Lecture 10 transcript

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Today we're going to talk about food webs and trophic structures.

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Learning Outcomes for this session are that we are going to be looking at theoretical work on food webs.

We will consider the feeding relations in and functions of soil food web. And we will consider the theoretical and empirical advances in food web ecology and we will be using soil food webs as a model.

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So a food web describes the relationships of feeding among all the organisms in the part of the community that you are interested in or an entire community. We can draw food webs as a diagram which links consumers and food and we use the arrows to show where the food has come from, like in this diagram below.

The links between these trophic levels are usually based on Lotka Volterra models of competition and predators and prey.

So food webs will be combining the theory of a lot of the lectures that we have been through so far.

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So one of the key points with food webs, is that energy decreases as you move up trophic levels. And so what we have here is at the bottom trophic level we have plants or plankton in the sea. The plant material will be making its own energy. So this is the first step of the trophic level.

At the next level, we have the plant consumers. They will be eating the plants. Then at the level above that we have the first level of predators. So they will be eating the prey, or plant consumers. And finally, we might have a top predator.

One of the other key things to notice is that there are fewer individuals as you move up each trophy level. So it's a pyramid. This is because energy is lost at each trophic level (each transfer). And it is thought that the energy efficiency rate is about 10% maybe even less. So the herbivore (plant consumers) will get 10% of the total energy of the plants and then the predators will get 10% of the total energy of the herbivores. Therefore you have less individuals at each level because there is not enough energy to sustain them.

Now some species may capture energy at more than one trophic level. So, for example, a bear is an omnivore, it eats both plants and animals. So, it feeds at more than one trophic level.

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So food web ecology has been very important for looking at the effects that humans have on ecosystems.

One of the most famous examples is the accumulation of DDT in the eggs of birds of prey. Now, this happens through bioaccumulation. Bioaccumulation is when toxins build up in a food web. So plants might take up the toxin through their roots and it would become part of the leaf tissue. And then a herbivore would come and eat the leaf tissue and then the herbivore will be eaten by a predator. So the toxins will build up in the food web. The toxin cannot usually be excreted. When eaten it remains in the food web, and because it accumulates in the fatty tissues of an animal body, the toxin will be most concentrated at the top level of the food chain. The top predator will have the highest level of bioaccumulation, and we can see this in many examples. This was found a number of years ago that in birds of prey, the DDT had accumulated, to the extent that it was found in the shells of the eggs and the shell was so fragile that the eggs could not produce live young because they just broke.

Food web ecology is also important because when we see removal of top predators from ecosystems, you see results and changes through the other levels of the trophic web and we have seen this a little bit with the lynx and the snowshoe hare.

And another example is if you remove prey or plant biomass, you get a resulting shift in food web dynamics.

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As well as applied ecological questions food web. Ecology is also used to answer some fundamental of theoretical because ecological questions. For example, we can calculate the flow of energy and matter through ecosystems.

We can use it to explore the green world hypothesis.

And we can model the behaviour and dynamics of very complex communities and this is useful to look for potential effects of changes or to predict what would happen if you remove certain organisms.

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The green world hypothesis states that the balance of predators and herbivores allows plants to grow.

This means the predators reduce herbivore numbers and this allows plants to live. As well as predators, we have parasites and diseases to reduce herbivore numbers. However, this section of the hypothesis is possibly unlikely because plant biomass is only eaten 7- 18% by herbivores. So grazing of plant material is actually quite a minor effect. But some herbivores do eat the entire plant.

Could a herbivore evolve that does eat all the plants?

Well Krebs, whose work we looked at in the last lecture on the predator lecture, he came up with six reasons why the world is green and not brown.

The first are the plants and not passive agents, they are not just sitting waiting to be eaten. They have defenses and they can grow in all sorts of ways that reduce the possibility of being eaten.

The second is that nutrients limit herbivores not energy. So therefore, the nutrient level in the plants might reduce herbivore numbers because they're not getting sufficient nutrition, even if there is a lot of plant biomass.

Third, is that herbivores are limited by abiotic factors. So they limited by temperature, moisture, salinity and so on, as well as predators.

The fourth reason is that spatial variation reduces the availability of plants so different types of landscape might mean the different plants are not found in areas where herbivores would want to feed.

The fifth reason is that herbivores limit their own numbers. So if they are overcrowded, if there are too many in an area then herbivores will reduce their birth rate.

And finally enemies might limit herbivore numbers and this could be through competition, parasitism predation or disease.

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More complexity in an ecosystem is assumed to be more stable. But Lord May in 1972 hypothesized that actually this is not true. He started the diversity stability debate. The diversity stability debate suggests that as you have more diversity in an ecosystem, it should be more stable to change or to disturbance than communities made up of a very few species.

So we might assume that functional redundancy means increased stability because if one species is lost, there will be another to fulfil its role.

But Robert May showed mathematically that complexity means instability. There are three reasons what to support May’s paradox.

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The first is that trophic coherence increases stability. And I recommend having a look at this website on the bottom, which is a blog post discussing this paper by Johnson, written by Johnson. So it's just a simple summary of his thoughts on this.

Tropic coherence is a measure of how neatly species fall into each level. On the left we have high trophic coherence. Each species only feeds on the level below.

On the right, there is less trophic coherence. There is no clearly defined structure.

In reality, food webs fall somewhere between this one and this one.

We would call the left one perfectly stratified, and the right one. Not coherent.

And Johnson found that trophic coherence is linked with stability. And when they carried out a statistical test, they found that more than 80% of the variance was explained by trophic coherence.

So Johnson said the trophic coherence is a better predictor of stability than the size or the complexity of the food web.

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The second reason to have support for Mays paradox is compartmentalization. This is where groups of species interact more frequently among themselves than other species in the community.

Compartmentalization increases the persistence of multi-trophic food webs. As the food web becomes more complex, the effect of compartmentalization will increase. So persistence is more likely. So you see here that each of these circles is one compartment. And the species in each compartment will mainly interact with each other. And there's only a few links with other compartments.

So this figure Stouffer and Bascompte look at what would happen if you have a single extinction in one of the compartments.

They hypothesized that a positive effect of compartmentalization would mean that the effect of the extinction, would mainly be in this compartment.

If there is no effect of compartmentalization working on this ecosystem then you will see the effects of the one to extinction throughout the community, regardless of the compartment.

Stouffer and Bascompte concluded that compartmentalization is an advantage because it reduces the effect of the extinctions. Measuring direct interactions is very difficult. So compartmentalization is useful for giving insight into community dynamics.

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The third reason for May's Paradox. Is where Wall and Nielsen hypothesized that food webs with many weak links are more stable than food webs, with strong links. This is because disturbance is less likely to lose a lot of species. And when we say strong links, meaning that each species is very dependent on only one or a small number of hosts.

So in this figure we see that A is dependent on two hosts. And B is dependent on two hosts and in turn those hosts are only dependent on two plants. Whereas if you have weak links. This means that A and B, and also the herbivores are generalists. And they will eat a wide variety of foods. Therefore, as we see after a disturbance event, if we lose the predator species A in the strong links you get a fairly big change in the different dynamics of the herbivore, and the plant.

Whereas over here, not much has changed, but you do see a very large shift in the community composition. So there are more herbivores and fewer plants and that will have cascading effects on all of these other species. If you have weak links, then not much changes really these herbivores might increase in number of very little bit. But there was very little effect on the plant community very little effect on the species because B will just take over the predation of this herbivore. So everything is kept approximately the same.

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A keystone species is a very important species in an ecosystem. The word Keystone is taken from the stone in an arch. That if it was removed the whole arch would fall. So a keystone species, traditionally in ecology was deemed to be a predator. So if you remove a predator, then everything changes.

More recently ecologists have realized that a lot of species at different trophic levels could be the Keystone. The function of the keystone species is to maintain structure and integrity of the community. And that means keeping all of the individual numbers approximately stable. So if the Keystone is predator, it will prevent competitive exclusion by dominant species. If you remove the keystone species very rapid change will occur in the community.

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The term was invented by Robert Paine in 1966- he worked on rocky intertidal shores and he was looking at this food web that I've put here. His definition was the keystone species exerts top down influence on lower trophic levels and prevent species at lower trophic levels from monopolizing critical resources such as competition for space or key producer food sources.

So he was interested in what happened if you remove the starfish *Pisaster*. He had observed during his work that diversity reduces as the number of predators is reduced. His hypothesis was that some consumers have a bigger role than others in controlling species coexistence.

He removed *Pisaster*. And he had two sections of the coast, one where he took away *Pisaster*. And one where he left it present. Remember, you need a control and the treatment.

So he compared the control to the area with *Pisaster* over time. And what he saw was that when you remove the *Pisaster* competition between other predators increases. And there is an increase in competition between the herbivore first level consumers. This is because they're not being predated to such an extent. And he came back after a few months, and he found that only mussels and barnacles were left. The species richness had fallen very, very significantly. So the mussels and the barnacles have driven out everything because competition increased. It actually went from 15 species in the food web to eight.

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Now we will look in depth at the soil food web. The soil food web is remarkably complex. There are millions and millions of species in the soil. And ecologists are only just starting to recognize how complicated and diverse the soil food web can be.

Trophic structure is divided into primary producers, which are plants, plankton, cyanobacteria, and so on. Those that harvest sunlight and make into sugars.

Then we have primary consumers, which are those that feed on plant material. And then we have secondary and tertiary consumers, which are predators. And you can have predators that feed on predators in the soil.

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The primary consumers tend to be microorganisms. So bacteria, fungi, algae and actinomycetes. And these are primarily responsible for breaking down organic matter, which is called decomposition, and recycling nutrients. So some form symbiotic relationships. They were also a few that are auto trophic they harvest sunlight.

In 10 grams of soil you get enormous numbers of bacterial species, and enormous amounts of fungal hyphae which we remember from the mycorrhiza lecture.

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In the soil we have secondary and tertiary consumers we have protists, we have nematode worms. We have Collembolans and we have mites. Science is just starting to attempt to characterize the types and goals of these groups in the soil. Nematodes are enormously complex groups and they fulfil roles such as predation, plant disease, and they attack each other. They eat bacteria, they eat fungi, they are enormously diverse. Collembolans tend to focus on eating dead plant material and dead animals, here they are called detritivores, so detritus is any dead material- dead plants and animals.

Mites as well have an enormous range of roles in the soil. So it really depends on which group you are interested in looking at.

So we're starting to use morphological efforts and DNA sequencing to really try and characterize what is happening in soils across the world and it is an enormous job. And protists actually quite late to this.

Protists are small Eukaryotes that will again have an enormous number of roles in the soil. So in order to try and simplify this complexity, we can look at soil food webs as those based on bacteria or fungus.

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The bacterial decomposition channel tends to mean that if you have a high fungal to bacterial ratio you have more fungi, you have a fungal decomposition channel. If it is low, so more bacteria, you have a bacterial decomposition channel.

And with bacteria if you have a bacterial based soil food web, this will tend to occur in more nutrient rich undisturbed habitats. So if you are adding fertilizer or regularly ploughing up the soil, we will tend to get more bacterial based food webs.

So they occur greatly in agricultural intensification. Everything is very fast growing fast moving and carbon and nitrogen cycling occurs very rapidly. Now with this speed of processing carbon and nitrogen, it is thought that more carbon and nitrogen is lost through leaching or through evaporation and so on. So it's quite a wasteful decomposition channel.

A fungal based food web occurs in more late stage undisturbed systems. Systems that have been established a long time and have very little interference. Now these are very easily destroyed in things like agricultural intensification or disturbance occurs in the fungal food web.

All the organisms that feed on the fungus and the fungus itself are all very slow growing. They don't lose much carbon and nitrogen. Everything is retained in the system. So the cycling is very efficient, but it's quite slow.

And the plant species that are grown in these food web can influence which food web that you get. So you get very fast growing inefficient plant species like agricultural crops and so on. And they might result in a bacterial decomposition channel. Whereas if you have slow growing trees, very slow growing species, then you might get a fungal decomposition channel.

We could say that bacterial decomposition food webs consist of r-selected organisms. While fungi and all of the organisms that feed on the fungi are based on a K-selected classification.

Now this is quite a simple idea and it has been challenged by ecologists as being too simplistic.

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This is the first example of the soil food web, and it combines primary producers and detritivores, so organisms that feed on dead material. And we can draw a very simple schematic like this.

But this was quite groundbreaking in 1987 because the interconnectedness so the fact that everything is linked together. That was quite a new concept at the time.

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And it was based on of ideas such as the microbial loop. And you can see that Marianne Clarholm in 1985 so before the soil food web. She was thinking about ways that the microbial and producer soil food web interact with plants to cycle nutrients.

Now the microbiome concept began in marine ecosystems, and in soil. It has been shown to be quite complex. Bacteria take carbon sugars from roots. This allows them to then break down the organic matter in the soil. Now organic matter is partially decomposed plant material or dead organisms and so on. And it creates what we know to be the organic part of the soil.

The bacteria want to take nitrogen from this organic matter. And they take the sugars from the roots as an energy source in order to help them do that. So the bacteria will change the nitrogen to a plant available form so ammonium. But it is locked up inside the bacteria and only a small part of this is released. And then the plant takes it back up again. Protozoa feed on bacteria, and when they feed on the bacteria they release the nitrogen. So then, much more is available to the plants. Clarholm conducted experiments which showed the nitrogen uptake, with and without protozoa in this system, and if you do have protozoa, the uptake of nitrogen by the plant increases by 75% so this loop is extremely important in nutrient cycling.

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The rhizosphere is the area around a plant root. Now Moore produced this figure in Ecology and they thought that productivity, which is the amount of biomass produced is the main thing that dictates how complex the food web is and also how many levels, it can support.

So we see here productivity is increasing as you go along here and trophic level increases so plant consumer, predator, predator, predator as we go up. So as we go up in productivity, we go up in trophic level that is the assumption. And the reason for this is as you move up the productivity gradient biomass would increase until there is enough energy to support a second trophic level. So if there are very few plants in an area, it will not support a herbivore. These dashed lines are thresholds in trophic structures so F2 is the threshold for being able to support a herbivore at this level of productivity. And then at F3, this is when you have enough energy to support a third level. So we might get a predator in the system as well.

If we don't get a predator, we get C2, and this means that there is too much consumption.

And the width of each of these equates to approximately the population size or each new group of each new trophic level. So you can see that you have more herbivores and then lots of herbivores and fewer predators. Here it's turned upside down. And this is because as we have discussed when you don't get a predator or the predator is removed, then you get over consumption of the lower levels and that means that you get derailed. Everything becomes unbalanced.

So there's too much consumption here and you get a bit of a collapse. So this is what is meant by the predator keeping the planet green, it keeps the herbivores in line.

Now this lambda is what happens if there is a disturbance. For an example, if you get a drought or some kind of land use change, you get an oscillation. So it goes back and forth between these. The disturbance means that you get changes that go back and forth until it will stabilize and settle.

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Just to clarify, top down, is how the structure of low trophic levels is driven by effects of consumers from higher trophic levels. Plant communities are affected by herbivores. Or herbivores are affected by predators. Bottom up means that the trophic levels and the sizes of these- the composition and the structure are affected from below. That means that the plant community structure is driven by abiotic factors such as nutrient concentrations and so on. And then that in turn affects the number of herbivores.

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Now we have seen in some of our examples that there is support for top town and maybe a bit less for bottom up. Here is another food web from the same more paper. And we see how different plant inputs. Remember how I talked about fast growing plants and slow growing plants selecting for a bacterial food web or fungal food web.

In the fast cycle, which is the bacterial side, notice it's all thicker lines more clear. So this fast cycle is the bacterial cycle and the plant input that is put into it is called labile detritus so the detritus is the dead material.

Labile means the molecular composition is quite simple. And this is very easily and rapidly broken down by the soil food web. Labile detritus might be very soft leaves or very rapidly growing root systems that don't put much energy into defence. It's all just created to grow very fast and grab all the nutrients.

On the right hand side we have resistant detritus. Is the detritus the dead material from slow growing plants and they are slow growing because they could be more woody so they have more wood and they could have a lot of defences so chemical defences that become unappealing for decomposers. These things break down very slowly. They have a very complex molecular structure they take a long time to break down. And these tend to be fed on by the fungi.

Different plant inputs selected for different soil food webs. But actually this is more evidence for the bottom up.

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We’ll look at the Jena Experiment again with a paper from Scherber in Nature. This is a really nice dataset. A lot of people work on the experiment.

Now the numbers that we see in the food chain are strength and the direction of the relationships here.

All of these arrows show the direction of the relationships. And these numbers are regression coefficients. The larger the number, the more significant. And this whole model is called a structural equation model, it is quite a complex statistical procedure, which is a useful way to link all sorts of relationships together in one diagram.

Scherber’s findings were that belowground relationships were less affected by disturbance than aboveground, and herbivores were most strongly affected by changes in plant diversity. Interestingly, parasites and predators were also affected by the plant effects on herbivores. So there is a relationship of plant diversity that runs through and ultimately affects the herbivores.

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Talking about stability, we have seen that the top trophic levels, the predators at the very top, reduce change of the lower trophic levels, they tend to keep everything under control, mainly because they are Keystone a lot of the time. And research has shown that slow fungal energy channel contains more weak links and more high trophic levels so it can support it. It has more energy to support more trophic levels and because these are all weakly connected and can feed and make use of many different organisms so it is more stable than the bacterial energy channel. And it's partly because if you are slow growing you are using your food resources for more complex molecules and you can put them into stress tolerance, defence and different things that will help you survive in times of stress or disturbance. And so we see much more stability in the slow growing soil food web.

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One of the things that we work on is looking at stability in response to disturbance.

And the two ways to look at the effect of disturbance on a system is resistance which is the amplitude or the size of the effect after a disturbance. And to do this, you do need to have a control that has not been disturbed really so that you can compare the size of the disturbance. So let's say you have a drought and everything dries out and you want to know how much soil nitrogen changes during the drought. And so you would have the soil nitrogen in soils that have not seen a drought and then the soil nitrogen and soils that have seen a drought and you would measure the difference.

And then the resilience is the magnitude. Does it return to the normal level or does it just become slightly different, and the speed of return. How long does it take to get to some kind of new normal stable state and is it the same stable state as if it had not been disturbed. If there had been no drought. Is this the same and the answer here is no that takes a long time and recovery is not complete. These are very useful parameters or factors to be able to tell if there is high stability or instability in a system. Here we see a very simple food chain, not a web, a chain of three organisms. And you can see that the disturbance means that the biomass, the amplitude of these fluctuations is enormous is very large, over time, and you see very little recovery. It's not flattening off. It's just a big problem in this system lots and lots of change over time.

You increase the complexity and you become a food web. More species at different levels. And you can see here when these are computer simulations, they're not real data. But you see that the size of these fluctuations decreases over time. So while still quite unstable, the stability is higher, with more complexity.

And if we continue here you have a link created here is quite a weak link as well. You see that the stability of the system is approaching a new normal level, it's, it's much more stable, the amplitude of the fluctuation is much lower.

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So in summary, so food webs are really good model system for formulating and testing ecological theories.

And we can affect above ground food webs through modifying nutrient availability, but we can also modify below ground food webs by changing the plant community.

And soil food webs are very important in driving soil processes that can form the basis of plant production and climate mitigation.

Reading

Chapter 20 Begon

Avolio dominant species

Paine food webs

Scherber

Discussion topics

1. What keystone species are present in Myanmar forests?
2. If you removed one of these species what would happen?
3. What is the significance of conserving these species?