversity could the animal space use which will affect the disease cycling. This speaks directly to the complexity that exists in all natural systems when all parts have direct or indirect effects on species interactions.

Lafferty, K.D. and Wood, C.L., It's a myth that protection against disease is a strong and general service of biodiversity conservation: Response to Ostfeld and Keesing. Trends in Ecology & Evolution, Volume 28, Issue 9, 2013, p. 503-504. doi:10.1016/j.tree.2013.06.012

Wood, C.L. and Lafferty, K.D., Biodiversity and disease: a synthesis of ecological perspectives on Lyme disease transmission. Trends in Ecology & Evolution, Volume 28, Issue 4, 2013, p. 239-247. doi:10.1016/j.tree.2012.10.011

II. **Specialization & Niche Dynamics**

A. Articles
1. Leiby & Marx 2014
2. Poisot et al. 2011
3. Konuma et al. 2013

B. Questions

1. ▌ A trade-off in performance across habitats is perhaps the most intuitive explanation for ecological specialization. With reference to whatever kind of specialization you like (diet breadth, environmental tolerances, etc.) describe the evidence that trade-offs (antagonistic pleiotropy) either are or not important for specialization in a particular group of organisms (birds, spiders, whatever).

Evidence for trade-offs being important

Several of the examples in class where trade-offs were evident was for fish. In one example we could clearly see that the perch could not have both body shapes (long and skinny or short and fat). However, the body type did not immediately convey what advantage caused one body type to occur more frequently in the shallow shore areas or the other body type in the deeper open areas of the lake. In the lab researchers found that attack velocity was negatively correlated with prey capture success when vegetation was present in lab tank and positively correlated when vegetation was not present. From this experiment there is evidence of a trade-off for this perch species in greater capture success based on attack speed controlled by body shape.

In the experiments conducted in Cooper and Lenksi (2000), multiple populations of E.coli adapted to a constrained medium. Interestingly, unused catabolic mechanisms decayed as well but not because of mutation accumulation. Catabolic mechanisms decayed rapidly. Thus, it was concluded that antagonistic pleiotropy resulted in specialization to the constrained medium.

Evidence that trade-offs are not important

Many studies hypothesized that trade-offs were the cause of specialization but were unable to show sufficient evidence for trade-offs. Many of these studies have also shown no disadvantage for the characteristics in the other environments, eating the other food, etc., when it would be expected for trade-offs. This may be due to methods unable to detect the trade-off or measuring the wrong mechanism of trade-off. However, this is more likely due to there not being a trade-off in a characteristic causing the specialization.

There are scenarios where simple loss of genetics is the cause of adaptation rather than better performance from one trait. Some cave-dwelling animals have lost traits or organs that are of little use in cave habitats. Darwin (1859), speaking of eyeless salamanders, thought that while eyes were of little use to these salamanders they were not deleterious and so disuse caused their loss. Which adds evidence to mechanisms other than trade-offs.

Darwin, C. On the Origin of Species by Means of Natural Selection, or the preservation of Favoured Races in the Struggle for Life. London: John Murray Eds, Albermarle Street; 1859.

Cooper, V.S. and Lenski, R.E. The population genetics of ecological specialization in evolving Escherichia coli populations. Nature **407**, 736- 739 (2000). doi:10.1038/35037572

2. ▌ Consider species A that eats food type 1 and species B that eats food type 2. To paraphrase the classic review of ecological specialization by Futuyma and Moreno (1988), a reciprocal rearing experiment that finds that A and B both die when reared on the other resource probably tells us more about the consequences rather than the causes of specialization. Explain that statement, and describe an experiment that should be done instead, to better understand the causes of specialization.

The reciprocal rearing experiment only presents evidence on the performance of each species under different conditions, specifically, feeding failure. However, this experiment does not present evidence on the mechanisms that lead to the development of the feeding strategies in the analyzed species, therefore, it indicates the consequences and not the causes of specialization. An experiment developed by Leiby and Marx (2014), is a good example of an analysis for determining the causes of specialization, as the authors investigated interspecific variation and presented evidence of substrate specificity in Eschericial Coli due to mutation accumulation.

3. ▌ Many authors have pointed out that the history of research in specialization has been too focused on the physiology and performance of individual organisms, often under laboratory conditions, while ignoring the complexity of interactions in the wild. Considering the community context (competitors, enemies, mutualists, primary producers etc.), describe at least three distinct hypotheses to explain the evolution and persistence of specialized phenotypes.

We looked at the example of Monarch butterfly wing coloration. Our three hypotheses are as follows:

Monarch butterflies have bright coloration to deter predators.

Monarch butterflies have bright coloration to deter hybridization.
Monarch butterfly wing structure that causes its coloration increases strength-to-weight ratio, which improves endurance on long-distance migrations.

4. ▌ Two part question on the macroevolution of specialization: (1) What is the evidence that specialization either is or is not an evolutionary “dead end”? (2) What is the macroevolutionary relationship between diversification and specialization? Neither of these are settled issues, and for both you should explain both what is currently known (from the literature) and explain your opinion (i.e. how do you think the issue might eventually be settled, pending lots more studies of course).

(1) Specialization is a dead end because of the large disruptions happening in the world. With the disappearance of the only resource used extinction is extremely high. We are seeing a mass extinction event unfolding and it is not the generalized species that adapt to changed habitats that are disappearing, but the specialized or limited species. When a species are specialized, the range is reduced to where the resources are found which leads to limited speciation, which ends the continuation of adaptation and is a dead end in the evolutionary line.

Species are specialization for the rich resources, not the poor ones (or at least specialized such that they can receive rich benefits from otherwise limited resources). This can increase the time available for other pursuits that increase fitness. Stability of those resources was needed to get the specialization in the first place and would indicate that those resources are more stable. Many if not all the species are specialized in some way and that is much evidence in the way that specialization increases fitness. Even our generalist species don’t run, swim and fly.

(2) As species or groups specialize on a resource, other resources are available for other species of groups to specialize on which reduces competition. Specialization also makes groups or species better competitors for a particular resource. Energy is passed through trophic levels, often in a damaging way to lower trophic level. Specialization by plants or prey animals to reduce damage also leads herbivores and predators to specialize further to continue exploiting resources. This leads to specializations increasing diversification as their interactions lead to more specialization in different ways.

Group B Discussion Notes 9/12

Danielle Miles (leader), Alison Agneray (note-taker), Lydia Doan, Benjamin Sonnenberg, Jamey Wilcher

Voyles- DISEASES OF WILD POPULATIONS

❙ The Dilution Effect is an appealing hypothesis, but it is also a highly controversial topic in the fields of disease ecology and epidemiology. What are some critical characteristics of hosts, parasites and vectors that would be key for a dilution effect to occur in a disease system?
-- Dilution effect = hypothesis that the overall effect of increased species diversity reduces or 'dilutes' disease risk through a variety of mechanisms. In order for the dilution effect to occur in a system, increased biodiversity must result in one or more of the following effects (taken from Keesing article and Voyles presentation): (1) Encounter reduction: the host species are limited in space and moving around less in their environment, i.e. mice will minimize their movement in an environment with coyotes/predators and "diminish contact with pathogen propagules." (2) Transmission reduction: added species reduce the pathogen load within the host and make the host less susceptible to disease transmission, i.e. mutualist mitochondria helping plants ward off disease and boost defense mechanisms. (3) Susceptible host regulation: added species alter birth or death rates resulting in limited susceptible host population, i.e. interspecific competition for the same limited resources constrains host population size. (4) Recovery augmentation: added species promote recovery after infection, i.e. added prey or food species may help infected host overcome disease and even gain immunity. (5) Infected host mortality: diseased hosts have higher mortality rates with interspecific competition and are not able to transmit pathogens posthumously, i.e. diseased individuals are targets for predators. All five of these mechanisms are able to co-occur and the effects of increased diversity can create complex disease interactions.

❙ Imagine a scenario in which high biodiversity could lead to an outcome that is opposite to the Dilution Effect (i.e., an amplification effect) and describe the conditions when this might occur.
-- There is no single relationship that is likely to be a 'universal truth' across all disease systems and often the Dilution effect is not applicable, instead increased species diversity results in an amplification effect. For example, if the added species increase vector numbers or act as alternative hosts, encounters with the pathogen and the overall transmission rate increases, i.e. having chickens near your house results in higher rates of Chagas disease (Keesing article). Alternatively, increased host diversity may amplify disease prevalence in cases with higher between-species than within-species transmission, i.e. multi-host pathogens like the Lyme disease bacteria and river blindness nematode rely on species diversity to spread

Forister- SPECIALIZATION & NICHE DYNAMICS

❙ A trade-off in performance across habitats is perhaps the most intuitive explanation for ecological specialization. With reference to whatever kind of specialization you like (diet breadth, environmental tolerances, etc.) describe the evidence that trade-offs (antagonistic pleiotropy) either are or not important for specialization in a particular group of organisms (birds, spiders, whatever).
--Note: Antagonistic pleiotropy "is when one gene controls for more than one trait where at least one of these traits is beneficial to the organism's fitness and at least one is detrimental to the organism's fitness: (Poisot article).
-- When considering the three photosynthetic pathways (C3, C4, CAM) in plants, there is strong evidence to show that trade-offs are extremely important for specialization. There is a direct connection between energetic cost to carbon fixation and water use efficiency. Plants with a C4

or CAM pathway are the most water use efficient (shorten stomatal opening time and store carbon prior to creating complex sugar), but expend far more energy on carbon fixation than C3 plants (stomata stay open longer, but carbon is fixed immediately with no storage 'cost').
-- Another example of antagonistic pleiotropy is crossbills: beak shape vs. food specificity http://www.jstor.org/stable/2937103?seq=2#page_scan_tab_contents This is a link to a paper describing the Crossbill complex in North America which gives an example of trade offs in foraging efficiencies between members. The author is arguing (continues to this day to argue) that these trade offs have led to not only specialization on a food resource but to possible speciation via ecological sympatric speciation.

-- Not important for E.coli in the Leiby article

- Consider species A that eats food type 1 and species B that eats food type 2. To paraphrase the classic review of ecological specialization by Futuyma and Moreno (1988), a reciprocal rearing experiment that finds that A and B both die when reared on the other resource probably tells us more about the consequences rather than the causes of specialization. Explain that statement, and describe an experiment that should be done instead, to better understand the causes of specialization.

-- Leiby's E. coli is a perfect example of an experiment to better understand the causes of specialization and test ***intraspecific*** variation. Specialization can only begin in the context of a single species. It may result in two different species after years of adaptation and evolution, but it is not enough to take two species and show how they are in fact, different species. A better experiment instead is to work with only species A and split into two subpopulations with the first eating the original food type 1 and the other eating food type 2. After observing several generations under these conditions, it is possible to then test for specialization (does the second subpopulation become intolerable to food type 1? etc.).

- Many authors have pointed out that the history of research in specialization has been too focused on the physiology and performance of individual organisms, often under laboratory conditions, while ignoring the complexity of interactions in the wild. Considering the community context (competitors, enemies, mutualists, primary producers etc.), describe at least three distinct hypotheses to explain the evolution and persistence of specialized phenotypes.

-- 1. There is a natural progression in evolution towards specialized phenotypes. As species stay in the same/stable environment over time, natural selection has a tendency to select those acquiring narrow ecological niches within this specific habitat (i.e. Darwin's finches on a stable island formed different beak shapes and body types to better utilize food sources).
-- 2. Symbiosis and mutualism can "propagate narrow niche breadth" (from Matt's presentation). For example, orchids have specialized with specific mycorrhizal fungi for nutrition and seed establishment, with some orchid species being holomycotrophic. The more an orchid relies on a specific fungus symbiont, the rarer it is in the wild. One hypothesis being that in stable environments (like Australia), the orchid's close association with successfully established fungi ensures that it too will become well-established in its habitat (example: doi:10.1111/j.1365-294X.2010.04736.x).

-- 3. Enemy-victim networks also different set of complex interactions that can result in specialization. For example in microbe and host networks, specialist bacteriophages are found to have very little overlap and compete with other phages far less, often creating a much smaller impact on the victim (https://doi.org/10.1186/2192-1709-2-13).

▌ Two part question on the macroevolution of specialization: (1) What is the evidence that specialization either is or is not an evolutionary "dead end"? (2) What is the macroevolutionary relationship between diversification and specialization? Neither of these are settled issues, and for both you should explain both what is currently known (from the literature) and explain your opinion (i.e. how do you think the issue might eventually be settled, pending lots more studies of course).

-- (1) Specialization is considered an evolutionary "dead end" since it leads to a narrow niche breadth and an inability to adapt to changing environments. The thought being that natural selection will drive species to diversify and specialize during times of stability and during extinction events, the specialists die out leaving behind generalists better able to adapt. Furthermore, specialists are considered 'derived' species, always a transition from a generalist species. Evidence to the contrary can be seen in Ruellia, a wild petunia, that is able to switch specialization from either hummingbird or bee pollination depending on its selective pressures (open-ended evolution), but it is not able to transition back from bat or hawkmoth pollination (dead-end). This indicates that there are certain thresholds under which specialization does not necessitate an evolutionary impasse (doi:10.1111/j.1558-5646.2008.00398.x). I think more tests studying this threshold and looking at what point specialization cannot be undone may help us better understand this generalist/specialist relationship.

--(2) This is a positive relationship where specialization increases diversification, reducing niche overlap.

--Other useful thought on subject: Specialization can occur as the result of an "accumulation of deleterious mutations due to relaxed selection associated with phenotypic plasticity " (Poisot article). For example, species living underground may not lose eyesight as an advantageous adaptation, but rather don't have a selective pressure to keep their eyes.

DISCUSSION 3: Population Ecology and Population Genetics

Group A Discussion Notes 9/19

Population Ecology - Kevin Shoemaker
Notetaker: Micaela Enger, Group A

1. Ecologists have been thinking about fluctuations in populations for at least one hundred years. Given that span of time, what do you make of the fact that we are still teaching and discussing some very simple models (like the Lotka-Volterra predator-prey model) that were first created pretty early on in that history?

- Turchin 2001 "The Lotka-Volterra equations are a horribly unrealistic model for real resource-consumer systems. It is, in fact, so bad that, to my knowledge, there has been no successful application of it to any actual population system, whether in the field or laboratory. But this is all beside the point, because the Lotka-Volterra model seems to get at some extremely basic feature of trophic interactions: their inherent proneness to oscillations (May 1974).
- It serves as a starting point and approximation or one layer of what happens in reality, which makes it still valuable. You can build on it, no model is universal, but it is a good place to start.

2. How can populations be regulated without density-dependent mechanisms? Can you think of real-world populations that might be regulated in this manner? Can density-dependent population regulation be considered a fundamental law of nature?

- Populations can be regulated by predation or through anthropogenic reasons like hunting or habitat fragmentation. Thus, those populations never have the chance to reach carrying capacity.
- The idea of exponential growth could be considered a law because it seems to be true unless there is some other interaction, much like Newton's law of inertia. An object (the population) will stay in motion (continue to grow) unless an outside force acts on it (another interaction occurs).
- There is also positive and negative density dependence to consider, in addition to age structure.

3. Given the diversity of mechanisms that can lead to population cycles, can we make any broad generalizations about population cycles in nature? Can you think of some reasons why some populations of the same species might exhibit cyclic abundance dynamics while other populations do not?

- Population cycles in nature can vary based on many different factors.
- Some population cycles may vary between populations of the same species because of overall variation. For example, the environment varies from year to year, stochastic

events occur, but even those examples can be somewhat cyclic like weather events (drought or precipitation). It doesn't necessarily have to be a pattern though.

- Some reasons that some populations may not have cyclic abundance dynamics is because of isolation. One population may have predators and one population may not if they're on an island, for example.

4. With respect to metapopulations, there are skeptics that say that the theory is not useful because "real" metapopulations don't exist. Critique this position, and describe at least one example of a metapopulation from the literature that was not discussed in class.

- The concept of metapopulations doesn't exactly fit all population dynamics. It can depend on the scale you're looking at or what you view as a population.
- An example metapopulation could be a herds of deer with different herds being different metapopulations. Seasonal changes or the geography of their habitat may cause the herds to roam in different areas, but if some sort of stochastic event or even resource availability causes the herds to travel to the same area, there could be some immigration or emigration between herds. Deer that get separated could also join a different herd.
- Another example could be wolves. They typically have specific packs, but if a wolf is pushed out of one pack it would be forced to join another pack. Offspring are also forced to join or start a new pack.
- Crossbills are also an example because different subspecies specialize on certain food resources. Populations may cross each as they move their food source, so they could breed between the different populations.

5. In a recent paper, Griffith et al (2016) state that "population-level processes are an ideal common currency within ecology and evolution". Explain why you either agree or disagree with this statement?

- We agree in terms of the idea that population demographics should be quantified in order to understand what drives population level processes. It can also provide into other fields like the spread of disease, evolution, and these processes can even help to indicate the health of an ecosystem.
- You could also disagree because you're only looking at subset of populations. There are differences between r and k selecting species. That makes it harder to use these processes as common currency within ecology and evolution.
- If we consider how different ecological processes occurring at one temporal and spatial scale can have repercussions in processes at different scales (for example, processes at the individual level can translate into effects at the population level) and vice versa, it does make sense to consider population level processes as an intermediate ground that can serve as a bridge between different subdisciplines.

Population Genetics - Marjorie Matocq

6. How have population biologists measured genetic differentiation within and among populations and what can we infer (or not) about evolutionary processes from commonly-used metrics?

- It seems that most studies use F_{st} to look at gene flow, but there are many other factors like drift that contribute to the story.
- We also discussed how sometimes you can have shared alleles between populations but this is because they share a common ancestor not because the populations are interacting.

7. Think of a particular species that you are familiar with. Based on the ecology and perhaps biogeographic/evolutionary history of the species, what predictions can you make about factors which are likely to be most important in determining the distribution of genetic variation in the system?

- Factors that can be important in determining the distribution of genetic variation in a system are natural selection, non random mating (sexual selection or inbreeding), genetic drift, isolation….
- Marjorie's example of the woodrat in the central California valley discusses how important female preference (sexual selection) is in determining the genetic variation in the three woodrat populations.
- Island species are a good example of genetic drift
- Trophy hunting is an example of selecting for small game
- Habitat fragmentation is also a good example of something that determines the distribution of genetic variation.

8. Whether we talk about a small number of microsatellites or a large number of SNPs, it is very unusual to find a wild system (population or species) without any genetic variation. Why is that and what maintains genetic variation?

- There are many factors that contribute to populations maintaining genetic variation.
- Dispersal like immigration and emigration.
- Genetic variation also increases fitness which would drive populations away from no variation.
- Populations would also be at risk for the extinction vortex. No variation essentially means the population consists of clones, so there wouldn't be any opportunity for individuals to adapt to environmental changes, thus putting them at risk for extinction.
- Mutation also helps to provide variation.
- An example of a population with low genetic variation: the cheetah population has undergone a bottleneck, resulting in the homogeneity of today's cheetah.

Group B Discussion Notes 9/19

Population Ecology and Population Genetics

- Ecologists have been thinking about fluctuations in populations for at least one hundred years. Given that span of time, what do you make of the fact that we are still teaching and discussing some very simple models (like the Lotka-Volterra predator-prey model) that were first created pretty early on in that history?
  - Although many of the simple models, such as the Lotka-Volterra equations, are not accurate when applied to real world systems, they describe fundamental and intuitive processes that form a basis for model refinement. They create a framework to which more intricate details can be added, and give ecologists a common conceptual base for teaching and discussion.

- How can populations be regulated without density-dependent mechanisms? Can you think of real-world populations that might be regulated in this manner? Can density-dependent population regulation be considered a fundamental law of nature?
    - Populations can be regulated by factors such as weather/climate, natural disasters, human disturbance, and mass immigration. These processes can affect the entire population of an area, regardless of population density.
    - Some examples of this might include insect diversity in high fire frequency habitats such as Florida longleaf pine (Knight & Holt, 2005)(http://onlinelibrary.wiley.com/doi/10.1890/04-1069/full), or wildflower abundances in deserts, which might be regulated mainly by rainfall.
    - If we consider a fundamental law of nature to be a regularity that applies to a broad class of phenomena, then yes, density dependence might be considered a fundamental law of nature, with some exceptions. However, if you define a law of nature more strictly, as a law that is true universally, in every situation, at every scale, then no, it would not qualify. It really depends on how you define a law of nature.
- Given the diversity of mechanisms that can lead to population cycles, can we make any broad generalizations about population cycles in nature? Can you think of some reasons why some populations of the same species might exhibit cyclic abundance dynamics while other populations do not?
    - There are a few broad generalizations we could make about population cycles. One is that they are often caused by changes in resource availability- either increases or decreases lead to the related changes in population size. Another generalization is that there is often a delay in the species' response to whatever is causing the fluctuations. In one classic example, the interaction between predation and food availability causes fluctuations in populations of snowshoe hares that is delayed by about one year (Krebs et al, 1995)(https://search-proquest-com.unr.idm.oclc.org/earthatmosphericaquatic/docview/213565620/18B982A5EC648A7PQ/1?accountid=452). A third generalization about population cycles could be that the magnitude of the fluctuations might be related to whether the species is r or K-selected; r-selected species produce far more offspring, but with less investment, so changes in resources, predation, weather, etc would cause greater changes in the population tallies. Alternatively, species that are K-selected might have offspring that are individually more resilient to stressors due to often higher parental investment, both in care and in body size. Since K-selected species tend to have fewer offspring, any fluctuations would most often act on smaller numbers of individuals and cause less dramatic changes to the overall population.
    - Some reasons that some populations of the same species might experience cyclic abundance dynamics where others don't could be due to geographic separation, and different pressures acting on different populations. For example, a population of rodents in a stable, verdant meadow with plenty of shelter might experience fewer fluctuations than another popualtion living in a sagebrush steppe with less forage and more exposure to predators. Ease of migration between areas may also

    influence fluctuations; for example, in a sink habitat, the population might not recover after a bottleneck if migration is reduced or eliminated.

- With respect to metapopulations, there are skeptics that say that the theory is not useful because "real" metapopulations don't exist. Critique this position, and describe at least one example of a metapopulation from the literature that was not discussed in class.
    - Our group worked off of a definition of metapopulations as populations with separate sub-populations that are equal, that reach carrying capacity once occupied, and with areas that are available for recolonization if their pops are wiped out.
    - Our group decided that the concept of metapopulations can be applied more easily over larger scales. With enough geographic area, it is possible to find populations that are separate but connected, and that experience different conditions. The idea that environmental or demographic variation can have different effects on different sub-populations is extremely useful in ecology, and even required to get a clear picture of the population dynamics of an entire species, especially one with a large range.
    - One example of a metapopulation from the literature is Spider Milkweed (*Asclepias asperula)*, which has scattered sub-populations ranging from Idaho to Texas.
- In a recent paper, Griffith et al (2016) state that "population-level processes are an ideal common currency within ecology and evolution". Explain why you either agree or disagree with this statement?
    - Population level processes, like BDIE, are things that affect growth, age distribution, mortality... Also catastrophe is often a population level process. Pop ecology gives you a foundation to study these processes, and then you can apply that to genetics, etc… Population level processes in ecology can help explain evolutionary patterns
    - Our group could not think of any reasons to disagree with this
- How have population biologists measured genetic differentiation within and among populations and what can we infer (or not) about evolutionary processes from commonly-used metrics?
    - Population biologists measure genetic differentiation within populations by looking at the frequency and number of different alleles for traits of interest, and at whether the proportions of heterozygosity match what they would be under Hardy-Weinberg equilibrium. They look at differentiation among populations by comparing levels of heterozygosity, which gives you Fst
    - Frequency of alleles can tell you how much drift is happening, number of alleles tells you about inbreeding and whether there is loss of genetic diversity happening.
    - Genetic analyses can tell you things about the history of the population or species in terms of when they started to diverge and whether there is immigration between populations, etc
    - Population genetics quantitatively shows why diversity matters
    - Evolutionary processes could tell you why you're getting speciation

    - Things to watch out for include when measured genetic differentiation doesn't reflect current processes of gene flow and drift. For example, many species have recently colonized large stretches of N. America after the most recent glacial retreat, and these species are showing lower genetic diversity in more northern latitudes, not necessarily because of drift or inbreeding, but just because they are a subset of larger southern populations.
- Think of a particular species that you are familiar with. Based on the ecology and perhaps biogeographic/evolutionary history of the species, what predictions can you make about factors which are likely to be most important in determining the distribution of genetic variation in the system?
    - One example our group discussed was bats, which only recently moved into Nevada after the last glacial retreat, facilitated by the advent of mining. Several factors are likely to affect the distribution of their genetic diversity. One is any founder's effects that might be happening from sub-populations splitting off from larger populations, either as the original colonizers of any of NV's mining caves, or as emigrants to new caves. These migrants would be likely to have lower genetic diversity than their source populations. Other factors that might affect genetic diversity in their populations might include habitat quality and rates of survival of bats with different genotypes, as well as how long the habitat has been occupied. Increased time could lead to increases in diversity through mutation, but it could also reduce diversity through drift or inbreeding in sub-populations, especially if there are low levels of migration between populations. Predation pressure can also affect diversity. While this may not be as much of a factor for bats, loss of diversity can be observed in populations like New Zealand's kiwi birds, which lost the ability to fly due to lack of predation pressure.
- Whether we talk about a small number of microsatellites or a large number of SNPs, it is very unusual to find a wild system (population or species) without any genetic variation. Why is that and what maintains genetic variation?
    - It's unusual to find wild systems with no genetic variation because they would not be able to survive any types of conditions that aren't ideal. For example, genetic diversity is very important in agriculture so that one disease can't destroy an entire field, or an entire crop species. The same idea can apply to any population, whether the pressure is disease, predation, cold-hardiness, resilience to disturbance...
    - Natl selection on mutations and gene flow between populations maintain genetic variation. Populations without any diversity would be removed any time they face a pressure that at least some of them are not adapted to handle.

Notes on the readings:

- Turchin, P. (2001). Does population ecology have general laws?. Oikos, 94(1), 17-26
    - He argues that it does have general laws, and compares them to the laws of physics
    - Laws he talks about include: the law of exponential growth, population self-limitation, and resource/consumer oscillations.
    - These basic concepts form a basis for further refinement
- Hanski, I. (1998). Metapopulation dynamics. Nature, 396(6706), 41-49

  - Goes through an overview of metapopulation dynamics and different processes that contribute to them (such as the extinction/colonization balance, spatial dynamics and connectivity, habitat loss/fragmentation, and community patterns in patches, such as food web structures), then breaks down to how these processes apply to different models
  - We were confused about the figures in this paper, especially figure 3, columns d-f...], and figure 5
  - We were also confused about the differences between different definitions of metapopulations
- Wang, I. J., & Bradburd, G. S. (2014). Isolation by environment. Molecular Ecology, 23(23), 5649-5662
  - Talks about a phenomenon that has only recently started to be investigated by ecologists and landscape geneticists.
  - The general idea is that species' genetic diversity can respond to changes in environmental conditions that are independent of geographic distance, such as continuous changes in elevation or humidity, or discrete changes in habitat or substrate type. IBE says that genetic diversity will increase with increasing environmental differences. The paper also talks about specific processes that can cause this, such as "when a temperature cline regulates dispersal among populations of an ectotherm", or "when genetic differentiation between plant populations is mediated by differences in their pollinator communities".
  - The authors break it down to 4 main processes that generate IBE patterns: (i) natural selection against immigrants, (ii) sexual selection against immigrants, (iii) reduced hybrid fitness and (iv) biased dispersal.
  - They also talk about challenges and considerations for studying IBE
- Marko, P. B., & Hart, M. W. (2011). The complex analytical landscape of gene flow inference. Trends in ecology & evolution, 26(9), 448-456
  - This paper advocates using models of population genetics that include their demographic history to tell causes of differentiation, rather than just assuming that observed differences are due to gene flow alone.
  - One suggestion is to use a model of landscape connectivity and compare it to spatial distribution of alleles, rather than just going straight to Fst to describe genetic changes.

DISCUSSION 4: Mathematical Models and Landscape Ecology

Group B Discussion Notes 9/26

Mathematical Models in EECB - Paul Hurtado

Notetaker: Micaela Enger, Group B

1. What are some of the foundational mathematical models in ecology and evolutionary biology? For one of these models, discuss its purpose (e.g., what does it seek to explain?) and key mechanistic or phenomenological assumptions (including simplifying assumptions). Is this model still useful today, or has the field advanced beyond it (or a little of both)?
    - Some examples of foundational mathematical models in ecology and evolutionary biology are the lotka-volterra predator prey model or something like logistic vs exponential growth.
    - Let's use logistic growth as a good example. The purpose of a logistic growth model is to observe how a population will grow over time with limited resources (k). One big assumption that this model makes is that there is a upper limit, the carrying capacity or k. It also assumes that the population is closed, meaning immigration and emigration are not taken into account.
    - The logistic growth model is also different from the exponential model because there is no lag time. The population will slow down the closer it gets to k.
    - The model is still useful because it serves as a good starting point. It can be built upon to use for more complex situations.
2. A key step in any statistical analysis is to check that the assumptions associated with your statistical model are not being egregiously violated. Discuss 2 or 3 approaches (e.g., statistical tests, graphical tools, etc.) for diagnosing possible violations of key assumptions. For each diagnostic method, discuss which assumptions they help check, and (if a violation were detected) how you might try to correct the problem.
    - Some typical assumptions are normality, homogeneity of variances, linearity, and independence
    - To test for normality, you can review the distribution graphically or use a statistical test like chi-square or Shapiro-wilk.
    - To test for homogeneity of variances, you can compare graphs, compare variance, standard deviation, or use a statistical test like levene's test, Fligner Killeen test, and Bartlett's test.
    - In order to fix these problems, you can transform data to make it normal or fix variances.

   - More generally, if the model you choose doesn't work for your data, then looking into other models may be the best approach instead of trying to fit your data to a model that isn't the best representation.

3. There has been recent controversy over p-values, including a rare statement by the American Statistical Association on their proper (and improper) use. Please discuss the proper and improper use of p-values within a broader discussion of other methods for model selection and hypothesis testing (e.g., Akaike's Information Criterion and related quantities).
   - The ASA states…
      i. P values can indicate how incompatible the data are with a specified statistical model
      ii. P values do not measure the probability that the studied hypothesis is true, or the probability that the data were produced by random chance alone.
      iii. Scientific conclusions and business or policy decisions should not be based only on whether a p value passes a specific threshold (0.05).
      iv. Proper inference requires full reporting and transparency.
      v. A p value, or statistical significance, does not measure the size of an effect or the importance of a result.
      vi. By itself, a p value does not provide a good measure of evidence regarding a model or hypothesis.
   - A p value should be used in combination with other statistics and figures. The 0.05 cut off is arbitrary. The cut off should make sense for specific data sets. Even if a p value reports one value, that doesn't mean there is or is not a relationship between variables. It should serve as an indicator taken with a grain of salt in many cases.
   - Even if your result isn't statistically significant, it could still be biologically significant.
   - The stats should always be outlined in the experimental design in order to prevent cherry picking data and other errors.
   - Akaike's information criterion (AIC) compares the quality of a set of statistical models to each other. An example from statisticshowto.com: you might be interested in what variables contribute to low socioeconomic status and how the variables contribute, so you can create several regression models for various factors like education, family size, or disability status. The AIC will take each model and rank them from best to worst. The "best" model will be the only one that neither under-fits nor over-fits.
   - So perhaps, the p value combined with another method like AIC could be the best way to make claims.

Landscape Ecology - Peter Weisberg

4. Landscape ecology is often characterized by its focus on spatial heterogeneity, and particularly on the reciprocal relationship between landscape pattern (e.g., resource mosaic; forest age structure) and ecological process (e.g., animal movement; disturbance propagation). In her review paper describing the state of progress in the discipline, Monica Turner notes that "…the relationship between processes that create patterns and

the patterns themselves still is not readily apparent.” Interpret this deceptively simple statement; why is this issue an important one? How can this problem be addressed?

  - Essentially, Turner is discussing how the relationship between process and pattern is not linear.
  - The relationship between process and pattern is context dependent. In some cases a certain pattern may not have a definitive process, and in other cases, a pattern may be caused by several processes. One cannot generalize in most cases.
  - This problem can be addressed by looking at different contexts and models in order to determine what models fit a specific pattern and go from there.
  - This is a difficult problem to address because disturbance and clear-cutting in a landscape like a forest may look similar so it is harder to determine the process.

5. Landscape ecologists study several kinds of fluxes, including (but not limited to) flows of genes, movements of animals, the rate and pattern of plant invasions, spread of disturbance agents, and the transfer and cycling of nutrients, energy and matter across heterogeneous landscapes. Does it seem to you that the same kinds of tools and concepts can be used (or are being used) to study these different kinds of fluxes? Or are there key differences? Please provide specific examples.
   - In some cases, the same tool may be used to look at many different fluxes. For example, gene flow and animal movement could be correlated, so similar tools could be used; however, gene flow and animal behavior are still very different.
   - There can be bigger differences when you think about how a nutrient may be carried by water from one place to another and stay, but if an animal moves, it is unlikely that it will stay in one place from that point on. The percentage of what stay could be a key difference.
   - There are also different barriers, so the scale is important in choosing a tool. Nutrients may have the ability to move to many more landscapes than an animal or gene. However, nutrients are often only available in specific forms which also plays into the bigger picture.
   - Like history is also a key difference to consider. An animal may be returning to a natal habitat, whereas that doesn’t really apply to nutrients or plant dispersal.
   - For example, in fragmented forests of the pacific northwest, elevated deer mice densities in clear cuts were associated with reduced recruitment of trillium (a plant) because of seed predation. This is an example of how animal movement and plant invasion, or lack of plant invasion are associated.
   - Simulation or predictive models may be better at looking at animal movement, while more empirical mechanistic models might help us better understand nutrient cycling.
   - Loreau et al. (2003) developed a metaecosystem framework by extending metapopulation models to represent fluxes of matter or energy.
6. How can our understanding of landscape heterogeneity be made functional, as opposed to merely structural?
   - We can look how organisms use landscape heterogeneity. For example, deer graze in open meadows, but they can hide in the cover of a thick forest. They use different landscapes for different purposes. We can also look at patterns of

movement to determine how often they visit different landscapes or what processes are driving them to use them differently.
    - Adding different structural layers can also help us look at a functional perspective. For example, if we look at age structure, some patches may have all adults or all juveniles.
    - Applied aspects of landscape ecology like habitat fragmentation also help to point out the functional side (composition and configuration).
    - Landscape ecology also plays a role in less obvious fields like determining carbon sinks and how well they function.
        i. This thought leads to a larger discussion on landscape ecology and its role in climate change in terms of nutrient sinks, range limits, loss of biodiversity, genetic drift, etc.…

7. How might species range shifts associated with climate change be affected by landscape heterogeneity? How might such shifts also be affected by climate-disturbance interactions? Is it therefore necessary to use dynamic, ecological simulation models to forecast species range shifts, or is it sufficient to use predictions from statistical models (e.g. Maxent, Random Forest)? Justify your response to this question.
    - The example from the Serra-Diaz paper shows that landscape heterogeneity may be harder on cold adapted species in a warming environment.
    - Warming will be advantageous for some species like grasses which will outcompete struggling species, while simultaneously increases fire frequency, which could affect population dynamics.
    - These sorts of examples show that predictive models are hard because changing ecosystems are not stable. Dynamic simulations with different mechanisms included and constraints could help us better understand what management strategies work best.
    - Disturbance is also going to limit where species can exist because it can destroy habitat, causing more landscape heterogeneity and more narrow corridors for species to travel through.
    - A dynamic simulation model can include changing climate and stochastic disturbance over different time and spatial scales. On the other hand, dynamic simulation models can also be limited by assumptions or scale if it is different to translate across scales.

Summaries of Each Reading

Ellner and Guckenheimer 2011 Chapter 1

- Discusses different types of general models.
- Dynamic models describe how system properties change over time like a gene's expression level or the abundance of an endangered species.
- Descriptive vs Mechanistic models
    - Decriptive models provide a summary of overall trends.

  - Mechanistic models are built by explicitly considering the processes that produce our observations. Relationships between variables emerge from the model as a result of the underlying process.
- Bathtub models
  - W(t+h)=W(t) + inflow rate x time elapsed - outflow rate x time elapsed
  - Essentially the water in the bathtub is equal to the inflow rate in ml/sec minus the outflow rate in ml/sec over time where time is continuous.
- Compartment models
  - Many bathtubs connected together
  - Example: enzyme kinetics
- The Modeling Process
  - 4 step process → dynamic equations can then be studied mathematically or translated into computer code to obtain numerical solutions for state variable trajectories
- Physical Models: models based on the physical laws of mechanics
  - Example: studying how animals move
- Optimization Models
  - Used when the modeler assumes that the study organisms are trying to achieve some particular goal.
  - Example: We might hypothesize that an animal will gather food in the habitat that gives it the best chance of getting enough food to survive, without getting eaten. The optimization model doesn't worry about how the goal is achieved. It just provides information when different assumptions lead to different predictions that can be compared to observations.
- Theoretical versus Practical Models
  - Theoretical understanding of how the system operates vs practical applications where model predictions will play a role in deciding between different possible courses of action.
  - Note the table on page 25

Waddington 1968

- The paper outlines the points discussed at the meetings in 1966 and 1967 on theoretical biology.
- Before this paper, theoretical biology wasn't really considered as a discipline.
- Discusses the idea that genes as units of information are the basic elements of life.
- Talks about several theories in biology and how the people that can prove theories or discover how to set up a computer will contribute most to the fundamental theory of evolution.

Turner 2005

- Discusses landscape ecology in general.
  - Landscape patterns and ecological responses
  - Pattern in important for spatially mediated interactions.

Serra Diaz et al. 2015

- Many tree species will experience changes in range limits as climate continues to change.

- Modeling efforts using climatic predictors and biotic interactions are good, but they need to integrate topographic complexity and the dynamics of disturbance along with forest succession to fully predict the dynamics of the forest with increasing climate changes.
- Serra Diaz used microrefugia in conjunction with disturbance and succession to look at range shifts.
- Results show that disturbance regimes play a major role in range shifts. Microrefugia had a significant but smaller effect on range changes. Microrefugia could enhance range persistence but that increases heterogeneity, and thus will disturb migration under some disturbance regimes for species with low dispersal capabilities. SPecies that gained suitable habitat with climate change depended on the interaction between species life history trains, environmental heterogeneity, and disturbance regimes to expand their ranges.

Group A Discussion Notes 9/26

Notetaker: Ben Sonnenberg

Mathematical Models

1. What are some of the foundational mathematical models in ecology and evolutionary biology? For one of these models, discuss its purpose (e.g., what does it seek to explain?) and key mechanistic or phenomenological assumptions (including simplifying assumptions). Is this model still useful today, or has the field advanced beyond it (or a little of both)?

-Several of the fundamental models include Lotka-Volterra, Michaelis-Menton, Population models etc etc.

-We looked at Population Growth equation as a specific example

-The purpose of this model is to measure population size at different points in time.

-Basic assumptions include birth, death, immigration, emigration rates

-The basic principle of the model is still valuable and in use today. The model has grown along with advancements in modern statistical tools and methods. Modern versions also vary in that they can be tailored to the specific target population and all of its parameters for maximum predictive accuracy.

2. A key step in any statistical analysis is to check that the assumptions associated with your statistical model are not being egregiously violated. Discuss 2 or 3 approaches (e.g., statistical tests, graphical tools, etc.) for diagnosing possible violations of key assumptions.

For each diagnostic method, discuss which assumptions they help check, and (if a violation were detected) how you might try to correct the problem.

-In order to use a statistical model, the data must fit the model. For example, in order to use a linear model the data in question is required to have a normal distribution. A simple but effective test would be to plot the data on a graph and look for the presence of a normal distribution.
-Several in our group mentioned that accurately observing at distributions on a graph can be difficult due to natural variability so that more advanced tests may be necessary such as (Bartlett's or Levine's test)
-If the data does in fact not fit a normal distribution and thus violates your model, a choice would be switching to a model that doesn't assume normality such as a Bayesian model and beginning again.

3. There has been recent controversy over p-values, including a rare statement by the American Statistical Association on their proper (and improper) use. Please discuss the proper and improper use of p-values within a broader discussion of other methods for model selection and hypothesis testing (e.g., Akaike's Information Criterion and related quantities).

- When testing for significance, it is extremely important to also look at effect size, as a large sample size can drive significance when an effect is not actually present.
- Another improper use of a p-value is to assume that it alone provides good evidence for a hypothesis.
- Margarete added: "It is improper to assume that incorrectly rejecting your null hypothesis ($p<\alpha$when your null hypothesis is true) is the only measure of error."
- A member of the group suggested model selection where a p-value is not an important value.

Landscape Ecology

1. Landscape ecology is often characterized by its focus on spatial heterogeneity, and particularly on the reciprocal relationship between landscape pattern (e.g., resource mosaic; forest age structure) and ecological process (e.g., animal movement; disturbance propagation). In her review paper describing the state of progress in the discipline, Monica Turner notes that "…the relationship between processes that create patterns and the patterns themselves still is not readily apparent." Interpret this deceptively simple statement; why is this issue an important one? How can this problem be addressed?

-multiple processes that create same/similar patterns can be present in a landscape. Cannot assume that the pattern observed in one model is caused only by one process.

-process and pattern may be impossible to separate
- In order to begin to understand the process vs pattern, one should start by analyzing the simple interactions and build to the more complex within a landscape. (Model construction or experimental design)
-One way to tease out the driving forces of the underlying processes that then create landscape patterns would be go out into the field directly measure interactions.
-recognizing the complexity of the interactions and not oversimplifying them can partially help to approach the problem.

2. Does it seem to you that the same kinds of tools and concepts can be used (or are being used) to study these different kinds of fluxes? Or are there key differences? Please provide specific examples.

-It does seem as though there are several popular tools and concepts being applied across different kinds of fluxes, such as simulation models and metapopulation models.
-There are hundreds of examples of fluxes throughout a landscape. The nature of a system in flux is that despite differences in scale or structure there are shared underlying concepts that all can be approached using a compartmental model.
-However, the different fluxes, depending on scale and structure, require completely separate tool kits for data collection and hands-on study.
Examples…
White-tailed deer migrations, movements of large herbivores across a landscape, require radio collars in order to track seasonal changes.
The spread of a particular gene in a Jeffrey Pine population requires collecting genetic samples across a wide range of landscapes and time spent in the lab comparing the genetic structures between locations.
The two situations are similar in that both are examples of fluxes traveling through different landscapes but the tools required to analyze the examples are completely different. This question hints at Dr. Weisberg's accusation that most ecological research has a component of landscape ecology.

3. How can our understanding of landscape heterogeneity be made functional, as opposed to merely structural?
- Approaching a landscape merely on the terms of its organismal composition gives a structural understanding but the investigation of how the composition allows for a landscape's homeostasis, flux, and interaction with other landscapes would allow for a description of its functional aspects.
- Observing the levels of organization across different scales (habitat, ecosystem, landscape) would also shed light on a landscape's functional components.

- Perhaps better mechanistic models relating to causes with degrees of effect on landscape heterogeneity will contribute to a more functional and therefore more predictive understanding, rather than a descriptive knowledge of the different component parts.

4. How might species range shifts associated with climate change be affected by landscape heterogeneity? How might such shifts also be affected by climate-disturbance interactions? Is it therefore necessary to use dynamic, ecological simulation models to forecast species range shifts, or is it sufficient to use predictions from statistical models (e.g. Maxent, Random Forest)? Justify your response to this question.

- Margarete said it well in her notes: “Serra-Diaz et al. 2015 concluded that species range shifts are directly affected by landscape heterogeneity in the sense of microrefugia. They used dynamic, ecological simulation models in their approach. Predictions from statistical models are still essential for forming a basic understanding of a system, and in some cases, we simply lack the data necessary to build a truly representative and informed simulation model.”
- In discussion, it was concluded that using statistical models to inform ecological simulation models and vice versa would be the ideal approach.
- These predictive simulations are necessary in that conducting an adequate experiment is completely unrealistic.

DISCUSSION 5: Soil Ecology and Microbial Ecology

Group A Discussion Notes 10/3

October 3
SOIL ECOLOGY

Group A

- Design an experiment to test how soil nutrient availability changes in response to a major disturbance event. What might this experiment be able to tell you about whether this ecosystem is at steady state?

To design an experiment to test how soil nutrient availability changes in response to major disturbance event we would compare a disturbed vs undisturbed site or design a disturbance is mesocosms. It is critical to know your steady state, once input is equal to output, for the site and for ending the experiment. Additionally, you should know your baseline NPP before starting experiment. It would be ideal to begin when things are in steady state. During the course of the experiment take measurements of nutrient inputs and outputs from the soil and/or water (may be both if at a field site). It would be most appropriate to perform this experiment over several years following your disturbance event.

- How would the theories outlined by McGill and Cole cause you to expect to see (and not expect to see) successional change in the soil microbial community as nutrient availability changes over the course of ecosystem development?

McGill and Cole asserts that as nutrient availability changes over the course of ecosystem development in distinct ways. Carbon and Nitrogen cycle together mainly because they are directly bound in most nutrient forms. Thus, as decomposition of carbon sources occurs can make nitrogen available. However, McGill and Cole also found that phosphorous is very different and disconnected from carbon mineralization. This is mostly due to the fact that phosphorus is not directly bound to carbon. Additionally, sulfur falls somewhere in between because it can be directly bound to either carbon or phosphorus compounds. The soil microbial community do not acquire these elements equally. The enzymes that break down each nutrient require specific other nutrient, ie phosphatase (enzyme that breaks down phosphate) needs a lot of nitrogen to operate. Thus, microbes are limited by the available nutrients in the soil. This framework provides a novel cycling theory to investigate in the context of microbial community.

One should expect to see differences in microbial processes if the nutrients in the soil are cycling over time scales. Understanding and incorporating where microbes fit and what they do fit into the cycles greatly improves our understanding of nutrient availability over time. Another interesting aspect is that soil age changes what nutrients are available as well. Additionally, plant communities can affect the nutrient availability as well, ie. specialized mycorrhizae in some plants can change nutrient compositions in soil.

▌Including microbial biomass and microbial growth efficiency may improve the ability of an Earth system model to predict carbon stocks and fluxes, but these coarse estimates fail to account for the tremendous variation of the microbiome. Please describe both why and why not explicitly including soil microbial community structure or functional groups would further improve Earth system model-development efforts?

It was previously believed the nutrients in the environment were not limiting (Vitusek) but we now understand that they are. In general, microbial processes and diversity are understudied thus their importance in soil carbon processes is understudied and underrepresented in current models. Including microbial biomass and microbial growth efficiency into models of nutrient cycling greatly improved model predictions but regionally there were some issues with correctly modeling the observations. There is tremendous variety on a small scale. Nearly 50% of spatial variation is still unexplained. For example, there were problems with modeling the tropical soil physiochemical properties accurately. Additionally, arctic soil heterogeneity was not represented in the models and needs to be examined properly. Thus, including microbial communities would allow us to include nutrient limitation but it does limit our predictability because we do not know the microbial communities as well. We cannot predict microbial community changes very well yet. It is likely and possible that the microbial community could change and change what is available in short time spans.

-maybe does not matter because have been in equilibrium for awhile (Tim)

MICROBIAL ECOLOGY

<u>David Vuono</u>

· Molecular phylogenetics has helped to pave the path forward for microbial ecology, why? What are the limitations of microbial community survey studies based on rRNA gene sequences from the environment? What factors need to be taken into account when interpreting these data? It is challenging and unfeasible to culture every microorganism in a given area so with molecular tools you can get more data and a wider breadth of what is in the environment and how they are related. Analysis of rRNA for molecular phylogenetics is a wonderful tool for determining molecular phylogenies but there are limitations. In general, rRNA has limited resolutions and lowered sensitivity. It is generally not useful for determination of close relatives at strain or species level because of rRNA's conservative nature, inconsistencies with determining time of divergence and domains have differences in average rRNA replication rates. Additionally, horizontal gene transfer and other mechanisms limit the ease of placing microbes into species concepts.

Another limitation to consider is selection of the 16S rRNA region to survey the microbial diversity significantly influences the estimation of bacterial diversity and species distributions. Gene region choice is critical. It must be conserved, not too large of a size, and reflect the line of descent. Caution is warranted when comparing data from different variable regions as well as when using different sequencing techniques. Additionally, reference sequences with low read accuracy, chimeric sequences and partial rRNA gene sequences with reduced phylogenetic resolution generated on short-read sequencing platforms such as 454 and Illumina remain problematic, resulting in incorrect or less accurate classification of environmental sequences.

· What role does the "rare' biosphere play in maintaining microbial diversity in environmental samples?

Less common organisms represent the “rare biosphere” but they have functional importance and important roles in the environment. For example, microorganisms which belong to archaea are often in specialized niches but often have key roles in these unique environments. Additionally, although they are in low abundance there is high diversity of these microorganisms, accounting for most of the diversity in microorganisms. For example, it is apparent that in some areas the rare taxa provide more nitrogen cycling than the abundant taxa. Thus, these rare species may have a significant role in global biogeochemical cycling. Also, just because they are rare now does not mean they were always rare. They may represent ancient or persistent taxa. And just because they are rare “today” or at time of sampling does not mean they will remain rare tomorrow or in the future. Many of these taxa have potential to become dominant taxa. For example, during El Nino events some rare taxa become more dominant in the soils.

· In Thompson et al, why was the 16S rRNA gene not able to resolve the tremendous amount of microdiversity with populations of Vibrio splendidus? Despite the <1% divergence of the 16S sequences from the strains isolated, how were the authors able to define these populations as ecologically differentiated groups and why is this important in the context of microbial ecology?

16S does not allow high enough resolution because of limited ability to determine differentiation between closely related species and problems with correct primer choice. Using culture dependent methods in conjunction with culture independent methods the authors could determine more genetic resolution and functionality. With culture dependent methods determining details of differentiation can be further analyzed. One method the authors used to improve genetic resolution was to compare a universal Vibrio protein, Hsp60, to determine sequence diversity of Vibrio isolates. Also, PFGE further analyzed differences in these genotypes by categorizing into genome size estimates which allowed classification into distinct genotypes and phylogenetic relationship analysis of Hsp60. PFGE has high discriminatory power, high reproducibility, and genotypying ability. This is important because if you are attempting to explain genetic diversity you may be greatly misinterpreting and underreporting it with the wrong primer choice or gene of interest. Additionally, it may be important to consider what level of diversity should one be looking for and comparing when making conclusions about microbes in an ecological framework.

- Microbiologist traditionally needed to isolate and grow microorganisms in the lab in order to understand an organisms potential role in the environment. How can traditional microbiology approaches (i.e., culture dependent techniques) be used in parallel with modern DNA and RNA sequencing to better understand the wealth of diversity, both taxonomic and functional, in the environment?

Cultivation of isolates from the environment are conspicuously different from those identified by sequencing techniques. In conjunction with high throughput techniques, such as DNA and RNA sequencing, culture based studies can elucidate questions of diversity in the environment, both functional and taxonomic. One can identify genomes better with culture based methods because isolates in the lab can be sequenced to a greater depth. Generally, culture methods allow for direct lab based studies for investigations on genetics, ecological roles, and models. For example, to compare fungal diversity in pine forests one would want to do sequencing at each site as well as collect multiple fungal isolates from multiple species. From the sequencing one could determine what fungi are present at least in abundant quantities. From isolates, one could find more diversity at sites and even further test these isolates for questions about functional diversity and ecological roles.

Group B Discussion Notes 10/3

Soil Ecology - Ben Sullivan

1. Design an experiment to test how soil nutrient availability changes in response to a major disturbance event. What might this experiment be able to tell you about whether this ecosystem is at steady state?

- The experiment presented by Vitousek and Reiners (1975) is a great example of an experiment designed to determine variations in nutrients availability. The authors evaluated seven watersheds at different successional stages after disturbance by logging, to identify variations in nutrients outputs as the ecosystems tend to a steady state after disturbance. The watersheds in the study had similar characteristics, such as similar elevational range, similar hydrological and precipitation regime, and the same bedrock substrate, which allowed for the results to be comparable. The authors found that the nutrient outputs in old age ecosystems where similar to the expected precipitation inputs, while the early successional ecosystems retain nutrients more effectively.
- Another example of an experiment to identify changes in nutrient availability implicates tracking the successional stage of a fire disturbed ecosystem and measure the concentration of nutrients from a source such as streams discharge, the water table or soil samples to evaluate if

the nutrient concentration variates through time. We would expect that at early stages of the succession the nutrient concentration in the samples would be low, and as the ecosystem regenerates and tends to a steady state, the nutrient concentration in the samples would gradually increase.

- Since experiments at landscape scales can be difficult to achieve, experiments with natural microcosms could be a useful alternative to assess soil nutrient availability. By using a microcosm, the conditions of the experiment could be more easily controlled and different disturbance conditions could be replicated. (For a reference on microcosms experiments see Srivastava et al., 2004. Are natural microcosms useful model systems for ecology? https://doi.org/10.1016/j.tree.2004.04.010)

2. How would the theories outlined by McGill and Cole cause you to expect to see (and not expect to see) successional change in the soil microbial community as nutrient availability changes over the course of ecosystem development?

- The theories presented by McGill and Cole 1981, indicate that the stabilization and mobilization of different nutrients in the soil are due to independent systems in which the microbial community play a fundamental role. Considering that during successional changes in the development of an ecosystem, the demand for nutrients varies (from an efficient intake of nutrients in early successional stages to similar values of input and outputs in mature ecosystems), we would expect to see clear variations in the microbial community composition and abundance accordingly to the nutrient demand and availability in the ecosystem.
- Furthermore, changes in the availability of limiting nutrient composition would also be relevant in determining variations in growth rates in plants and in microbial composition during the ecosystem development.
- We would also expect that, as the ecosystem reaches a steady state, the recycling of nutrients through litter decomposition would help in maintaining the microbial composition in the soil.
- Finally, we would expect that the seasonal variations in nutrient availability would also affect the microbial community composition, particularly as ecosystems in different successional stages experiment different seasonal variations in soil nutrient availability, as indicated by Vitousek and Reiners (1975).

3. Including microbial biomass and microbial growth efficiency may improve the ability of an Earth system model to predict carbon stocks and fluxes, but these coarse estimates fail to account for the tremendous variation of the microbiome. Please describe both why and why not explicitly including soil microbial community structure or functional groups would further improve Earth system model-development efforts?

- Including soil microbial community structure in Earth system models would improve model development efforts, as this information would lead to more accurate estimations of soil nutrient availability and to better informed predictions of primary productivity. As presented by Wieder et al., 2013, accounting for future variations in microbial growth efficiency due to climate change, would allow for better predictions of C pools. However, the accuracy of Earth system models that include variations of the microbiome is limited by our current knowledge of the soil microbial community. Considering the voids in information regarding the composition of microbial communities and their specific function in different nutrient cycles, the microbiome could be thought as a “black box”. The information input for the models might be incorrect, or we might be attributing certain functions to the incorrect microbial community structure. Nevertheless, even coarse estimations derived from current knowledge on the microbiome, should be closer to the reality that estimations from models that do not consider these important sources of carbon variation, as can be seen in the results presented by Wieder et al., 2013, who describe a better performance of their model, as they were able to explain a higher proportion of the spatial variation in contemporary soil C stocks.

Microbial Ecology - David Vuono

1. Molecular phylogenetics has helped to pave the path forward for microbial ecology, why? What are the limitations of microbial community survey studies based on rRNA gene sequences from the environment? What factors need to be taken into account when interpreting these data?

· Molecular phylogenetic allow us to compare the phylogenetic variation of different types of organisms, from large animals to microbial organisms by comparing genetic sequences. This has helped in the establishment of relationships between microbes and other organisms, the development of a more accurate classification of microbes and to determine phylogenetic groups or domains which allow us to track evolutionary history into a tree of life.

· Microbial community survey studies based on rRNA gene sequences from the environment aid in the characterization and classification of microbes that cannot be cultured. However, low differentiation of rRNA gene sequences of related microorganisms difficult their differentiation. As indicated by Pace (2009), the high conservation of rRNA does not allow for a reliable discrimination between humans and mice.

· When interpreting rRNA is it important to consider how to align and compare sequences from different organisms, how to extrapolate from a rRNA sequence to a taxonomic differentiation, the database information available for comparison, other sources of gene sequence differentiation (as in the Thompson et al., (2005) paper), among other factors.

2. What role does the "rare' biosphere play in maintaining microbial diversity in environmental samples?

· Rare genotypes can be the ones with the most important functions.

- The rare biosphere acts as a pool of genotypes that are only active in specific environmental conditions. Large parts of the pool can remain dormant for periods of time. These periods of dormancy could shield inactive microbes from being wiped out during times of disturbance maintaining overall microbial diversity in an environmental sample. The periods of disturbance could also activate dormant microbes allowing the environment to maintain microbial diversity during disturbances.

3. In Thompson et al, why was the 16S rRNA gene not able to resolve the tremendous amount of microdiversity with populations of *Vibrio splendidus*? Despite the <1% divergence of the 16S sequences from the strains isolated, how were the authors able to define these populations as ecologically differentiated groups and why is this important in the context of microbial ecology?

· Thompson et al., (2005) show that 16S rRNA sequences across the population sample are very similar, which define a clear cluster of *V. splendidus* population, but fails to identify differences in genotype. Due to the lack of variation in 16S rRNA sequences, the authors identified a high heterogeneity of genomes in the *Vibrio splendidus* population using the sequence diversity of the *Hsp60* gene. Moreover, by using pulse field gel electrophoresis, Thompson et al, were able to confirm the high levels of genotype heterogeneity in the population. The authors conclude that genotype diversity is likely due to different processes introducing variation such as horizontal gene transfer and that such variations have little adaptive value in the coastal ecosystem. The authors indicate that selection of different genotypes is probably neutral, which allows for the maintenance of the genotype diversity, and that such genotype heterogeneity can be averaged across the population, which results in genotypic diversity coexistence. These results are important in the context of microbial ecology, because genomic diversity in microbial populations is largely unknown, and such differences might be useful in defining subpopulations or niche differentiation in the microbial population.

4. Microbiologist traditionally needed to isolate and grow microorganisms in the lab in order to understand an organism's potential role in the environment. How can traditional microbiology approaches (i.e., culture dependent techniques) be used in parallel with modern DNA and RNA sequencing to better understand the wealth of diversity, both taxonomic and functional, in the environment?

· Analysis of environmental sequences has largely contributed to the current knowledge of microbial ecology because most microbes cannot be cultured (Pace, 2009). While cultured samples would present a solid evidence of the existence of a microbe, and would facilitate the study of phenotypic traits, cultured microorganisms might not perform the same functions when taken from its environment into artificial medias. In such scenario, traditional microbiology approaches might not be sufficient for determining the role of an organism in the environment and modern DNA and RNA sequencing techniques would still be useful in determining taxonomic and functional traits. If new methods for culturing microorganisms are developed, modern and traditional microbiology approaches can be used in conjunction to improve the understanding of the microbiome and of microbial ecology.

DISCUSSION 6: Ecoimmunology and Applied Evolution

Group A Discussion Notes 10/10

Trade-offs

As resources are a limited factor in development and growth, organisms often losing one aspect or amount of something in return for gaining another aspect or amount. In other words, a trade-off involves the allocation of limited resources among costly physiological functions with the allocation to one function decreasing the allocation amount to another. Trade-offs can also be specifically defined as, "beneficial change in one trait is linked to a detrimental change in another trait" (Jessup and Bohannan 2008).

As trade-offs tend to occur among highly costly life history traits, an investment in immunology can result in decreased reproductive rate. Another example of a trade-off occurs between immunology and decreased chemical effects (eg: sequestering secondary chemicals) in insects. Measurable traits that could potentially demonstrate a trade-off in an organism include weight, developmental time, and survivorship. As a result of the large energy investments and fitness costs associated with immune responses, it may also be possible to document a trade-off in life history traits of mate choice and mating itself. For instance, research has found sexes have different evolutionary interests that influence their investment in immune defense. Additionally, mate choice could serve to optimize offspring immunity by choosing immunocompetent males with high diversity of immune genes that complement the female immune genes. To demonstrate a trade off in mate choice exists one would have to identify a model species and keep individuals in the lab or track their populations for several generations in order to measure key trade off traits. Mate choice experiments could be done and MHC diversity could be measured as a proxy for immunocompetence.

Although it is difficult to experimentally authenticate that a trade-off exists, it possible to determine that a correlation between increased immunology with decreased life-history traits. For instance, an observational study could capture wild caught insects across populations (but within a species) and then test the insects for those who have a disease and those who do not. Then we could analyze common life history traits that would relate to growth and development. As another option, we could infect high number of females within a species (with a short gestation period) with parasites, control for injection in a second treatment group, then breed the females with males, and finally analyze the mean reproductive output for both treatment groups.

Understanding the causes of variation in the immune response

The immune system is a highly complicated aspect of an organism physiology with multiple pathways and different levels of energy investment. Understating the factors that lead to variation in a trait is important for many reasons, including that understanding variation in ecological immunology is important to understanding health and wellness in any species. In addition, understanding the evolution of virulence and an organism's ecoimmunity defense strategies is critical to species conservation. Likewise, being able to predict immune response is dependent on knowing the causes. Furthermore, if you want to study an organism with a host-parasite relations you need to know the ecological and evolutionary history of the organisms. However, it should also be noted that studying one aspect of the immune system greatly underrepresents the breadth of the immune response. For example, the interplay of hormones and the immune system muddies the organism's immune response to an ecological factor. If an organism is being chased by a predator or stressed by a territory invasion by a competitor the hormonal response will vary and so will the immune response. Additionally, hormones vary how they affect different aspects of the immune response.

It is worth noting that biotic and abiotic factors both contribute to variation in immunity, two of which are nutrient availability and presence or the presence of a symbiotic organisms. Temperature is another important factor in ecoimmunology and an organism's immune responses. There is also some natural variation in how well an organism's immune system functions, for instance the level of tolerance to being immune compromised can vary from individual to individual. In addition, the continuing levels of exposure to immune stressor would impact an organism's quality of immune response.

Measuring natural selection measured in the wild

Natural selection can be measured in the wild by looking at observable and adaptive response to selection which favors specific changes. This can be done both by looking at phenotypical variation as well as genotypical. For instance, one could track the fitness of a population that is responding to a changing environment using life tables and look for phenotypic variation in the individuals with higher reproductive rates. In addition, one could observe adaptation in wild populations by graphing a mean trait shift that could show a shift towards favored phenotype. For instance, the pattern of earlier maturation and smaller adult body size in heavily harvested populations of Atlantic cod. Other known trends include the shifting of smaller mean antler size in ungulates as an effect of hunting pressures.

In general the documentation of the a shift in specific characters within a species can be observed and quantified to show an adaptive response to changing conditions. This can be done by observational studies or by carefully designed field experiments. For example, Dr. Leger analyzed grasses that survived in post-fire restoration work done by the BLM and compared the survivors to a sample of original seed mix to see what traits produce a higher survival rate. Then seeds from the surviving field are grown in a common garden for multiple generations to control for environmental variability, before comparing seed traits again. Other experiments might include putting farm fished into habitats that already had local extinction to document which genotypes perform the best.

Natural selection can ultimately be measured by assessing population dynamics that depend on fitness, counting offspring that transmit genes to future generations. Evolution can happen fast enough to be observed, typically in response to colonization events or human related disturbance. There have been numerous documented cases of evolutionary change. One example is the Peppered moth that occurred in Europe before the industrial revolution as a white moth with a black speckled coloration. After the industrial revolution, the moth melanized into a dark color in response to the soot that covered the environment (Rice 2007 Encyclopedia of Evolution). Later when the pollution was cleared up the moth changed back to the lighter color.

historical reference community and the "novel ecosystem" concept

A historical reference community provides a measurable goal for habitat restoration and presents a measurable metric that is important for the construction of grant proposals. It can also be used for evaluation of the success of the project. Having a reference for each community may allow ecological restoration to be more relevant, understandable and effective in social, economic and cultural terms (Balaguer et al 2014).

The idea of an irreversible threshold that prevent restoration to a historic state is descripted within the “novel ecosystem” concept. The irreversible seems dogmatic and overly deterministic. Although, ecosystem may be so degraded that it may be wise to use conservation efforts in another area, there are few ecosystems that have had a truly irreversible loss of biodiversity. Furthermore, defining the difference between a historic and novel ecosystem is challenging and may dangerously under value the practice of restoration. On the other hand, it is also important to realize that “novel ecosystems”, when considered from less dogmatic definition, are abiotic and biotic components differs from those that prevailed historically due to anthropological alterations, and are increasing in abundance globally. These areas could be studied to determine the dynamics occurring in such an ecosystem, particularly to see if some native plants are able to persist in the altered landscape due to an increase of adaptive genotypes or phenotypes. If the goal of ecological restoration is to re-establish as closely as possible the historical trajectories of ecosystems before human actions drastically changed them, with the hope that the restored ecosystems can continue to respond to environmental changes as these arise, then having genotypes with a higher tolerance to degradation would be certainly beneficial.

Evolutionary potential mean in the context of restoration
Some genotype may contain greater phenotypic variation, which could in theory have a higher degree of resistance or resilience to disturbance. While it is important to protect and preserve diverse habitats through habitat restoration, there also has to be some consideration for the rapidly changing environmental conditions and continued pressures from human-mediated disturbances. Evolutionary potential is important in that genotypes within a species with a higher degree of tolerance or ability to respond to changes will be critical to the persistence of a species in the face of the anthropocene. Furthermore, as there is limited conservation funding, it is important to invest in restoration wisely, which would mean considering the evolutionary potential of each species within the historical framework of the ecosystem.

Group B Discussion Notes 10/10

Trade-offs in life-history traits are a large part of the literature in ecological immunology. What does it mean to have a trade-off? What sort of trade-offs would you expect to occur between immunity and life-history traits? How would you demonstrate that such a trade-off exists?

- A trade-off is a situation in which an organism has one trait that allows it benefit in some aspect (such as increasing fitness) to the detriment to another trait. In other words, it's losing a quality in exchange for gaining another quality.
- Trade-offs one would expect to occur between immunity and life-history traits would be:
  - Cost of reproduction and cost being paid in survival and cost being paid in future reproduction.
    - Reproduction vs. Survival – ex: High & low fecundity (quality vs quantity). With high fecundity, an organism will have a large number of offspring, invest less in offspring development but have a better chance to survive to keep having more offspring. With low fecundity, an organism will have a few number of offspring, invest more in offspring development, but have lower chances of surviving to keep having more offspring.
    - Reproduction vs. Future offspring – ex: Semelparity (gain: reproduction, cost: fitness to have more offspring) & Iteroparity (gain: fitness to have more offspring, cost: living long enough to keep reproducing).
  - Cost of development and cost being paid in immunity
    - Development vs. Immunity – ability to gather resources and mature sexually to reproduce at the cost of a strong immune system to fend off parasites or disease (priorities of resource allocation).

- Demonstration of trade-offs: Investigate the trade-off of reproduction and survival in Buckeye caterpillars when exposed to a virus -> infected caterpillar invests all resources to develop faster in order to reproduce, versus investing in its immunity to survive.

Understanding the causes of variation in the immune response is an important component of ecological immunology. First, explain why understanding factors leading to variation in a trait is important, then describe at least two possible ecological factors that could cause variation in the immune response.

Factors leading to variation in a trait is important because environments are always changing, so the organism must be plastic to any changes to survive and reproduce. Abiotic and biotic ecological factors could cause variation in the immune response. Abiotic factors such as climate change could change an organism's environment influencing their immune system to evolve. Biotic factors such as other species in an environment can influence an organism's immune system to evolve, for example, coevolution with parasites. Coevolution with parasites is where parasites and host species are in a close and long term association to where if a host develops a new defense mechanism to fend off the parasite, the parasite will eventually develop a way around that new defense mechanism to attack the host.

How is natural selection measured in the wild? and describe some examples of recent evolutionary change that have been documented.

One could measure natural selection in the wild by utilizing a population's life history and comparing, contrasting, and keeping records of morphologic traits, changes in behavior, changes in phenology, or changes in genotypic variation.

- Some examples of recent evolutionary change:
    - Island of Daphne Major – Study by Peter and Rosemary Grant on the natural selection of beaks of ground finch birds & seed sizes (depending of the seasonality of the year, selection favoring beak sizes depended on food availability)
    - Caribbean lizards – Introduction of large predatory lizards changed behavior of small lizards. Before predatory lizard introduced, small lizards perched on ground and rocks– when predatory lizards are introduced, small lizards had to escape into higher vegetation and adapt by evolving shorter limbs.

Why is the idea of a historical reference community central to the intellectual content of biological restoration? What do you think about the "novel ecosystem" concept: helpful new way to look at restoration, or muddying the waters with imprecise terminology?

The idea of a historical reference community is central to the intellectual content of biological restoration because without an idea of the history of ecosystem, how could we know how to restore an ecosystem back to a previous state? A historical reference community gives an idea of what is an obtainable goal in restoring an ecosystem (costs and available resources) and how to manage an ecosystem until it is considered a successful restoration. But, even then what constitutes a successful restoration?

The idea of a novel ecosystem is that an ecosystem is so altered by abiotic or biotic conditions that it is irreversibly different from the history of that ecosystem. Novel ecosystems require new approaches to restoration and conservation practices, so it is a helpful new way to look at restoration. It also makes the idea of restoration to be more of a human centric idea of what makes an ecosystem valuable, productive, or successful. It puts into perspective that an ecosystem is ever changing and makes one evaluate the costs and benefits of restoring an ecosystem that will still change over time.

What does the idea of evolutionary potential mean in the context of restoration?

The idea of evolutionary potential mean in the context of restoration is that since ecosystems are continuously changing, one could harvest that potential to create predictive models to improve restoration practices. Having such models could help with estimating the costs and benefits of restoring a particular ecosystem and setting short and long-term goals in planning.

DISCUSSION 7: Community Ecology and Physiological Ecology

Group A Discussion Notes 10/17

Community Ecology - Beth Pringle, Ph.D.

1. *Clements described an ecological community as an integrative whole, a superorganism. Gleason declared that communities could not be defined because species overlap is merely coincidental—species end up where they do independently of all others. Vellend says that ecologists currently define a community as "a set of species in sometimes arbitrary units of space." How to define a community has remained a central dilemma in the field of ecology. How do you think a community is best defined? Explain your reasoning and why you think your definition will be useful to the field moving forward.*
    - A community is an assemblage of species that coexist in time and space, and that interact directly or indirectly.
    - Communities are bounded by common environmental or abiotic conditions such as vegetation or geography. The relevant scale depends on the individual species or research question of interest.
    - One problem with scale: some plants or animals have very large distributions.
    - Similar question: how do you define a landscape in landscape ecology?
    - Interactions must be included in the definition because they drive processes, abundances, and distributions.

2. *In the Gotelli et al. 2010 paper, they report that biotic interactions, including Allee effects within species and competition between species, may affect species distributions at regional spatial scales. With reference to any system you like, describe how another species interaction (e.g., mutualism, parasitism, predation, herbivory, etc.) may produce patterns that "scale up" in space well beyond the spatial scale of the community or territory of any particular individual.*
    - Ex: Herbivory by caribou and reindeer prevents encroachment of the boreal forest into the tundra. Such herbivory affecting habitat composition and vegetation communities in a predictable way can be seen at different spatial scales. Example paper: Van der Wai, R. (2006). Do Herbivores Cause Habitat Degradation or Vegetation State Transition? Evidence from the Tundra. Oikos, 114(1), 177-186. Retrieved from http://www.jstor.org/stable/40234861

- Ex: (from lecture) Commensalism: nursery plants enabling establishment of a second species (e.g., sagebrush and pinyon pine). This scales from the level of the individual to the level of the community in terms of species distribution.
- Ex: (from Gotelli et al. 2010) "... conspecific attraction combined with interspecific territoriality could result in mutually exclusive distributions of species at relatively large spatial scales." (p. 5033). For another example of conspecific attraction leading to local aggregations of a species, crows have been shown to follow individuals demonstrating good body condition to find territories with high quality habitat.

Physiological Ecology - Jack Hayes, Ph.D.

1. *A fundamental goal in physiological ecology has been to establish mechanistic connections between physiological traits and fitness. In your opinion, have we already learned what we need to know (more or less), or should that remain an important goal moving forward? Be specific with respect to areas of ecology and evolutionary biology for which that physiology and fitness connection is (or has been) most important.*
   - No, we know little about:
     - Genetic underpinnings of traits
     - The extent to which behavioral plasticity can moderate physiological responses
     - Information for whole taxa and understudied species
     - The extent to which laboratory experiments fail to address physiological mechanisms and responses to environmental conditions actually experienced in the field
     - Potential for evolution in traits, and what is the source of variation for physiological responses.
   - The link between traits and fitness are important for:
     - Understanding species in extreme environments, or that are sensitive to change (e.g., tropical species that experience less extreme differences in temperatures throughout the year compared with species at higher latitudes).
     - Understanding species distributions
     - Predicting species occurrence, distribution, and abundance in novel environments

2. *A distinction can be made between statistical and physiological (or mechanistic) approaches to niche modeling. What is the distinction? and why might the two approaches produce very different results? Illustrate with a real example from the literature.*
   - Statistical approaches to niche modeling rely on presence or abundance data and correlate that with habitat variables to determine where a species is predicted to occur on the landscape. In contrast, mechanistic approaches use physiological data such as minimum/maximum temperature constraints, energy requirements,

etc., to predict species ability to persist on the landscape given habitat characteristics.

- Re: mechanistic models
    - Stochastic environmental events or conditions (e.g., weather events on trees) can have strong effects on individuals, but may not be accounted for in the model.
    - Finer-scale predictions (e.g., individual breeding pond level).
    - Depends on what variables are included in the model and how they are chosen.
    - Assumptions need to be made in the case of missing information. For many species, a lot of physiological information is simply not known.
    - Could be good for invasive species because there may be little or no data on the correlation between species presence and the novel habitat they might encounter.
- Re: statistical models
    - Environmental variables are used as proxies for what affects fitness
    - Could be something else affecting presence of individuals that is not accounted for in the models
- Different results between the two approaches were reported in Kearney and Porter (2009) in which they summarized the findings from a study on cane toads in Australia (Kearney et al. 2008) - the mechanistic model revealed that much of the southern continent was unsuitable to toads based on the locomotor performance curve, whereas the correlative model predicted the species' occurrence in the southern portion.

3. *Explain what type I, type 2, and type 3 statistical errors are. Which of these types of statistical errors do you think is the most important to avoid or minimize?*
    - Type 1 error: Alpha (α) error, in which the null hypothesis is true but you incorrectly reject it in favor of the alternative hypothesis.
    - Type 2 error: Beta (β) error, in which the alternative hypothesis is true but you incorrectly fail to reject the null hypothesis.
    - Type 3 error: In which your hypothesis is fatally flawed so that you reach the "correct" answer but your conclusion as to the reason/cause/relationship you are studying is therefore wrong.
    - Type 1 and Type 2 errors are known errors arising from the nature of the frequentist approach. The common approach is to minimize Type 1 error, so that an effect is not claimed to be significant by mistake. However, this approach means that Type 2 error is increased, such that it becomes harder to reject the null hypothesis although the null hypothesis is false. In contrast, Type 3 error is a reasoning error, and arises from the approach taken by the researcher(s) for the study design and rationale. This seems a more dangerous error, as the erroneous conclusions could result in serious management or conservation implications when decisions are made based on whatever incorrect claims were supported by the study. This error may also be more difficult to detect during the peer review process.

Group B Discussion Notes 10/17

COMMUNITY ECOLOGY (12-1pm)
Beth Pringle

Vellend, M. 2016. Chapter 3: A brief history of ideas in community ecology. pp 20-35 in The Theory of Ecological Communities, Princeton University Press: Princeton.

Gotelli, N. J., G.R. Graves, C. Rahbek. 2010. Macroecological signals of species interactions in the Danish avifauna. PNAS 107: 5030-5035

Recommended but not required:
Sandel, B. 2015. Towards a taxonomy of spatial scale-dependence. Ecography 38: 358-369.

- Clements described an ecological community as an integrative whole, a superorganism. Gleason declared that communities could not be defined because species overlap is merely coincidental—species end up where they do independently of all others. Vellend says that ecologists currently define a community as "a set of species in sometimes arbitrary units of space." How to define a community has remained a central dilemma in the field of ecology. How do you think a community is best defined? Explain your reasoning and why you think your definition will be useful to the field moving forward.

-> A community can be defined in many different ways, depending on what makes sense for your system. Most broadly, it can be viewed as either a collection of species that inhabit the same space and are interacting with each other in some fashion (may or may not include abiotic factors). The biggest dilemma for defining a community is defining the boundaries and setting the spatial scale, which is often done on a case-by-case basis. Natural boundaries can make this process easier (i.e. defining sagebrush community by presence or absence of sagebrush), but it is not always straightforward (i.e. salmon ‘community’ includes both riverine and ocean systems far too large to be a single community).

- In the Gotelli et al. 2010 paper, they report that biotic interactions, including Allee effects within species and competition between species, may affect species distributions at regional spatial scales. With reference to any system you like, describe how another species interaction (e.g., mutualism, parasitism, predation, herbivory, etc.) may produce patterns that "scale up" in space well beyond the spatial scale of the community or territory of any particular individual.

-> In the Gotelli et al. paper, they describe the allee effects within Danish avifauna and how individual choices scale up into larger regional patterns.
-> Mutualism: positive interactions between plants (i.e. pinyon pine and sagebrush) can be the driving force in species distribution at a communtiy/landscape scale Callaway paper https://link.springer.com/article/10.1007/BF02912621
-> Plant-pollinator interactions (mutualism and facilitation): Hegland paper http://onlinelibrary.wiley.com/doi/10.1111/1365-2435.12223/abstract Pollination success in red clover is scale-dependent. At a small scale, “the bumblebee visitation rate to red clover inflorescences increased with both intra- and interspecific floral density, indicating facilitative interaction for pollinator visitation among red clover flowers and its nearest floral neighbourhood.

Increased visitation of bumblebees led to subsequent increased fruit set, but there was a saturating effect as fruit set did not increase when visitation rates exceeded a certain level. As the floral neighbourhood became denser at a coarser scale, the interactions for pollinator visitation changed towards competition.”
-> Other example: pigeons following humans (commensalism)

PHYSIOLOGICAL ECOLOGY (1-2pm)

Jack Hayes

Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A., Jess, M., & Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Phil. Trans. R. Soc. B, 367(1596), 1665-1679.

Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species’ ranges. Ecology letters, 12(4), 334-350.

❚ A fundamental goal in physiological ecology has been to establish mechanistic connections between physiological traits and fitness. In your opinion, have we already learned what we need to know (more or less), or should that remain an important goal moving forward? Be specific with respect to areas of ecology and evolutionary biology for which that physiology and fitness connection is (or has been) most important.
-> No, too much remains unknown! For instance, little is known about physiological ecology in entirely new fields (immune system function, hormones, hibernation and genetics) and certain families (bats, endotherms and aquatic species).
-> It is crucial to better understand the mechanistic connections between phys. traits and fitness, if we are to understand how species will react or adapt to climate warming. Being able to better identify the appropriate variables (or proxies) and their relationship with climate will become increasingly important with looming climate uncertainty. “Physiological information is fundamental here: one needs to know whether a species is a thermal specialist or a thermal generalist, is warm versus cold-adapted, has marked acclimation capacities or is sensitive to other physiological variables” (Huey et al paper).

❚ A distinction can be made between statistical and physiological (or mechanistic) approaches to niche modeling. What is the distinction? and why might the two approaches produce very different results? Illustrate with a real example from the literature.
-> Statistical (correlative) approaches to niche modeling generally require very little knowledge of the organisms and their environments, simply trying to link species occurrence to GIS data based on statistically significant variables. This approach is best suited for environments/organisms that are poorly understood and understudied. On the other hand, the mechanistic approach takes species data (i.e. functional traits) and compares it to a relevant spatial (GIS) dataset (i.e. climate or terrain) based on a model to capture key processes and interactions in the environment. This approach is considered more “robust in contexts of environmental change that require extrapolation of correlative SDMs.” (Kearney and Porter paper). →see Kearney Figure 1

-> Correlative models are best suited for developing hypotheses to be tested further and to determine potential variables for a mechanistic model. Two different results using the two approaches were reported in several studies → Kearney Fig 5 has specific examples. Since the correlative approach cannot take physical traits or capacities into account, it has a tendency to overlook crucial environmental barriers to organisms (i.e. Cane toad's presence predicted in southern continent, which is physically not possible for the cane toad based on mechanistic approach).

- Explain what type I, type 2, and type 3 statistical errors are. Which of these types of statistical errors do you think is the most important to avoid or minimize?

-Type 1 error = alpha error: the null hypothesis is true, but you incorrectly reject ("false positive")
-Type 2= beta error: the null hypothesis is false, but you incorrectly accept ("false negative")
-Type 3: the null hypothesis is correctly rejected, but for the incorrect reasons. You are giving the right (statistically speaking) answer to the wrong questions. This is a flaw in the underlying hypothesis and how you are interpreting your data
-> Could make an argument for any of these errors being the most important to avoid. I would argue that Type 3 is the hardest to pin down and can lead an entire field of work down the wrong path. Alpha and beta error are accounted for in most statistical models, generally favoring to minimize the amount of alpha error since a false positive is considered more serious.

DISCUSSION 8: Phenotypic Plasticity and Chemical Ecology

Group A Discussion Notes 10/24

Phenotypic Plasticity - Jenny Ouyang, Ph.D.

1. What is a reaction norm? How do we quantify plasticity? What is the difference between phenotypic and genetic accomodation? What are possible mechanisms of plasticity?

- A reaction norm is an array of phenotypes that will be developed by a genotype over an array of environments.
- We can quantify plasticity by using clonal organisms in a common garden setting. This way you know the genotype and can control for environmental variation.
- Phenotypic accommodation is the adaptive mutual adjustment, without genetic change, among variable aspects of the phenotype, following a novel or unusual input during development. Essentially, a change in phenotype without a change in genotype.
- Genetic accommodation is simply quantitative genetic change in the frequency of genes that affect the regulation or form of a new trait.
- Mechanisms of plasticity as stated in the Pigliucci book chapter include development, genetics, and epigenetics.
    - Development meaning whatever mechanical forces may be applied during development. The mechanical environment can act as a selective environment, provide cues for the developmental process, be itself modified by the organism, and alter the morphogenetic process by means of the inherent plasticity of the developing organism.

2. What is the role of plasticity in niche construction and speciation?
    - The possibility that plasticity may facilitate the evolution of fast phenotypic changes could have consequences in the study of invasive species and speciation.
    - Levin says, “An ecological shift most often involved the occupation of novel habitats in the physical and genetic vicinity of the source population...plasticity buys populations time to adapt, in that they may persist across generations without genetic alteration...Long-term population survival of the newly found population in conditional on genetic refinement.” This is essentially what Pigliucci thinks in terms of invaders in a community.
    - There a examples of plasticity modifying ecosystem effects on organisms. Hansen et al. 2014 looked at whitefish in different levels (benthic and limentic) of a common garden structured lake.
    - Plasticity and niche construction is harder to provide examples for. In some species of birds, only some individuals migrate. Plasticity may determine who

  migrates and who doesn't, which in turn may allow the birds to fill different niches.

3. Can there be selection on plasticity? How? Which ecological conditions would favor stabilizing or directional selection on reaction norms? How would you test which life-history traits would respond to such selection pressures?
    - The Pigliucci 2005 paper discusses three examples of selection on plasticity. He also talks about how the experiments are difficult so there aren't many examples.
    - The little brown butterfly has two different forms depending on the season. The wet season form has eyespots on the wings in order to scare predators, whereas the dry season form is spotless in favor of crypsis. The deflection of predators and crypsis serve as two different selective regimes that maintain phenotypic plasticity for eyespot formation.
    - Ecological conditions like trying disease and temperature cause birth weight to be stabilized. If an organism is too small it won't be able to survive disease or cold temperatures. If an organism is born too big, it might succumb to other complications like developmental issues, killing the mother, etc…
    - Ecological conditions like a tree that only grows leaves at the top might cause directional selection in that organisms that can adapt will survive. The organisms don't necessarily need to vary in genotype, so the reaction norm could be affected.
    - To test which life history traits would respond to which selection pressures, one could go back to the clonal organisms in the common garden experiment in order to control genotype and environmental variation.

Chemical Ecology - Lora Robinson, Ph.D.

1. Explain the potential trade-offs between an organisms investment in producing primary metabolites and secondary metabolites. How can changes in the abiotic and biotic conditions affect these trade-offs?

- Investing in metabolites is very costly. This may result in trade offs between these investments and growth, weight, performance, immune function, defense strategies, etc..
- Nutrients can be limiting. A plant cannot invest endless energy and resources in metabolites if it can't acquire nutrients.
- Herbivory can also affect these trade-offs. If an herbivore induces a higher chemical response, a natural enemy like a parasitoid wasp may be attracted to the caterpillar for example. This will hurt the immune function and eventually survival of the caterpillar.
- Lack of water like a drought year could affect the growth trade-off, making it more severe.
- Disease or pesticide usage could also affect these trade-offs.

2. Why do organisms produce a diverse array of secondary metabolites? How does chemical diversity contribute to species diversity?

- The obvious answer is that the organism would be better protected.
- Chemical diversity can also help to throw specialist herbivores off track because volatiles can confuse the herbivore in a plant situation. Chemical diversity can also help plants survive against generalists in that they have many options to eat.
- Chemical diversity helps to prevent many species from adapting to be able to detoxify certain secondary metabolites.
- The Salazar et al. 2016 paper discusses how volatile chemical diversity negatively affected total specialist and generalist herbivore damage. However, there were differences between high-volatility and low-volatility chemical diversity. High-volatility diversity reduced specialist herbivory and low-volatility diversity reduced generalist herbivory. This could be the driver behind the idea that increased plant diversity is expected to reduce average herbivore damage.

➔ The Raguso et al 2015 paper about chemical ecology summarizes the many different subfields of chemical ecology and the different ways that chemical ecology is studied. For example, an insect may sequester secondary metabolites for chemical defense or may use pheromones in order to attract a mate. A field in which chemical ecology may be applied is pest management.

Group B Discussion Notes 10/24

PHENOTYPIC PLASTICITY - Jenny Ouyang

1. What is a reaction norm? How do we quantify plasticity? What is the difference between phenotypic and genetic accommodation? What are possible mechanisms of plasticity?

- First, what is plasticity? According to Kelly, 2012, “Phenotypic plasticity can be broadly defined as the ability of one genotype to produce more than one phenotype when exposed to different environments, as the modification of developmental events by the environment, or as the ability of an individual organism to alter its phenotype in response to changes in environmental conditions.” This is different from the range of phenotypes that can be produced by different genotypes.
- A reaction norm is the range of phenotypes produced by a certain genotype across a range of environments. This is the line in a G*E graph. Often, the reaction norms of several phenotypes are plotted on one graph in order to compare the plasticity of different genotypes.

- We quantify plasticity by characterizing the variation in a certain phenotypic quality (such as height) across different environments. This is depicted on a G*E graph, where the angle and height of the slope of the reaction norm from a genotype or a group of genotypes can tell you whether that trait is plastic or not, how plastic it is, and how that plasticity varies between genotypes. If the line has a non-zero slope, the trait is plastic. The height of the curve for the reaction norm can tell you how plastic the trait is. Comparing the slopes and heights of reaction norm curves between genotypes tells you whether the plasticity of a certain trait is variant or invariant between genotypes.
- Phenotypic accommodation occurs when one genotype produces, through mechanisms such as development, potentially adaptive variations in phenotype in response to environmental conditions. Genetic accommodation can follow phenotypic accommodation b/c, even though your underlying genotype might remain the same over time with phenotypic accommodation, inheriting (perhaps epigenetically) a certain phenotype can buy time for genetic changes that might fix those genotypes. Genetic accommodation can also happen when you get changes in frequencies of certain genes that might be more plastic and adaptable to certain environments than others. Also, individual behavior is a potentially plastic trait that can lead to other genetic changes like speciation.
- Possible mechanisms of plasticity are development, genetics, and epigenetics. Development can be a mechanism of plasticity by creating variations in an organism's phenotype in response to environmental conditions, especially conditions which mechanically affect development (such as wind affecting plant height, temperature regulating growth speed, etc…). Genetics can be a mechanism of plasticity by coding for plastic responses. Epigenetics can be a mechanism of plasticity by regulating expression of certain traits in response to the environment.
- Heterozygosity- when heterozygosity increases, plasticity decreases. Heterozygosity is different from plasticity b/c heteterozygosity is already having two different genes that can be activated, versus when one is producing different phenotypes.

2. What is the role of plasticity in niche construction and speciation?

- Plasticity can determine which environments organisms or populations are able to tolerate. If an organism moves into (or is forced to occupy) a new environment, plasticity can allow it to survive these novel conditions, and buys time for genetic change that might code adaptation or even specialization to that environment. Theoretical example: Populations of moths in places with pollution might become darker in color in response to predation pressure. This could result in a unique ability of these moths to occupy polluted niches. It could also lead to speciation between moths in polluted and non-polluted areas if the color of the moths' wings is related somehow to their reproductive compatibility.

- Plasticity can allow sympatric populations to specialize to different resources.

3. Can there be selection on plasticity? How? Which ecological conditions would favor stabilizing or directional selection on reaction norms? How would you test which life-history traits would respond to such selection pressures?

- There can be selection on plasticity if there is a cost to having plasticity; it could be selected for in cases where environments are really variable, then species that are more plastic would be more likely to survive, whereas in more stable environments plasticity might not be selected for. Phenotypic plasticity can influence the fitness of individuals, and can then be a target for selection. Stable environments where only one phenotype does well favors stabilizing selection on reaction norms (genotype slope is flat in G*E graph). Directional selection on reaction norms would be favored in environmental conditions where more than one phenotype could do well (such as darwin's finches with either really large or really small beaks). You could test which life history traits would respond to stabilizing or directional selection on reaction norms (which is basically creating more or less plasticity) by quantifying variation in certain life history traits, and comparing the levels of variation in those traits found between populations in more or less stable environments. You could also test this by monitoring a population over time and seeing whether some life history trait changes in response to changing environmental conditions. One example can be found in the Charmantier paper, where they investigate whether the birds' timing of reproduction is responding to climate change, a potential source of directional selection on variation in the reaction norm for that trait.

CHEMICAL ECOLOGY- Lora Robinson

1. Explain the potential trade-offs between an organism's investment in producing primary metabolites and secondary metabolites. How can changes in the abiotic and biotic conditions affect these trade-offs?

- Secondary metabolites, such as those produced for defence, or chemical signals to pollinators, can be highly beneficial to an organism's fitness when it has enough resources to produce them. These metabolites can prevent the organism (plant) from being killed by herbivores, can increase pollination (and thereby reproduction), attract natural enemies of herbivores, etc- all things that might help a plant survive and reproduce better than its competitors. However, producing secondary metabolites is energetically expensive, so by allocating resources to them, you might be reducing allocation to other functions (like growth, reproduction, etc), which could reduce fitness when resources are limiting or when other pressures are high. Changes in abiotic and biotic conditions might affect the plant's ability to perform basic functions, which would make producing secondary metabolites even more costly (potentially to the point that the costs involved in producing them outweigh the benefits of having them). Examples of changes in abiotic conditions that might have this effect include changes in resource availability, which could alter balance of key nutrients, energy availability (such as sun and shade), etc,. Changes in biotic conditions could involve levels of competition, levels of herbivory affect priorities for energy investment.

2. Why do organisms produce a diverse array of secondary metabolites? How does chemical diversity contribute to species diversity?

- Organisms produce a diverse array of secondary metabolites because there is a diverse array of ecological interactions that the plant could have to respond to. Examples include: defense from herbivory, pathogens, UV damage, attracting pollinators and natural enemies of herbivores, etc...
- Chemical diversity contributes to species diversity through specialization of mutualists, through an arms race of increasing specialization with attackers, and with coevolution of pollinators, etc...

DISCUSSION 9: Species & Speciation; Paleoecology

Group A Discussion Notes 10/31

Matt Forister:
#1 Dobzhansky-Muller model of speciation = “The critical point is that, while A and B both function properly on their “normal" genetic backgrounds, we have no guarantee that they will function correctly when brought together in a common genome.”

- It is not selecting for infertility of hybrids
- Alternative fixation

Reinforcement = barriers to reproduction would happen because it is bad to waste reproductive energy for nonviable offspring. Could be seasonal shifts, mate discrimination. Keep failures from happening

- This promotes speciation
- Hybrids have less survival than either parental form

Haldane’s rule = “the preferential sterility and inviability of hybrids of the heterogametic [XY] sex”
Book suggestion: The ecology of adaptive radiation (2000)
#2 The history of research into speciation has moved from a focus on the geography of speciation (allopatry, parapatry and sympatry) to a focus on the ecology of speciation. Define "ecological speciation" and explain the shift in emphasis from the previous geographical framework.

- Divergent selection from different environments

o Natural selection has to be working on it
o An example said was assemblage of predators
o Ciclids in lake Victoria is also an example of sympatry – can be behavioural or ecological
o Stickleback is an example – Ecological Speciation Rundel and Nosil 2005
o TREE Review ole seehausen – hybridization and radiation

#3 Consider the following proposition: “The real controversy with respect to 'species' is not about the definition of species, the real issue is whether or not you believe species are entities that can be characterized by differences that are biologically more important than differences among other levels of organization and diversification, such as differences among individuals, populations or communities." Explain your own position regarding the priority or importance of species as a unit of study.

· Option 1 = species are relevant:
o Conservation/management of a species over a habitat/community
o Communicating to nonscientists decline in a species over preservation of land/area
§ Even communication amongst scientists
o Canary in coalmine – by seeing species change monitoring environmental change
o How else to measure diversity in a study area – species richness and diversity as buffers/health/ecosystem services/function
o Species respond physiologically/behaviourly even broader than the local population being studied
§ Model organisms have relevance, but can’t be generalized too far
· Option 2 = species are irrelevant
o We could be protecting/restoring more habitat or ecosystems instead of one species – what about umbrella species?
§ Not every species is an indicator of health and needed management of the area
o Missing population variability
§ An example is bird morphology for some species across the united states
o Not many species concepts consider functional traits
§ Related to policy focus
§ Is it related to novel species concept?

Paleoecology

#1 Considering the ecosystem or organisms that you work on in your own research, how might the environment of your system or organism have been different during the Little Ice Age? Middle Holocene? Late Pleistocene? How might this past history be reflected in the modern populations/distribution patterns/communities that you find today?
· Option 1: Great Basin
o Pinyon Juniper wildly different because of no pinyon pine and now they share woodland
o Ponderosa pine and douglas fir did not recolonize all of their previous habitats
o Different gradient of conifer trees can lead to different cognitive traits for caching etc in mountain chickadees
o Around lake lahontan is area that would have been underwater at some point so relativity in how new study systems are

#2 If you were to add a paleoecological component to your analysis, what tools would be best suited to answer your questions? What temporal resolution of analysis would you need? What evidence would you need to collect? Explain your reasoning.
· Option 1: PJ Woodlands
o Pollen counts
o Tree rings
o Charcoal
· Option 2: areas near volcanoes

- The magnetic poles
- Transverse range in California
- Areas undisturbed can use lichen measurements

Group B Discussion Notes 10/31

Species & Speciation - Dr. Matt Forister

Readings

Orr, H. A., & Presgraves, D. C. (2000). Speciation by postzygotic isolation: forces, genes and molecules. BioEssays, 22(12), 1085-1094.

- Reviews genetics of post-zygotic reproductive isolation. Gives useful definitions of fundamental concepts.

Rabosky, D.L. (2016). Reproductive isolation and the causes of speciation rate variation in nature. Biological Journal of the Linnean Society, 118(1), pp.13-25.

- Questions the field's overwhelming focus on post-zygotic reproductive isolation as sole explanation for speciation. Raises ideas about speciation rate in addition to mechanisms explaining speciation.

Questions

1. Explain the following terms and ideas that have been important in the history of speciation research: 1) the Dobzhansky-Muller model of speciation, 2) reinforcement, 3) Haldane's rule.
    a. Dobzhansky-Muller model: "[P]ostzygotic isolation results from an interaction between two or more genes." (Orr and Presgraves 2000)
        i. Hybrid sterility and inviability can evolve without either lineage having passed through an adaptive valley
        ii. Two alleles, though singly fit, are unfit in combination
        iii. Characterized by two properties: epistasis and recessivity
        iv. Not mechanistic - could be result of genetic drift or selection
    b. Reinforcement:
        i. The acceleration of the rate of speciation. "For example, the occurrence of partial intrinsic postzygotic isolation between populations might trigger reinforcement, such that complete prezygotic isolation evolves rapidly in response to maladaptive hybridization" (Rabosky 2016)
        ii. Evolution of mate discrimination - natural selection favors isolation to avoid wasting reproductive effort
    c. Haldane's rule: "[P]referential sterility and inviability of hybrids of the heterogametic [XY] sex." (Orr and Presgraves 2000)

        i. Population genetic theory of speciation
        ii. Comparative pattern of hybrid problems
        iii. Orr and Presgraves 2000 discuss complicating examples
2. The history of research into speciation has moved from a focus on the geography of speciation (allopatry, parapatry and sympatry) to a focus on the ecology of speciation. Define "ecological speciation" and explain the shift in emphasis from the previous geographical framework.y of speciation (allopatry, parapatry and sympatry) to a focus on the ecology of speciation. Define "ecological speciation" and explain the shift in emphasis from the previous geographical framework.
    a. Geographic framework - physical or environmental circumstances or niches that explain isolation
    b. Ecological speciation - role of natural selection (or genetic drift, or sexual selection) in explaining how species might form
    c. Shift from geographical to ecological framework
        i. More answerable questions
            1. Geographical == relies on unknowable historical elements
            2. Ecological == Under what conditions can selection on an ecological trait lead to reproductive isolation? How will different kinds of isolation (pre- or post-zygotic) evolve? How strong does selection on these traits have to be?
            3. Introduction of new tools - we can now see inside “black box”
                a. New ways to collect and analyze data
            4. Case studies
                a. From matching your hypothesis to testing predictions
                    i. *Rhadoletis pomonella* - hawthorn and apple trees (example from lecture)
            5. Giraffes - how many species?
                a. Geographic isolation versus biological species concept (example from lecture)
3. Consider the following proposition: “The real controversy with respect to 'species' is not about the definition of species, the real issue is whether or not you believe species are entities that can be characterized by differences that are biologically more important than differences among other levels of organization and diversification, such as differences among individuals, populations or communities." Explain your own position regarding the priority or importance of species as a unit of study.
    a. What would you use if you didn’t use species?
        i. *E.g.*, monarch
            1. Migrating subspecies is the one that people care about
        ii. Conservation implications

            1. At what level should protections be applied
        iii. Human value system
            1. Motivation to care
            2. Political protections
    b. How do you define an alternative unit?
        i. How do you define a “community”?
    c. Continuum
        i. Species concept limits the way we think about things
        ii. Degree of difference - different metric for determining units of organization?
    d. Depends on the research question
    e. Utility
        i. Biological species concept and reproductive isolation - clear criterion(?)

Paleoecology - Dr. Scott Mensing and Dr. Adam Csank

Readings

Mensing, S. A., Tunno, I., Sagnotti, L., Florindo, F., Noble, P., Archer, C., ... & Piovesan, G. (2015). 2700 years of Mediterranean environmental change in central Italy: a synthesis of sedimentary and cultural records to interpret past impacts of climate on society. Quaternary Science Reviews, 116, 72-94.

- Through pollen, magnetism, stable isotopes, and charcoal, authors reconstructed the story of the climate, hydrology, and plant communities in a site in Italy since Roman occupation.

Roberts, N. (2013). The Holocene: an environmental history. John Wiley & Sons. Ch. 2.

- Summarizes methods used to determine geological history.

Questions

1. Considering the ecosystem or organisms that you work on in your own research, how might the environment of your system or organism have been different during the Little Ice Age? Middle Holocene? Late Pleistocene? How might this past history be reflected in the modern populations/distribution patterns/communities that you find today?
    a. Coastal ecosystems
        i. Sea level
    b. Hibernating behavior
        i. Cost of behavior in warmer climates
        ii. Enable persistence during cooler climates
    c. Oaks in CA - persist to the present due to presence of small populations in isolated refugia during glacial periods (example from lecture)

   d. Tools to predict future responses over next 100 years of projected climate change
      i. Stationarity - how things have reacted in the past may not predict whether or how they will continue to respond to the same environmental variables
      ii. Limiting factors
2. If you were to add a paleoecological component to your analysis, what tools would be best suited to answer your questions? What temporal resolution of analysis would you need? What evidence would you need to collect? Explain your reasoning.
   a. Great Basin
      i. Pack rat middens
      ii. Atriplex - establishment of two different species at two different times
   b. Temporal resolution depends on research question

DISCUSSION 10: Philosophy of Biology; Genomic Variation & Architecture

Group A Discussion Notes 11/7

- Should we expect species concepts to be consistent across the tree of life? What impact might this sort of thinking have? For example, with respect to the units of evolution, understanding biological theory, or the politics of species conservation.

No, we should not expect current species concepts to be consistent across the tree of life. Currently there is no universal species concept-one that applies to all organisms- and this is for a reason. To encompass everything on the tree of life would create such a broad definition that it would be pretty much useless for use. The most well known species concept, the biological species concept (BSC), defines a species by if it can interbreed but has its' limitations. Ernst Mayr states the BSC as 'a biological species is a group of interbreeding or potentially interbreeding organisms that can produce viable offspring' (Mayr 1963). The biological species concept has been useful for the growth of the field of evolutionary biology but does not include asexual organisms, hybridization, most prokaryotes including bacteria (ie horizontal gene transfer) and is logistically challenging to demonstrate. Other species concepts may expand this definition in useful ways for certain applications (ecological species concept, recognition species concept, phenetic species concept, phylogenetic species concept, and 26 more), however currently none can cover the tree of life.

The impact of this is that we do not have a universal species concept and thus the use of species may be the wrong focus for a number of applications. Perhaps we have been thinking about how we group things incorrectly. Classes of things share properties of having a certain time and space that has an ending and beginning where as individuals of things have a continuous history. The latter sounds more like a species and the former is what we have been attempting to categorize species as. Perhaps we need to treat species as individual things classified by their shared properties, such as functional groups, at least in certain fields or systems. This would allow science to move forward and the species to remain. Additionally, the confusion about what a species is could have consequences in policy, such as the Endangered Species Act, which relies on a strict definition of a species. However, there have been a number of issues with this already because of inconsistencies with phylogenetic analysis, ex. four species of girrafes (Fennessey et al 2016).

It would be great to have a universal species concept spanning the tree of life, but we may not be able to at the moment. It is useful for scientists to group things in an identifiable unit or terminal unit. Having groups of things in useable units allows the science to move forward. The current species concepts generally groups things that are similar and is useful in understanding how that group changes. It doesn't have to be a historical biological species concept necessarily and could be more of a functional group or subspecies or other species concepts. Perhaps it is important to decide what matters for your question and/or context and to be flexible on changing your definition as you change your scientific question, system or field. Context is what matters for a species concept.

Politics extend beyond the species concept and need to focus on a clear and identifiable unit to keep policy moving forward. However, this definition may not be biologically useful. Inconsistencies in definition can create problems for politics of species conservation. Fields may disagree on how important species is or how to use it.

▌ Advocates of the EES view it as theoretically on par with the Modern Synthesis. Is there anything important the EES account leaves out? Is there anything trivial it includes? Is the EES necessary, important, irrelevant, or harmful to contemporary biological thinking?

The extended evoluntionary synthesis (ESS) was proposed in 2013, much after the Modern Synthesis prompted by Huxley and established from 1918 to 1942. Importantly, the EES leaves out epistasis, extinction, genetic variation and is eukaryotcentric in how it synthesizes evolutionary biology. What the ESS adds is certainly not trivial. It adds important fields, concepts and ideas that are critical to evolution such as morphology, evolvability, plasticity, evo-devo theory, niche construction, epigenetic inheritance, multilevel selection and genomic evolution.
However, a new name for the field is likely not as important as some advocate. To revamp the Modern Synthesis is extreme. It could even be harmful. Generally, it doesn't help to add more terms if unnecessary. Biology already has the problem of creating new terms throughout fields that mean essentially the same things. This has the consequence of obstructing and clouding science which leads us away from moving science forward. Currently, it is better to have a united front in evolution. There is no need to have a tremendous disagreement on semantics on a controversial subject.

Nice synthesis via https://en.wikipedia.org/wiki/Extended_evolutionary_synthesis

Pigliucci and colleagues make the following predictions:

1. change in phenotype can precede change in genotype

2. changes in phenotype are predominantly positive, rather than neutral (see: neutral theory of molecular evolution)
3. changes in phenotype are induced in many organisms, rather than one organism
4. revolutionary change in phenotype can occur through mutation or facilitated variation
5. "repeated evolution in isolated populations may be due to convergent selection and/or developmental bias"
6. adaptation occur due to natural selection, environmental induction, non-genetic inheritance, learning and cultural transmission (see: Baldwin effect, meme, transgenerational epigenetic inheritance, ecological inheritance, non-Mendelian inheritance)
7. rapid evolution can result from the simultaneous induction and natural selection
8. biodiversity can be affected by features of developmental systems (evolvability, constraints)
9. heritable variation is directed towards variants that are adaptive and integrated with phenotype
10. "niche construction will be systematically biased towards environmental changes that are well suited to the constructor's phenotype, or that of its descendants, and enhance the constructor's, or its descendant's, fitness"[42]
11. multilevel selection[4]
12. kin selection[3]

❚ What is the difference between selected effect and causal role functions? Are they exhaustive of all options? Are they exclusive? How are they relevant to biology?

In the new age of genome biology, there is renewed debate among biologists about the meaning of “function”. The controversy is mainly about the meaning and use of words. The debate about the word “function” began mostly in response to the ENCODE Project in which researchers have claimed to at last disproven the 40-year-old notion that our genome is mostly informationally nonfunctional “junk”.

There are two main concepts of function, selected effect and causal role functions (Graur et al 2013). The selected effect functionality is history dependent (etiological) and evolutionary (explanations based on natural selection) —that is, how that feature contributed to enhanced survival and reproduction now and/or in the past—in other words: Why it is there. This distinction is typically applied at the level of the whole organism or its genome: Effects at the intragenomic or super-organismal level are often neglected or assumed to be reducible to function at the genomic level. By contrast, casual role functionality is ahistorical and simply addresses the way(s) in which a component contributes to a stated capacity of some predefined system of which it is a part: What it in fact does. A "system" could be any structural component (such as the heart or brain) or process (such as circulation of blood or cognition) recognized as coherent and biologically relevant by an investigator. Simply, it is solely defined as a trait which performs a function. Thus, it may or not be selected for.

The causal role concept does not tell us if a trait is under selection thus cannot tell us anything conclusive about its' adaptiveness. This can lead to erroneous conclusions in biological studies which do not examine adaptive or maladaptive consequences of traits. The causal role concept is useful as an ad hoc device for traits whose evolutionary history and underlying biology are not well known. However, the distinction is important because a selected effect function suggests a "clear and conservative method of inference for function in DNA sequences" and allows us to determine which sequences are under selection based on function. In other words, we can determine if a trait must have a real biological function if it meets the requirements of the selected effect concept.

However, in practice it can be tricky to decide what has a selected effect functionality in genome biology. Casual role functionality is easier to demonstrate experimentally. However, not all causal roles that can be conceived or demonstrated empirically are biologically meaningful. Pleiotropy and epistasis muddy the actual studies that attempt to answer these questions. Thus, we are still left with the question, how do we determine selected effect? Everything falls into these two definitions of "function" but are likely not exhaustive of all groups. Making the distinction between these two types of "function" is of course relevant. Selection is important to know for any studies concerned with true function.

❙ Years ago, non-coding DNA was thought to represent "junk". Now we know that is not the case. What are some of the functions of non-coding DNA, and what are some of the consequences of non-coding DNA that does not have an apparent function?

It is now known that non-coding DNA has a role and is not simply "junk" DNA. Some non-coding DNA is transcribed into functional non-coding RNA molecules. Non-coding DNA functions in transcriptional and translational regulation of protein coding sequences, scaffold attachment regions, origins of DNA replication, centromeres and telomeres. At least 80% of non-coding DNA has biochemical activity in the human genome such as modifying histones, binding transcription factors, regulatory elements, and methylating CpG dinucleotides. The potential consequences of non-coding DNA are that the amount of non-coding regions or activity of these regions (ie. recombination, mutations and insertions) may be disadvantageous due to a metabolic costs or adaptive consequences. Additionally, it is likely that the more DNA an organism has the more deleterious. There also may be consequences to function and metabolism at the organism level.

- Recombination rates vary across the genome, across species, and across populations. What are some evolutionary consequences of variation in recombination rate? How does this relate to the idea of 'divergence' islands mentioned in the Ellegren et al. 2012 paper

Recombination occurs during meiosis to produce new allelic combinations in natural populations, and thus strongly affects evolutionary processes. Genetic maps, which document the way in which recombination rates vary over a genome, are a novel and essential tool for many genetic analyses because it allows researchers to study speciation by examining recombination rates. Ecological speciation is the evolution of reproductive isolation between populations adapting to a contrasting environments. A major factor determining the extent to which migrant alleles penetrate a population is recombination. Recombination would appear to have contrasting effects during ecological speciation with gene flow. This field has produced important consequences for evolutionary studies. Low recombination doesn't contribute to gene flow. Areas with low recombination, or recombination deserts, are large. Determining areas of high divergence allows us to focus on areas that may lead to speciation. Additionally, there are important differences in how different groups recombine. For example, birds tend to have many inversions and by contrast mammals tend to have many translocations, entire pieces of chromosomes that move.
Ellegren et al 2012 was a notable study in that it used bioinformatics to uncover speciation very precisely between two hybridizing flycatchers. The researchers demonstrated that recombination occurs non-randomly within the genome in areas called which they called "divergence islands". Divergence islands occur in hot spots and happen. They are often located in repeat regions and found in centromeres and telomeres.

Nice review on the study:
https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3630805/

- What is the population genetic mechanism(s) that Lynch argues best explain genome size expansion?

Lynch argues the best explanation for genome size expansion is population size. The larger the population, the faster the generation rate. In taxa with smaller population sizes, natural selection is less efficient (largely due to the increased impact of drift and reduced genetic variation). In these populations, there is consequently a reduction in the ability to eradicate excess DNA that accumulates as a result of random mutations and insertion of transposable elements. For taxa with large population sizes, selection is typically highly efficient and able to purify and streamline the genome by removing potentially deleterious or burdensome genetic content in

relatively few generations. In these populations, we see a high ratio of coding to noncoding DNA.
Additionally, taxa with extremely large population sizes, such as bacteria, typically tend to be smaller in size and have smaller cells. The inverse is true for taxa with small population sizes. Cell size is directly correlated with genome size, thus there is also a correlation between organism body size and genome size. However, there appears to be no metabolic costs to maintaining and replicating extra DNA, such as longer division time. This was initially proposed as a reason these smaller organisms have smaller genomes and a low percentage of 'bulk' DNA, however it appears that purifying selection is simply more efficient in those populations, acting to reduce excess non-functional DNA and 'streamline' the genome.
Additionally, the presence of selfish genes may add to growth of genome size.

Group B Discussion Notes 11/7

Philosophy of Biology, Dr. Carlos Mariscal
1.Should we expect species concepts to be consistent across the tree of life? What impact might this sort of thinking have? For example, with respect to the units of evolution, understanding biological theory, or the politics of species conservation.

A single, consistent concept of species for designating all organisms across the tree of life is a very appealing idea. Having a unifying concept would certainly facilitate communication of ideas among the scientific community and with the public, the study of nature, as well as the implementation of management policies. However, if we consider all the different mechanisms that intervene in the evolution and development of life on Earth, expecting a consistent concept of species does not seem very realistic. For every concept of species developed so far, there are always a lot of exceptions, that undermine its ideas and assumptions. Moreover, even if a largely unifying concept were to be developed in the future, it is highly possible that not everybody will agree with its implications or that exceptions will be found.
Considering all the above, a pluralist concept of species, in which we acknowledge the diversity of mechanism intervening in speciation, seems like a good solution, although this approach also presents some challenges. For example, having different concepts of species would impact how we study nature. The concept you use will influence how you approach your study objective and vice versa. Your field of study might also determine which concept you prefer. Furthermore, understanding biological theory might become messy as well as other aspects such as

conservation, and as mention before, it would affect efficient communication within the scientific community, and the public.

2. Advocates of the EES view it as theoretically on par with the Modern Synthesis. Is there anything important the EES account leaves out? Is there anything trivial it includes? Is the EES necessary, important, irrelevant, or harmful to contemporary biological thinking?

When evaluating the EES in comparison to the Modern Synthesis, there are different positions that arise. On the one hand, the EES includes explicitly different processes that might be relevant in evolution. These processes could be underestimated in the modern synthesis, and including them in an extended synthesis could improve our overall understanding of the mechanisms of evolution. On the other hand, how can we determine what to consider as relevant for evolution? Different scientific fields might want to include their concepts as fundamental. How do we know for sure that the additional processes included in the EES are significant? While we can find examples of organisms where these additional processes are highly relevant, that is not always the case. So, are these additional processes important for specific cases or are they really a fundamental part of the mechanisms of evolution? While we do not believe that the EES includes trivial concepts, depending on your study objective, these processes might not always be relevant. Moreover, we do not consider that exploring other approaches for studying nature is harmful, as debating is a fundamental part of science. However, the division in the scientific community created by this debate might be harmful, as it undermines collaboration among scientists. Finally, and as mention before, depending on different fields of study the EES might be leaving out important concepts such as cryptic genetic variation, epistasis, lateral gene transfer, extinction, among many others.

3. What is the difference between selected effect and causal role functions? Are they exhaustive of all options? Are they exclusive? How are they relevant to biology?

Selected effect refers to a trait that has undergo natural selection, which indicates the trait having a specific function that increases fitness in an organism, and this result in such trait been selected for. Causal role could be understood as a side effect or random result functions. Which means that a function was not selected for, but that casually is part of the functions of a specific trait. Selected effect and casual role functions are not exclusive as a casual role might derive in a selected effect, and a selected effect trait might have different casual role functions associated with it. These concepts are relevant to biology for understanding mechanisms in evolution and for establishing the distinction between different types of function. Finally, if we consider intelligent design as part of the options regarding the function of traits, then selected effect and casual role are not exhaustive.

Genomic variation and architecture, Dr. Tom Parchman

1. Years ago, non-coding DNA was thought to represent "junk". Now we know that is not the case. What are some of the functions of non-coding DNA, and what are some of the consequences of non-coding DNA that does not have an apparent function?

Non-coding DNA is important for chromosome structure. These sequences also control where transcription factors attach and can affect gene expression. Non-coding DNA might protect the genome from mutations, as a mutation in a non-coding region may not have deleterious effects on the whole chromosome. However, non-coding DNA is prone to mutation (especially in regions of intron-exon boundaries) and can gain deleterious function due to these mutations. Therefore, non-coding sections can be related to diseases. This consequence of non-coding DNA does not have an apparent function.

2. Recombination rates vary across the genome, across species, and across populations. What are some evolutionary consequences of variation in recombination rate? How does this relate to the idea of 'divergence' islands mentioned in the Ellegren et al. 2012 paper?

Variation in recombination rates across species and population can lead to adaptive benefits as for example, higher recombination rates purges deleterious mutation faster. Moreover, recombination would affect the size of the effective population of a species which has evolutionary consequences. Recombination relates to the idea of divergence islands in that these areas of divergence may not be only a result of adaptation but of recombination. Therefore, the information interpreted from divergence islands should be evaluated carefully, as it might not be a direct result of adaptation.

3. What is the population genetic mechanism(s) that Lynch argues best explain genome size expansion?

According to Lynch, the size of the population is the mechanism that best explain genome size expansion. A population with a small effective size will lose genetic diversity quickly, as compared to a population with a large effective size, in which natural selection is more effective. For species with large effective population, natural selection will intervene in preventing the addition of extra non-coding DNA, so we would expect a species with a large effective population to have a smaller genome size, than a species with a small effective population.

DISCUSSION 11: Comparative Genomics and Gene Evolution; Ecology and Evolutionary Epigenetics

Group A Discussion Notes 11/14

David Alvarez-Ponce - Comparative genomics and gene evolution

Readings

Cork, J. M., & Purugganan, M. D. (2004). The evolution of molecular genetic pathways and networks. Bioessays, 26(5), 479-484.

- Discusses the evolution of genetic pathways and how highly connected genes may function differently, influence more important drivers, and be more conserved. Paper also discusses how evolutionary selective forces may influence genetic pathways.
- Example: There is typically a negative relationship between connectiveness and rate of protein evolution.

Alvarez-Ponce, D., & McInerney, J. O. (2011). The human genome retains relics of its prokaryotic ancestry: human genes of archaebacterial and eubacterial origin exhibit remarkable differences. Genome biology and evolution, 3, 782-790.

- Paper discusses that the human genome is made up of archaebacterium and eubacterium and that the archaebacterium genes are expressed across more tissues. These genes are also inovled with more informational process and and ecode more central proteins in protein-protein interaction networks

Questions:

Can you find any parallels or areas of overlap between the study of genetic networks and the study of ecological networks (food webs)? Put another way, are there any questions that might be pursued in both areas using similar approaches and techniques.

1) Yes, we can use network analysis to look at how populations, communities and ecosystems may function. From the properties of a specific node we can figure out how specialized or generalist is a specific node based on the number of edges
2) Utilization of networks to model and explain the spread of diseases. For example, the way disease is spread through turtles.

3) Prairie dogs burrows: understanding how interconnected a population is. What is the “best burrow” that is used. This can then be used to prioritize conservation efforts for the most important nodes.
4) Social networks among birds or dogs, can we use social networks to distinguish “important” individuals in a population.

Evolutionary biologists have often conceptualized selection and drift acting on genes in isolation, i.e. abstracted from the genomic context in which they interact with other genes. How do you
see our understanding of evolution being affected by a knowledge of the structure and function of genetic networks?

1) Where genes located upstream vs downstream. Depending on where the gene is on the activation chain can determine how evolved you are, and consequently, more conserved genes are typically more important to a primary function.
2) Co-evolution between proteins and genes, were older and more conserved genes interact other similar older and more conserved genes. Similarly, more evolved genes interact more frequently with others.
3) We can also utilize the structure of networks to infer how susceptible genes are to mutation, which can infer how evolved a gene is over time.

<u>David Zeh - Ecology and Evolutionary Epigenetics</u>

Bonilla MM, Zeh JA, Zeh DW. 2016. An epigenetic resolution of the lek paradox. BioEssays 38, 355-366.

- This paper discusses how the lek paradox may be resolved by epigentics.
- The lek paradox suggests that if females continuously select the best fit males, or males that are displaying the best coloration, then we should be eroding genetic diversity.
- Evidence from epigenetics suggest that the genetic diversity is actually conserved because it is the variation in the environmental conditions which is actually driving how genes are expressed. Thus, the genes are there but they are not being expressed, and the genetic diversity is conserved.
- Be sure to watch the video abstract!

Zeh DW, Zeh JA, Ishida Y. 2009. Transposable elements and an epigenetic basis for punctuated equilibria. Bioessays, 31, 715-726.

- This paper discusses how Transposable elements (TE’s) increase in different environments which can cause mutation may be very important for how organisms evolve.

- More specifically, it discusses the epi-transposon hypothesis which suggests that increased amounts of TE's may drive organisms off of their fitness peak in poor environmental conditions and mutate the genome to find a new fitness peak, all within a fitness landscape.

Recommended but not required:
Klironomos FD, Berg J, Collins S. 2013. How epigenetic mutations can affect genetic evolution: Model and mechanism. BioEssays 35, 571-578.

Questions: (Note we discussed 4 of the 8 questions)
Explain why the classic view of the co-adapted genome is an incomplete representation of eukaryotic genomes, using the human genome as an example.

Did not answer

What is the Lek Paradox and how might discoveries in epigenetics help resolve this paradox?

1) The Lek Paradox is the idea that females select males that are most well endowed and "best fit" which would eventually erode the genetic diversity of the population, so why do it?
2) Epigenetics suggest that environmental conditions can influence expression, in other words individuals in a good environment grow the best and genes are expressed differently based on environmental conditions. Because environment has such an effect on the gene expression the genetics among "well-endowed" males are actually conserved, just expressed differently. Thus the genetic variation is actually intact as time progresses.

The parasite hypothesis views transposable elements as genomic parasites that replicate within the host genome purely in their own interests, even at the cost of reducing host fitness. By contrast, the helpful transposon hypothesis argues that transposons enhance host evolvability by elevating the rate of large-scale alterations of the genome. Which hypothesis is correct? Explain your answer.
Did not answer

How might transgenerational epigenetic effects be important for organisms adapting to new environments or responding to changing biotic and abiotic conditions (including toxins in the environment)?

Did not answer

Discuss the evidence from comparative genomics that the domestication of retrotransposon genes and DNA transposon sequences has been critical in the origin and elaboration of the *mammalian placenta and the physiology of pregnancy. Explain how the transposon-driven origin of the placenta differs from conventional view of live birth as an adaptation to enhance maternal fitness.*

Did not answer.

What is the difference between intergenerational and transgenerational epigenetic effects? Can intergenerational epigenetic effects have evolutionary implications?

1) Intergenerational – Stressor has effect on the female, and offspring but stops there
2) Transgenerational – Goes beyond when the stressor happened, so that stressor is expressed in future (>F2 generations).
3) Intergenerational epigenetic effects can have an evolutionary effect by causing behavior or phenological responses in the offspring which can effects its breeding thus cascading to an evolutionary response to a stressor over time.

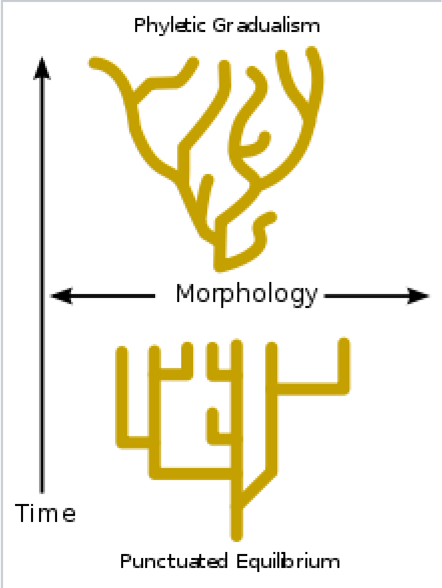
Ecologists and evolutionary biologists typically view epigenetic mechanisms as facilitators of adaptive phenotypic plasticity and accelerated evolutionary response. By contrast, biomedical researchers often focus on the negative fitness consequences of environmentally-induced epigenetic disruption. Can both views be correct? Which view is more accurate? Why did epigenetic mechanisms evolve and how might this insight address the question of whether epigenetic effects are adaptive or maladaptive?

1) Both views are correct, because they both have support, and could plausibly be true. There are negative effects of epigenetics if coming from a poor environment (i.e. slower growth, smaller, less complexity). But the same epigenetic effects may be beneficial to organisms adapting to a new environment. Perhaps, the environment is changing and by incorporating epigenetic effects into gene expression, it allows a wider variation of phenotypic variation to be displayed and handle a wider variety of environmental conditions.
2) Epigenetic mechanisms can be maladaptive because they are costly to do. If the epigenetic is responding to a positive environment then they are likely adaptive and beneficial, but poor environments are more maladaptive.

According to Zeh et al.'s (2009) epi-transposon hypothesis, physiological stress shifts the balance of power in favor of parasitic sequences in their struggle with the epigenetic defense mechanisms of the host genome. How is this significant for Sewall Wright's shifting balance theory, Stuart Kauffman's complexity catastrophe hypothesis, and punctuated equilibria?

1) SW’s shifting balance theory suggests that a population will divide and move to higher fitness peak, and has the potential to then outcompete the other populations. Similarly, the complexity catastrophe hypothesis suggests that the organisms may undergo multiple transformations searching for the highest peak in a fitness landscape. The epi-transposon hypothesis supports this by suggesting that in poor environmental conditions, there are more transposable elements (TE’s). The increase in TE’s drives novel gene formation, re-wiring of genetic networks and increased mutation rates. This allows for increased phenotypic and genotypic variations, and paves the way for populations to colonize new peaks and potentially outcompete the old phenotypes/genotypes.

2) The punctuated equilibria, suggests that instead of gradual changes over time to phenotypes and genotypes, that there are actually distinct and relatively rapid changes between evolutionary stable states in a taxa’s life history. The epi-transposon hypothesis would back this back this theory up, by supporting the idea that unstable environmental conditions or large disturbances can cause rapid mutation, and genetic re-wiring, leading them to mutate and find a higher fitness peak in that particular landscape.



Punctuated equilibrium, bottom, consists of morphological stability and rare bursts of evolutionary change via rapid cladogenesis, and is contrasted to the much more gradual, continuous phyletic gradualism, top

Group B Discussion Notes 11/14

Comparative Genomics and Gene Evolution

- *Can you find any parallels or areas of overlap between the study of genetic networks and the study of ecological networks (food webs)? Put another way, are there any questions that might be pursued in both areas using similar approaches and techniques?*

Our group was immediately reminded of Dr. Lee Dyer's presentation at the beginning of the semester regarding niche formation/interaction. Many of Dr. Alvarez-Ponce's figures depicting protein interaction networks (especially in hierarchy) were very similar to predator-prey interactions within the Piper model system.

There are many other parallels including social networks! The Pravosudov lab is beginning to look at chickadee social networks and their impact on the fitness of individuals within the population.

In other words, yes! There are many examples of ecological networks that could be examined using similar mathematical models or overarching concepts.

- *Evolutionary biologists have often conceptualized selection and drift acting on genes in isolation, i.e. abstracted from the genomic context in which they interact with other genes. How do you see our understanding of evolution being affected by a knowledge of the structure and function of genetic networks?*

It is logical to assume that genes involved in required cell/organism function and survival would be more highly conserved in the genome. Understanding the gene/protein interactions and gene/protein hierarchies could have major impacts in understanding patterns of inheritance.

An example given in the reading was that proteins that are farther up in biosynthetic pathways (plant anthocyanin production) were more highly conserved than proteins near the end of the pathway. This is a pattern of inheritance that is most likely impacted by the proteins place/function in the synthesis network.

Ecological and Evolutionary Epigenetics

- *What is the difference between intergenerational and transgenerational epigenetic effects? Can intergenerational epigenetic effects have evolutionary implications?*

Intergenerational epigenetic effects impact only a few generations before receding. The number of generations effected depends on the sex of the individual with the epigenetic marks. For example, parent generation females and first generation females retain somatic genetic markers while first generation females can also pass along markers to germline cells spreading the impact over three generations. In males, the parent generation shows epigenetic markers in somatic tissue as well as in sperm (2 generations).

Transgenerational effects refer to the inheritance of epigenetic markers after the stress-inducing environmental influence has receded. Transgenerational effects also differ from intergenerational effects because they can continue to be inherited for more than three generations.
According to the Epigenetic resolution to the Lek Paradox, intergenerational epigenetic effects do have evolutionary implications. Females select for high quality males based off phenotype(s). The Lek Paradox suggests that female choice will erode variation in male fitness. The epigenetic resolution suggest that epigenetic variation has the ability to renew this lost variation. Males that are of lesser quality may be more susceptible to stress and the accumulation of negative epigenetic markers. So males exhibiting lesser quality/higher degrees of epigenetic effects may be selected against leading to a potential increase in fitness for the female.

- *Ecologists and evolutionary biologists typically view epigenetic mechanisms as facilitators of adaptive phenotypic plasticity and accelerated evolutionary response. By contrast, biomedical researchers often focus on the negative fitness consequences of environmentally-induced epigenetic disruption. Can both views be correct? Which view is more accurate? Why did epigenetic mechanisms evolve and how might this insight address the question of whether epigenetic effects are adaptive or maladaptive?*

The views that epigenetic mechanisms can have both positive effects (i.e. phenotypic plasticity) and negative effects (i.e. disruption of cell regulation leading to disease) are both correct. I would say that neither view is more correct than the other. Epigenetic effects are simply a mechanistic explanation for environmental variation both positive and negative. The research perspective and questions being addressed would lead to the epigenetic effects being labeled as negative versus positive.
Epigenetic mechanisms evolved, in the case of transposable elements, as parasitic insertions into foreign DNA with a likely viral origin. Other mechanisms like histone modification arose through the need to consolidate the volume of the DNA strand for cellular storage. Transposable elements are selfish in nature and will copy and insert as much as allowed. These processes may lead to maladaptive losses in function for “host” organisms. Histone modification is highly beneficial to the function but if new environmental stresses cause a disruption in regulation this could lead to more maladaptive losses in function. In summary, all epigenetic mechanisms have the potential to be both maladaptive and/or adaptive. Some mechanisms having greater potential for one side versus the other.

- *According to Zeh et al.’s (2009) epi-transposon hypothesis, physiological stress shifts the balance of power in favor of parasitic sequences in their struggle with the epigenetic defense mechanisms of the host genome. How is this significant for Sewall Wright’s shifting balance theory, Stuart Kauffman’s complexity catastrophe hypothesis, and punctuated equilibria?*

Sewall Wright’s shifting balance theory: Evolution rates increase when a population divides into smaller subpopulations with restricted gene flow.

Stuart Kauffman's Complexity Catastrophe hypothesis: Small sudden environmental shifts can cause large changes in ecosystem structure (species composition etc.)
Here is the link to Lydia's resource: https://arxiv.org/ftp/arxiv/papers/0707/0707.0854.pdf
Punctuated Equilibria: Periods of rapid evolution after long periods of stability. The breakdown in epigenetic mechanism control methods leading to higher activity in transposable element action (genome disruption) is a possible mechanistic explanation for Punctuated Equilbria.
The three aforementioned ideas all focus on historical increases in the rate of evolution. The epi-transposon hypothesis is a potential answer to the mechanism behind these increases in evolutionary rate.

DISCUSSION 12: Conservation Biology & Ecosystem Management; Phylogenetics

Group A Discussion Notes 11/21

- Compare and contrast taxonomy with phylogeny. Considering the ambiguity in some phylogenetic relationships caused by lineage sorting of ancestral polymorphisms and hybridization, discuss ways you think evolutionary taxonomies could reflect discordant associations among taxa for different genomic loci. You should ignore homoplasy and other sources of error in phylogenetic inferences in your answer.

-taxonomy is to group for whatever reason you want - Sometimes we use to find similar species that our research can also apply to or to work in similar systems

Body form
Related habits
Related niche space

-phylogeny is supposed to be based on evolutionary history
Ambiguity in some phylogenetic ways to group species (ie birds and amphibians and reptiles)
-HGT, gene duplication, hybridization, recombination, natural selection and other phenomena are cited as potential causes of gene tree incongruence.
-Rapid evolution doesn't have enough time for allele differentiations to die out (eventually)
species radiation
- The whole genomes make up the organisms but we want to use loci or smaller sets of the genome to try to differentiate the organisms

- Discuss the advantages and disadvantages of model-based approaches to phylogenetics, such as Maximum Likelihood and Bayesian methods, with non-model-based approaches, such as Cladistics based on the Maximum Parsimony criterion. Under what conditions would you choose to assume or avoid assuming a detailed model of the evolutionary process in your phylogenetic analysis? Consider using a variety of data sources (e.g., DNA sequences, amino acid sequences, morphology, …) in your answer.

-Maximum likelihood - simple DNA sequences - not good when there are many processes happening
- model is needed and outcome is based on the basic model matching the mechanisms of evolution - wrong model will give wrong results
- The model can be better tuned by letting your data determine parameters
- estimation of uncertainty from model based design

- models can create many more trees to calculate the likelihoods of each one
- maximum likelihood has lower variance?

see the optional Science paper as reference for this

Conservation Biology

Preamble to study question: Ecologists employ scientific approaches (populations modeling, habitat conservation models, etc.) to conserve ecosystems and biodiversity. Yet there continues to be larger scale, global environmental degradation, due to local (e.g. habitat loss, invasive species introductions), regional, and global disturbances (e.g. climate change, atmospheric pollution). In the last decades, an emerged field of combining conservation science studies with partnerships with religious and faith organization has emerged to facilitate environmental conservation efforts. Some researchers and scholars in policy and social science suggest these partnerships are required to make significant and meaningful change that lends itself to conservation.

❙ Pick one of the dominant religions from eastern and western world, compare and contrast the environmental philosophies of these two religions and how they may contribute to conserving a natural resource. What are the limitations of using a faith based approach to developing natural resource conservation plans?

Within any religion it is as diverse as any other group, culture, geographic area; Not everyone has the same understanding, opinions, purpose, methods

Christianity -
Can be seen as more anthropocentric
Environment is often not one of the topics most focused on
It can feel mutually exclusive with science and this religion

Buddhism -
It appears to be more essential to be connected with nature
Caring for the environment is probably a more important part of living the religion

Our perceptions of differences between eastern and western religions, in general, could be due in part to a lack of familiarity with those that practice this religion. Possibly we know a lot more people that practice western than eastern religions (both the good and the bad).

Both religions can have real estate that maintain biodiversity or use working methods to maintain or promote biodiversity and research efforts. They may not all be in natural states but maintain some aspect or assemblage of native plant communities.

- reservations or sacred sites that are not for commercial or industrial use but for spirituality and connecting with deity and creations
- commercial properties such as ranches, farms, orchards that have some areas or aspects of preserving natural ecosystems

Limitations to working with religious groups
- Giving bigger role to a minority opinion of the community
- Large amounts of continual communication to bridge divide and maintain
- change in leadership - New leaders may place less importance for environment - Is there really long term sustainability?
- More effort involved to work with a different group

Group B Discussion Notes 11/21

ECOSYSTEM MANAGEMENT AND FAITH BASED CONSERVATION, Sudeep Chandra

❙ *Pick one of the dominant religions from eastern and western world, compare and contrast the environmental philosophies of these two religions and how they may contribute to conserving a natural resource. What are the limitations of using a faith based approach to developing natural resource conservation plans?*

- Christianity (varies wildly by denomination, from Genesis: humans have “dominion” over Earth and need to tend to the garden of Eden, disagreement on ownership vs. stewardship, many sects do advocate for conservation and taking measures to not over consume resources [i.e. seventh-day adventists and methodists])
- Buddhism (vegetarianism, karma and reincarnation place humans in the middle of a grand cycle in nature so there is less distinction between humanity and nature, humans are inherently part of the environment [came from it and shall return!], respect for all sentient beings is a core concept in buddhism)
- Related to both: Religious leaders have a lot of influence in their communities and can create profound change amongst their congregations (i.e. illegal ivory trade crackdown in Tanzania, try to reach out to Catholic priests in the area to spread message)
- Potential Contributions: From AAAS news article, “Conservation depends on science (tools, methods), but also on human values and engagement.” Reaching out to people on the basis of religion is a way to connect on the basis of values and engage in a more meaningful way, especially since most (84%) of the world identifies with a religion. Furthermore, these religious communities are often politically connected and highly organized “at local and regional levels, and some function nationally and internationally” (Schaefer 2017). They are often huge landholders in countries with limited space to

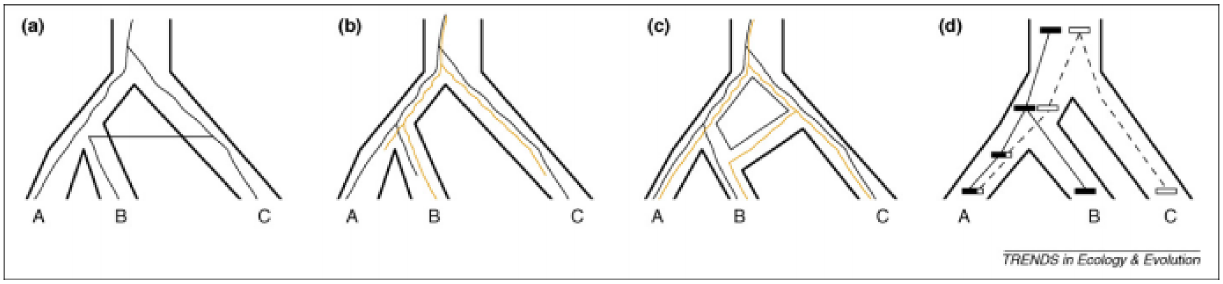
commit to preservation, which could open up opportunities for “maintaining biodiversity” (Bhagwat 2009).

- Potential Limitations: It can be difficult to navigate multiple faith communities for a single project and come to agreement on a morals/ value basis. Negotiation is key! This trust building process can be very time-consuming and is not guaranteed to succeed, particularly if there are other pressing issues (i.e. Sudeep’s example of working in Mexico). Additionally, there is an inherent ‘openness to interpretation’ of religious texts which can pose complications when trying to find a common ground.

PHYLOGENETICS, Guy Hoelzer

❚ *Compare and contrast taxonomy with phylogeny. Considering the ambiguity in some phylogenetic relationships caused by lineage sorting of ancestral polymorphisms and hybridization, discuss ways you think evolutionary taxonomies could reflect discordant associations among taxa for different genomic loci. You should ignore homoplasy and other sources of error in phylogenetic inferences in your answer.*

- Taxonomy is the simplest classification of organisms and is organized on the basis of shared characteristics. Phylogeny is a more nuanced form of classification that accounts for organisms’ shared evolutionary history and the relationships among groups of organisms.
- Incomplete lineage sorting causes gene trees to not match species tree (discordant association) as a result of a polymorphism in the shared ancestor. Other sources are in Figure 2 below taken from Degnan 2009.



TRENDS in Ecology & Evolution

Figure 2. Sources of gene tree–species tree discordance other than incomplete lineage sorting. **(a)** HGT: a lineage jumps from the population ancestral to A and B to the population ancestral to C, leading to the gene tree (A(BC)). **(b)** Gene duplication and loss: through extinction of lineages, gene duplication can produce apparent relationships incongruent with the species tree. Even if paralogs are not lost, the sampling of lineages that are not true orthologs can cause lineages from A and C to appear more closely related to each other than either is to B. **(c)** Hybridization causes some genes sampled from species B to descend from the population ancestral to A and B, whereas others descend from the population ancestral to B and C. The two gene trees depicted in (c) are ((AB)C) (black) and (A(BC)) (orange). Hybridization affects whole genomes, whereas HGT typically affects only small DNA segments. **(d)** Recombination can lead to different histories for neighboring segments within a gene. For the DNA segment depicted in black, the gene tree is ((AB)C), but for the segment in white, the gene tree is ((AC)B).

-

❚ *Discuss the advantages and disadvantages of model-based approaches to phylogenetics, such as Maximum Likelihood and Bayesian methods, with non-model-based approaches, such as Cladistics based on the Maximum Parsimony criterion. Under what conditions would you* *choose to assume or avoid assuming a detailed model of the evolutionary process in your phylogenetic analysis? Consider using a variety of data sources (e.g., DNA sequences, amino acid sequences, morphology, …) in your answer.*

- Non-model-based approaches, such as Cladistics based on Maximum Parsimony, don't result in any significance values (i.e. p-value) and are only based on "hypothetico-deductive models" built on Occam's razor principles (Felsenstein 1988). These approaches can work with relatively small data sets and require relatively few resources [time and money].
- Model-based approaches, like Max Likelihood and Bayesian methods, become more consistent as the size of the data set increases.
- The Felsenstein article provide more in-depth discussion of examples ~35 pages. Guy's powerpoint slides also break down the benefits and disadvantages of each.

DISCUSSION 13: Global Change and Conservation

Group A Discussion Notes 11/28

Readings

Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. Trends in Ecology & Evolution, 22(1), 42-47.

- Because predictions of species distributions under future climate scenarios are so variable among different methods, the authors argue that ensemble forecasting is an improved way to make more robust forecasts of species distributions in future novel environments

Kearney, M. (2006). Habitat, environment and niche: What are we modelling? Oikos, 115(1), 186-191.

- Argues for specific definitions of "niche" versus "habitat" versus "environment" and then operationalizes these definitions in the context of species distribution modeling
- "Niche models" take into account the mechanistic interactions between organisms and their environments, and their fitness consequences
- "Habitat models" describe associations between distributions and numbers of organisms across a landscape and the physical or biotic features of that landscape, without explicit mechanistic links between the landscape and the organism

Buckley, L. B., Urban, M. C., Angilletta, M. J., Crozier, L. G., Rissler, L. J., & Sears, M. W. (2010). Can mechanism inform species' distribution models? Ecology Letters, 13(8), 1041-1054.

- One of the few papers to explicitly compare performance of correlative versus mechanistic species distribution models
- Discusses some of the benefits and drawbacks to the different approaches, and points out flawed assumptions regarding each

Questions

1. Given the uncertainty involved in species distribution modeling how can we possibly use these models to inform conservation efforts now and into the future?

    - Better than nothing.

- Models should at a minimum describe known sources of error, and account for error as much as possible.
- Use an envelope encompassing the range of scenarios used for predicting, so that the model is more honest about how much range there actually is in its predictions.
- Good approach: using ensemble forecasting such as described in Araújo and New (2007). See especially Figure 1 on page 45.
- Be careful to use the model only for how it was intended to be used.
- Avoid the problems and uncertainties associated with species distribution modeling entirely. We know things are going to change. Instead of persisting with species-specific approaches (resulting in unbalanced protections, vertebrate-biased, etc.), an alternative is to conserve "land facets". See the following paper for a good explanation of this approach:
  Beier, P. and Brost, B. 2010. Use of land facets to plan for climate change: Conserving the arenas, not the actors. Conservation Biology 24:701-710.

2. Do mechanistic (vs. correlative) "niche" models provide better distribution models since they are based on real limiting interactions of a species and environmental limitations?

- Neither necessarily provides "better" models. See Buckly et al. (2010) who directly compared mechanistic and correlative models and found that each had advantages and limitations. In theory, mechanistic models should provide better predictive models for novel conditions; however, it is not possible to acquire perfect knowledge of a species' physiological interactions with the environment. Because we will never know enough to have a "true" mechanistic model, sources of error will inevitably be present, and thus a correlative model can actually perform better for certain species or certain environments.
- Mechanistic models are often developed based on physiological experiments performed under laboratory conditions. Such experiments can result in conclusions about species' responses to environmental conditions that are heavily biased or misleading for species in the wild.
- Developing an understanding of mechanistic responses to environmental conditions is effort-intensive, and the mechanisms themselves can and do vary across space and time.
- Incorporating more parameters into a model means that more sources of error are incorporated, especially when the parameters are themselves based on models for which there are multiple sources of error.

3. What does it mean for an ecological relationship to be "mechanistic" versus "correlative"? How would you justify (or test experimentally) that a putative "mechanistic" relationship of environment and performance (e.g., sprint speed as a function of ambient temperature) is not just a correlation?

- A mechanistic relationship is causal rather than correlative. It uses the *why* to predict the response of a dependent variable to an independent variable. A correlative relationship is descriptive, and only describes *how* one variable changes with another.

- For example, a mechanistic relationship would use the increase in metabolic rate as a function of temperature in an ectotherm such as a lizard to predict how that lizard's sprint speed would increase with temperature. In contrast, a correlative relationship would simply describe the positive relationship between sprint speed and temperature.
- An experimental design to determine the causal relationship between sprint speed and temperature would involve measuring metabolic rate under different temperatures, and would test sprint speed in different temperatures immediately (when metabolic rate would not have time to respond to the different temperature) or after a period of acclimation (once enough time had passed to ensure the metabolic rate had responded to the new temperature).

4. Each of the statistical relationships ~~for mechanical~~ for both mechanical and correlational variables that are used to define habitat or niche relationships imparts error into the modeling process. Should mechanistic model error be accounted for differently than that of correlational models? How would one best account for these sources of error?

- Error should be accounted for.
- An error in a mechanism could have a larger effect on the model predictions than an error in a parameter in a correlative model's predictions (Buckley et al. 2010).
- A mechanistic model for species distribution is a model based on other models - it models species distribution based on models describing mechanisms for physiological responses to environmental conditions. Thus, the error in each individual mechanism should be carried through when building the species distribution model.
- The type of modeling approach used (e.g., Bayesian versus GLM), will determine how errors can be accounted for.
- The model could be run on a range of values describing the parameter estimate to identify the possible magnitude of the effect of any single mechanism on resulting model predictions. Effects that are very large could be used to justify additional research into that mechanism to ensure our understanding of that mechanism is sound before building predictions.
- A possible approach to a lack of sufficient information to build a purely mechanistic model could be to incorporate specific mechanisms into a correlative model. For example, Inman et al. (2016) first built a correlative model using MaxEnt to describe the habitat suitability for the Mohave ground squirrel in southern California. They then "augmented" that with a model of juvenile dispersal. This was then used to compare species distribution under various climate and land use scenarios and how the species distribution could change over time. While the dispersal distances they used came from an observational study and was not a mechanistic description of dispersal, this study illustrates the possibility of how a particular mechanism (of forage availability and fitness, or anything else that could be limiting) could be incorporated into a correlative species distribution model to better understand possible range shifts under various future scenarios.

Inman RD, Esque TC, Nussear KE, Leitner P, Matocq MD, Weisberg PJ, Dilts TE. 2016. Impacts of climate change and renewable energy development on

habitat of an endemic squirrel, *Xerospermophilus mohavensis*, in the Mojave Desert, USA. Biological Conservation 100:112-121.

Group B Discussion Notes 11/28

❙ Given the uncertainty involved in species distribution modeling how can we possibly use these models to inform conservation efforts now and into the future?

For this question, the Araujo paper would be the best paper to reference.

- No one model can truly be accurate on the circumstances of a system. All models are essentially flawed but provided useful information nevertheless.
- Ensemble models are simulations of a system, each representing a possible state that the real system may be in at a specified point in time.
- A forecast ensemble is where the multiple simulations consider more than one set of initial conditions, model classes, parameters, and boundary conditions.
- Using multiple ensemble models creates more robust forecasting and can reduce mean error.
- Ensemble forecasting shouldn't be viewed as an alternative to good old fashion model building with better/more accurate data. Also these forecasts are dependent on individual predictions -> if you don't have the right predictions, your forecasts could lead you into the wrong direction.
- In addition, it really depends on your system and what you're trying to accomplish to know how and which forecast to use correctly. "…whether the benefits of using a set of combined forecasts in decision-making outweigh, on average, the costs. In reserve selection, it has been shown that acting upon ignorance and opportunism can be more expensive than acting with the support of data and models, " (p46).

❙ Do mechanistic (vs. correlative) "niche" models provide better distribution models since they are based on real limiting interactions of a species and environmental limitations?
(Buckley et al, 2010)

Mechanistic	Correlative
Function: Derive hypothetical biological processes using phenotypes of organisms. These models require very accurate understanding of fitness relationships in terms of environment and phenotype.	Function: Modeling involves incorporating biological processes by approximating environment-range interactions from occurrences.

Advantages: Better predicts range dynamics than correlative model -> to predict a geographic range, these models rely on our understanding of what processes cause survival and reproduction Mechanistic has layers of information (while correlative may have more information than you need).	Advantages: These models usually require only data on the localities and associated environmental conditions of a specimen. Can predict range dynamics if range constraints are omitted by the model, if they remain constant, and the independent variables correspond to the processes that constrain the range.
Caveats: Since these models require understanding of a species fitness relationship with environment and phenotype, any errors in parameters can add up and lead to poor accuracy in prediction. Good, up-to-date data (and need a lot of it) to have good mechanistic model May fail to predict species' current range: mechanistic focuses on a "limited set of abiotic constraints (primarily thermal constraints), the interaction between different abiotic constraints and those between abiotic and biotic constraints could cause observed ranges to deviate from predicted ranges" p1048 -> over predicts for Buckley's models	Caveats: Correlative models might not reflect the mechanisms underlying a species distribution (correlative uses a lot presence only data). The major assumption of correlative is that processes setting range limits are fixed in time and space – so these would be violated when making dynamic predictions, such as range shifts during climate change. It makes predictions based on the species occupying a grid rather than using rate of population growth. Also changes in the environment or the range itself is not at equilibrium.

▌ What does it mean for an ecological relationship to be "mechanistic" versus "correlative"? How would you justify (or test experimentally) that a putative "mechanistic" relationship of environment and performance (e.g., sprint speed as a function of ambient temperature) is not just a correlation?

- Mechanistic relationship looks at the organism (its phenotypes) and its relationship to the environment, while correlative looks at locality and environmental conditions to infer any biological processes of an organism.
- How to justify –> "what's in the black box?" Test assumptions to see if the relationship is real

  - Paint tortoises and test their performance experiment –> explore the relationship between temperature and activity of the tortoise
    - See if performance varies if you change the environmental conditions

❙ Each of the statistical relationships for both mechanical and correlational variables that are used to define habitat or niche relationships imparts error into the modeling process. Should mechanistic model error be accounted for differently than that of correlational models? How would one best account for these sources of error?

For mechanistic modeling, if you don't include enough mechanisms, particularly since there is a lot of overlapping, you could get a lot of error.

  - To best account for sources of error: don't use the model if you don't know your parameters or your species very well -> know if there is information missing -> find more data, and tests your mechanisms. Try to include biotic interactions because these interactions can constrain a species' range.

For correlative modeling, if you have inappropriate thresholds or climate characterization, you can have a lot of error.

- To best account for sources of error: Actually check your presence data on the ground and expand your map to see if your species is abundant in other areas than just the area you're interested in (where species currently occur vs an inaccurate survey done 20 years ago).

To best account for sources of error for both models: Know what parameters to include in your model, test sensitivity of the models and how they handle parameter uncertainty– play around with adding or excluding independent variables to see what noise does to the structure of your modeling. OR merge the two models to improve model performance.