**Summer 2005: Exam 2** **Name _______KEY______________________**

**Part I: Definitions.** *[5 points for each term]* For each term, provide a brief definition *that also indicates why the term is important in ecology or evolutionary biology*. Where I've provided two terms, choose one to define. *Circle the one that you're defining.* Where appropriate, feel free to provide an example or draw a diagram to accompany your written answer.

1. Coevolutionary arms race **or** host switching

   **Coevolutionary arms race**: a term used to describe a form of antagonistic or negative coevolution where two species are coevolving and one benefits from the relationship and the other is affected negatively. It is referred to as an arms race because the species that has a negative effect creates selective pressure for resistance in the other species. Once resistance evolves in the second species, this, in turn places selective pressure on the first species to evolve a means of overcoming the resistance, which in turn places selective pressure for a new form of resistance in the second species, etc.

   **Host switching**: a situation where a parasite, disease or herbivore begins using a new host that is not a direct descendant of its original host. In other words, the organism does not cospeciate with its host. Important as an example of a host/parasite-disease-herbivore relationship that is not coevolved.

2. Equilibrium community theory **or** climax community

   **Equilibrium community theory**: an early form of community theory in ecology that postulated that communities were tightly coevolved sets of species that when through a regular and predictable succession process, culminating in a climax community that would be stable for an indefinite period of time

   **Climax community**: in equilibrium community theory, the final stage in succession, differing from the earlier stages of succession because the habitat produced by the climax community would sustain the climax community rather than facilitating a new stage in succession

3. Competition

   For either intraspecific or interspecific competition, competition occurs when members of the same species or two different species, respectively, attempt to use or defend the same resource(s) such that use or defense limits the resource's availability. Important because competition has been demonstrated to often be an important force that structures ecological communities

4. Facilitation model **or** Tolerance model

   **Facilitation model**: a model of ecological succession where the community moves from one stage of succession to another (or individual species in the community are replaced by others) because the earlier stage (or species) creates new conditions that provide a habitat better suited for the next stage (or new species) than for the original stage (or species)

   **Tolerance model**: a model of ecological succession where all of the species that will be in the community at later stages are present at the outset. Community composition changes over time because different species have different life history strategies (r-selected and K-selected) , e.g., annuals dominate initially because they are r-selected to grow rapidly, reproduce quickly and copiously, whereas woody species dominate later because they eventually shade out the annuals by growing slowly over a number of years until they dominate the space.

5. Fahrenholz's rule **or** coadaptation

   **Fahrenholz's rule**: this rule states that parasites and hosts that live in close association with one another will usually cospeciate approximately simultaneously with one another. This is one

of the essential expectations for coevolving species.
**Coadaptation**: one of the critical features of coevolution, it states that each of the species in a coevolved pair will has adapted by natural selection to the other. The critical feature of this idea is that the species have reciprocally acted as a selective agents on each other

6. Zero isocline **or** carrying capacity
**Zero isocline**: the line on a phase-space or state-space graph of Lotka-Volterra interspecific competition that represents the combinations of population sizes for which one of the species will have zero population growth, i.e., when $dN_1/dt = 0$. Important because it is used to help interpret what the outcome of competition between two species will be
**Carrying capacity**: the maximum number of individuals of a species that a given environment (having a particular set of resources) can sustain indefinitely. An important concept in ecology, used in several theoretical constructs, particularly competition

7. Top-down regulation **or** genetic drift
**Top-down regulation**: a form of community regulation where the presence of species in a higher trophic level control the composition of species at a lower level, e.g., the top predators in a community might control the composition of herbivores, which in turn might control the species of plants.
**Genetic drift**: the change of gene frequencies in a population from one generation to the next due to chance events. Drift is only a strong source of evolutionary change in small populations, but is an important example of neutral evolution.

**Part II: Short answer.** Make your answers economical and to the point. Draw a labeled diagram if that will help you to make your point.

8. Under what circumstances might we expect a parasite-host relationship to evolve to one where the parasite has lower virulence? Why? *[7 points]*
A parasites is expected to evolve lower virulence when it is subject to kin selection. Otherwise, we would expect selection to favor the most virulent type over the short term since it will reproduce most rapidly. Kin selection is favored when individual hosts are only infected with a single parasite genotype at a time. (This allows the less virulent types to persist longer while the more virulent types kill their hosts, and subsequently, themselves). Kin selection is also favored when the mode of transmission is vertical (parent-to-offspring) rather than horizontal (one individual to any other individual) because the parent needs to survive long enough to reproduce or the parasite will die along with its host.

9. You're studying a plant community in the Davis Mountains of west Texas. Using a historical series of aerial photographs you note that the cover of woody bushes is steadily increasing. What evidence might you use to test whether a change in the abiotic environment is responsible for the change? (I'm not talking about a controlled experiment in this case.) *[5 points]*
Since you can't perform a controlled experiment, you're going to need to look for correlations between the increase in woody plant species and various aspects of the abiotic environment, e.g., rainfall, temperature, pollutants. To strengthen any conclusions you might make from these correlations, you should also check to see if other biotic factors are similarly correlated with the increase in the woody species. If you cannot find any biotic factors, but can find one or more abiotic factors that correlate with the increase in woody species, you can have greater confidence that the abiotic factor(s) are driving the change.

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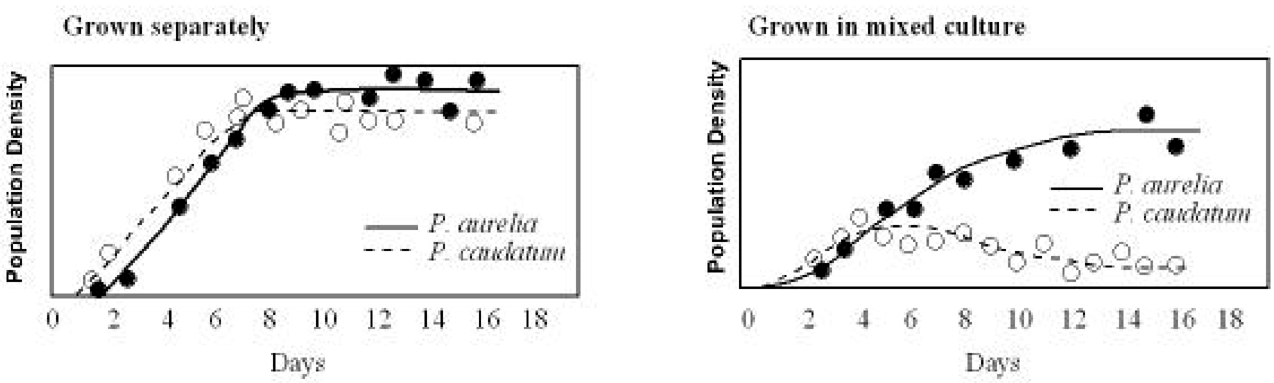
10. Explain why the addition of the term $\left(\frac{K-N}{K}\right)$ to the unrestrained growth equation $\frac{dN}{dt} = rN$ puts a limit on population growth? What process does this equation model? *[7 points]*

Without the $\left(\frac{K-N}{K}\right)$ term the equation describes unrestrained exponential population growth. The new term adds the concept of carrying capacity (K). As the population size (N) increases the numerator in the fraction approaches 0, which means that the equation for population growth rate approaches 0. When N is small relative to K the equation behaves more or less like the unconstrained equation. This equation models intraspecific competition because as a species population grows and resources become scarce, it's growth is slowed by competition for those resources.

11. How did Egler's initial floristics hypothesis begin to challenge the equilibrium succession theory? *[6 points]*
In the 1950s Egler developed his initial floristics hypothesis for old field succession because he found that even at the earliest stages of old field succession all of the species were present that would be found at later stages of succession. This contradicted the equilibrium community theory, which hypothesized that the earlier species facilitated later inclusion of species from later stages by changing the environment to favor the later species at the expense of the earlier species. If all of the species were present in a community at the outset, the equilibrium theory could not be correct. (Nonetheless, it took another couple of decades before the equilibrium theory was overturned.)

12. Look at the graphs below for two species of *Paramecium*. With no other information than this, what process would you say is operating when the two species live in the same environment? Why? *[5 points]*




When grown separately each species follows a standard logistic growth curve by growing until it reaches its carrying capacity, probably due to intraspecific competition. When grown together, *P. aurelia* has a nearly normal growth curve, but it does not reach the same population density as when it grows alone and it takes longer to reach equilibrium. *Paramecium caudatum*'s population growth is highly altered and either appears to be going to extinction or a much lower equilibrium level when compared with its other growth curve. This is probably most easily accounted for by interspecific competition between the two species where *P. aurelia* is the better competitor under the conditions in the experiment.

13. Given the graph below, what evidence do you see for and against lynx being a controlling influence of snowshoe hares? *[7 points]*

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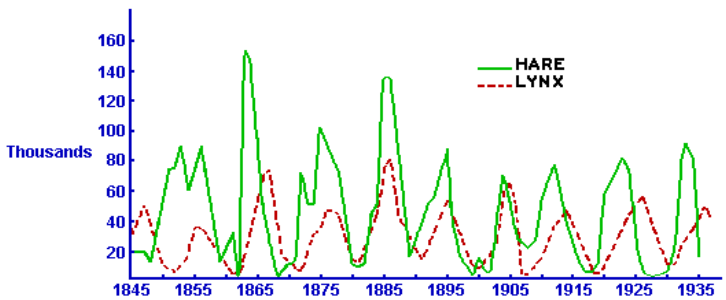
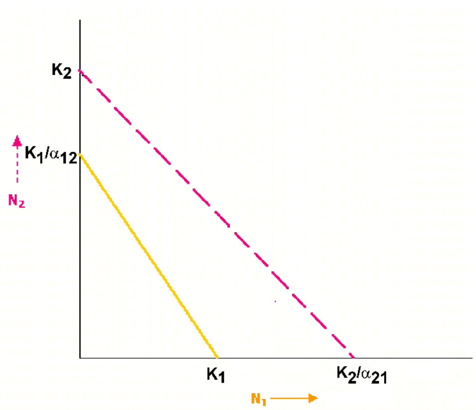



**Evidence for lynx being the controlling influence**: the population cycles of the lynx and the hares appear to be approximately in synchrony, which would be expected if the lynx were limiting the population size of the hares. In addition, in at least some of the cycles, there is a slight lag in the response of the lynx population to the hare population, which would be expected under a standard predator-prey model.

**Evidence against**: In some cases the cycles of the lynx and the hares move in synchrony without the expected time lag, e.g., the cycle that peaks around 1905. There are also times when the hare populations rise and fall without changes in the lynx populations, e.g., the hare population from about 1870 to 1880. Finally the height of the hare and lynx population peaks do not maintain a consistent relationship between one another, e.g., the hare peaks in 1905 and 1915 are about the same height, bu the lynx peaks for the same times are different heights.

14. Below is a phase-space graph for two species that are competing with one another. What will be the outcome of this competition? Why? (The dotted line is for species 2.) *[7 points]*




The outcome of this competition will always be that species 2 competitively excludes species 1. The reason for this is that the zero isocline for species 2 is always at a higher population level for that species for any combination of population sizes of the two species than it is for species 1. In other words, whenever species 1's population size is large enough to be at or above its zero population growth rate, species 2 will still be at a population size where its population growth rate is still positive. Hence when species 1 can no longer compete effectively for limiting resources in the environment, species 2 will still be able to get enough of those resources for its population to continue growing at the expense of the population size of species 1.

**Part III: Essay.**

Answer *one* of the two choices (A or B) for each of the two essay questions that follow. *[15 points each]*

15. **A**. Some species of ants are known to tend aphids on plants. You think this might be a coevolutionary mutualism. What will you need to do to produce the best evidence for your hypothesis?
**B**. You're studying succession in an old field. Present two different experiments you might perform to determine whether the disequilibrium theory or the equilibrium theory is a better explanation for what is happening in that community.
**A**. Coevolution is usually considered to have two components: coadaptation and cospeciation. In the case of coadaptation, because you suspect the relationship to be mutualistic, you will need to determine whether the ants and the aphids positively affect each other's fitness. You can accomplish this by setting up experiments where you exclude ants from some plants where aphids are while leaving the ants on other plants where there are aphids. If the aphids have lower mortality and/or higher rates of reproduction in the presence of the ants then the

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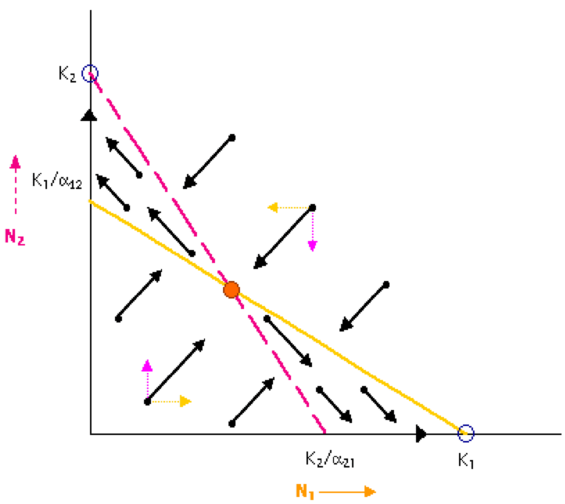
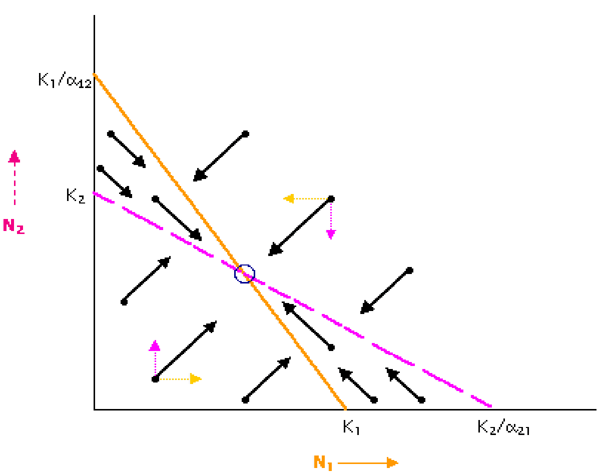
relationship is positive. Similarly, you could remove aphids from the plants in an area while leaving them in another and see what sort of effect this has on the ants fitness. You'll also need to demonstrate cospeciation between the ants and the aphids because, if there hasn't been a long term association between the species, the mutualistic relationship between the ants and the aphids might just be the result of each being preadapted to one another and not true coadaptation. To test for cospeciation, you can produce phylogenies for each of the species groups and see if there is topological congruence between the phylogenies of the ant and the aphid species that are associated with one another.

**B**. You all avoided this question like the plague. Not a single one of you chose to answer it. I'm curious what it was about it that made it seem harder than the first question.

16. **A.** Look back at question 14. Draw and explain the other two types of interspecific competition graphs. Be sure to explain what the outcomes of competition are for those graphs and why.
**B.** Remember the example of what happened to the various trophic levels in Lake St. George after a large winter fish kill. Which aspects of the recovery supported top-down control of the populations and which aspects supported bottom-up control? Why? You can use the graph to help explain your points.




**A.** The top graph shows a situation where interspecific competition can lead to one of three equilibria. There is an unstable equilibrium at the orange dot where the two isoclines cross and two stable equilibria at the points where the isoclines for each species are at the carrying capacity for the species, i.e., $K_1$ and $K_2$. Which of the three equilibria the species will end up at depends on what their initial population sizes are. A very small number of initial population sizes will end up at the unstable equilibrium point. Once at the unstable equilibrium, any change in their population sizes will cause them to go to one of the two stable equilibria, leading to competitive exclusion. Whether species 1 competitively excludes species 2 or vice versa depends on which area of the graph their population sizes are in. If their population sizes end up in the area of the graph where the isocline of species 1 is above the isocline of species two, species 1 will exclude species 2. If their population sizes end up in the area of the graph where the isocline of species 2 is above the isocline of species 1, species 2 will exclude species 1. In the first competitive exclusion case, species one is a better interspecific competitor than species 2, and interspecific competition predominates over intraspecific competition. In the second competitive exclusion case, species two is a better interspecific competitor than species 1, and interspecific competition predominates over intraspecific competition.




The second graph shows a situation where interspecific competition leads to just one stable equilibrium at the point where the isoclines for the two species cross. Here interspecific competition is much weaker than intraspecific competition, so each species ends up primarily competing with members of its own species, rather than with members of the other species, leading to a stable coexistence. It doesn't matter where the two species' population sizes begin on the graph. They will always end up at the stable equilibrium point.

**B**. The evidence in the graphs make it appear that the first level of fish carnivores and the zooplankton are subject to top-down control, whereas the phytoplankton are more likely to be subject to bottom-up control. In the case of the first level of fish carnivores, we can see that they are initially killed off along with the top fish carnivores during the winter fish kill. Then as the top fish carnivores remain at a low level the lower level fish carnivores' populations increase, followed by a decrease as the top fish carnivores begin to recover. The zooplankton respond to the initial fish die-off by significantly increasing their population sizes and then their population sizes inversely mirror the population sizes of the first level fish carnivores. In the case of the phytoplankton, at the time that the zooplankton have their initial spike of population growth following the fish kill, the phytoplankton also have a spike of population growth, precisely the opposite of what would be expected if there were top-down control of the phytoplankton by the zooplankton. In fact there is no evidence in the graph that the phytoplankton's population sizes are inversely mirroring the population sizes of the zooplankton, suggesting the possibility of bottom-up control for this trophic level.