Chapter 7 – Network Structure and Metrics

7.1 Introduction

The purpose of the "network" view is to look holistically at an environmental problem. In the "systems" view, we broke down the problem into sub-models and expressed those using five icons. In the "network" view we want to learn to describe the behavior of the whole collection of relationships. We also want to be able to predict that behavior from characteristics of the network of processes. The description of these behaviors will require a new and specific vocabulary.

The "network" view is very useful for systems that have a medium number of objects that interact in specific ways. We will be using the network view to understand the behavior of food webs; with some questions such as: are they stable? Do they bounce back after a stress event? And, how important are the specificity of the linkages that have developed?

In networks with a small number of objects and processes, the "network" view can easily be made to be congruent to the "systems" view. To demonstrate this, we will examine a food web (with only a few organisms) from both a "systems" and a "network" view. Even though we can force congruency in these simple network/systems, the goal is to learn to approach more complex networks. A holistic network approach can be very different, and provide additional insight into the problem to the dynamic systems approachs. The network view looks at the web of relationships and the systems view tries to describe all objects, flows and controls with a standardized format. The viewer will help us focus on network structures such as loops and metrics as they relate to the general state of the network and its health.

Side Bar: Definitions

- Node - An object or organism that has some relationships to other.
- Links or edges - the relationships between two nodes.
- Connectivity - the degree that the overall network is linked together. (See the calculation of this metric in the text).
- State - the condition of all the nodes and links at any one time.
- Attractor - the concept is that the states of a network will tend toward a particular set of states.
- Resilience - if a network is perturbed enough it may jump to a different structure and behavior. The resilience is how far the network can be pushed and still return to a similar structure and behavior.

We can use a small natural meadow as example of how a network and systems view might be different. In the "systems view" we would look at the major flows of energy and nutrients. Our description might cover most flows by focusing on the grasses and a few herbivores. Even a study limited to just the dominant energy flows might be extremely useful. In contrast, a network model might include all the different species that inhabit the meadow. Some of these might not contribute any significant amount to the gross flows of energy but might help structure the entire ecosystem. For example, fruit-eating birds disperse seeds from many different plant types all across the meadow. The combination of these two views can help us look at energetics or nutrients in one case and focus on biodiversity processes in the other.

7.2 The node and arrow network diagram

The network diagram looks very similar to the systems diagram we used before. There are nodes and connections between the nodes. For example, we might construct a network diagram for a simple 5 species food web (Figure 1).

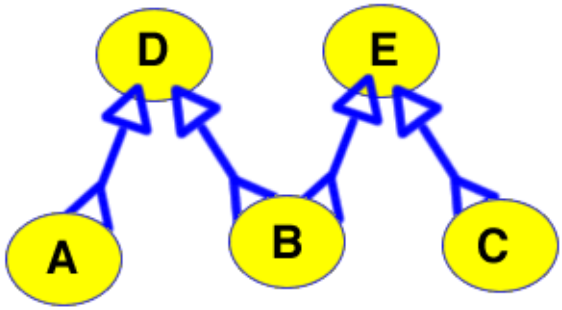


Figure 1. A node and arrow network diagram for a food web with five participants. "A" and "B" can pass energy or materials on to "D". "B" and "C" can pass energy or materials on to "E". The focus in the network view is on the interactions, in this case there are four unique interactions, AD, DB, BE, and EC. The nodes are where these connect. In this diagram all of the connection strengths are the same. For simplicity subsequent figures will show only the lines rather than the arrows.

In this food web, "D" and "E" are the predators and "A"; "B" and "C" are the prey. There is also some competition, for example "D" and "E" compete for "B".

In this network, the changes in any one component will have immediate effects and subsequent compensatory responses. For example if the amount of "A" is diminished, there could be an immediate negative effect on "D" which could be compensated if "D" switches to consuming more of "B". The decrease in "B" would effect "E" and that would ripple over to effect "C". Thus a change in one species could affect the entire network. All the species help the network adjust to the initial perturbation.

7.3 Description of network structure

Network structure and function are related. The structure of the food web network is also called the "trophic" structure. The first level of the description is the network diagram, the nodes and arrows as shown in Figure 1. Two important characteristics of this network structure are the connectance and the linkage density. The connectance is the proportion of the number of links to the total links possible. The total number of links possible can be easily calculated from the number of nodes as:

$$total\_possible\_links = n*(n-1)/2$$

Thus the connectance in Figure 1 is (4 links) / (5 nodes*4 nodes/2) = 0.4.

The link density is simply the average number of links per node. In this example that is 4 links/ 5 nodes = 0.8 links/node. This value is low for natural food webs in part because in our simple diagram there are no links from D and E and no links to A, B and C. Natural food webs can be very complex however even if they only have a link density in the range of 2 links/node.

7.4 Description of network behavior

We are going to focus on attempting to describe the stability of a food web or other network. Stability could broadly be considered the ability of the network to return to its starting condition after a perturbation. Assuming that the food web is in a healthy state to start with, having the appropriate number of connections, it will return to that state after an amount of time.

The ability to tolerate these perturbations is called the "resilience" but it has two different interpretations in the current literature. Some authors use the term "resilience" to indicate the amount of time the network takes to return to its original state whereas others use the term "resilience" to indicate the maximum magnitude of a perturbing stress for which the network will recover. We will be using the second definition in this book. The general sense of resilience is that it indicates the ability of the network to handle stress.

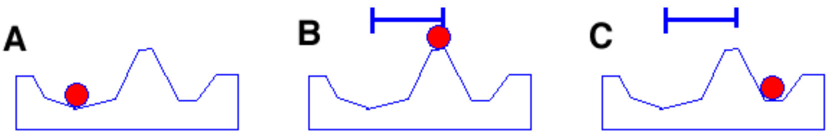


Figure 2. A common metaphor for the resilience of a system. Figure A is the stable state. Figure B shows how far you need to move the ball and yet have it still roll back to its original state. The bar represents the resilience of the left basin (or attractor). Figure C shows that the system was pushed to far and moved to another stable state, different from the original.

7.5 Visualization of a food web network response to a single perturbation

The following food web diagram (Figure 3a) is used to describe the linkages in network that is assumed to be in a stable configuration. Imagine that the links are springs and that the tension of the links is equal. If one of the nodes is pulled a little out of its current position (Figure 3b), there will be an immediate effect on all the springs that are attached to that node and a subsequent, compensatory effect of the entire network to re-establish equal tension (Figure 3c). In this visual/mechanical metaphor for a network, the position of each node in XY space represents how a species deals with its environment. A shift of position of a node should be interpreted as a required change by a species to acclimate to new environmental stresses or conditions. In this metaphor, it is also necessary to envision that the nodes don't move instantaneously, but rather slowly drift toward a new position.

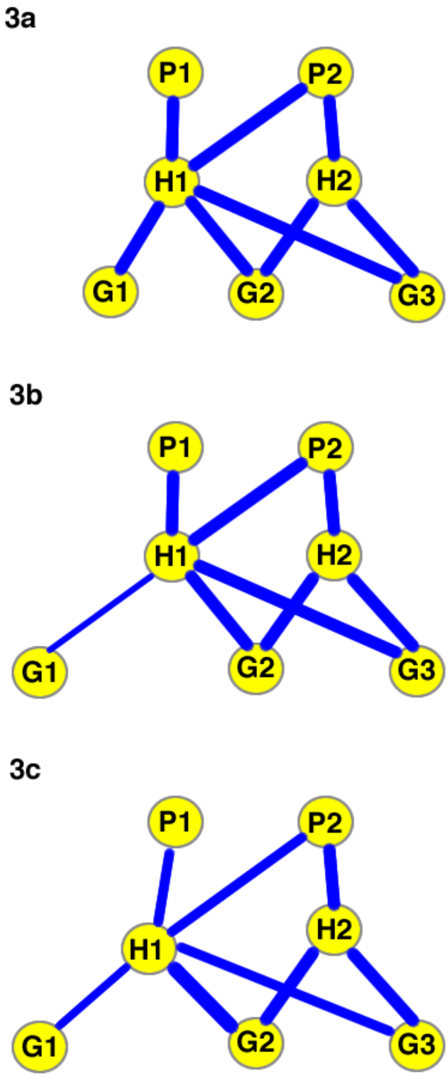


Figure 3. A network that starts in a stable state in which all the links have equal tension (a) until one node is disturbed and the link is stretched (b), followed by compensation by the entire network (c). During the period of compensation, some links are stretched a

little and others may actually be compressed (such as the link between H1 and G2).

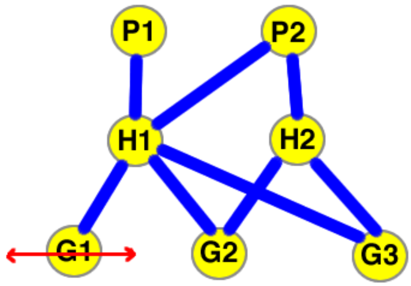
If the perturbed node is also allowed to respond, the entire network should return to the same geometry as it started with. If the perturbed node is held in a position for a period of time, the rest of the network may readjust itself to the same geometry but shifted over a bit.

This visualization of network behavior is supposed to give you a feel for how a change in any one of the nodes will lead to a compensation response by the entire network. This view seems to be a cause and effect type system and you can imagine that a systems diagram could also represent it. The visualization of a shifting set of nodes and rearrangement of the links however can be applied to more variable systems that include more parameters than just material and energy flow.

Visualization of the behavior in a network with variable nodes

In the previous diagrams, the position of the node in XY space represented both the environmental condition that the species was dealing adapting to. For example, the shift to the left of G1 could represent how a species of grass dealt with a particularly dry spell of weather. What we need to visualize now is what the network behavior would be if the nodes were constantly varying on their own (or being driven by environmental conditions) and what a network of constantly moving nodes and stretching/condensing links would look like. This will be represented below in a series of figures that show how the oscillation in just one node, "G1", would propagate oscillations to other nodes in the network. The oscillation in G1 could be caused by a daily or tidal environmental forcing function for example. In a real food web network, we should expect that several of the species might be responding to environmental conditions and that the network behavior could be described more as a set of dancing nodes than a simple response to a perturbation.

4a



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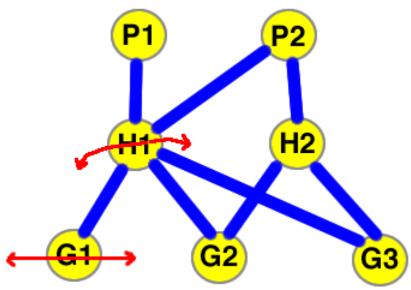

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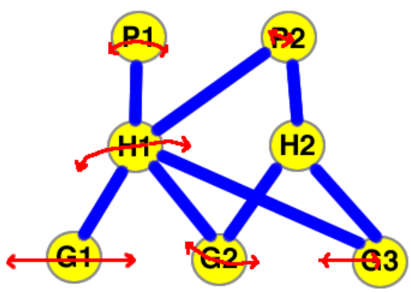

Figure 4. Propagation of an oscillation from G1 to other nodes in the network. Each subsequent diagram shows how the oscillation from the previous diagram might propagate next. As the nodes are further away from G1, the response can be considerably attenuated.

An important part of this analysis is the number steps that it would take to have the original perturbation propagate through the entire network. In the above example, the next two steps after the perturbation are shown and it would only take one more step to effect all of the nodes. The level of connectivity determines the number of steps.

7.6 Intermediate levels of connectivity

More is not always better in complex and natural systems. If a network has connections between almost all the nodes (Figure 5a), the action at one node has a direct effect on the others and the overall network tends to act like one object. For example a small tree farm where all the trees are the same age and closely packed will act like one stand of trees rather than individual trees. If one gets a disease, it is likely to pass that off to the other trees. If a fire starts anywhere on the farm, it is likely that the whole stand will burn. At the other extreme (Figure 5c), if a network has minimum to no connections it really acts as two separate networks. The action in one part of the network has no way to affect the behavior of the other part. This is often associated with fragmentation of habitats. Each of these sub-networks may also be too small to compensate for perturbations or variations. The optimal behavior for ability to share stress and diversity of response is when there is a medium, or intermediate, level of connectedness (Figure 5b).

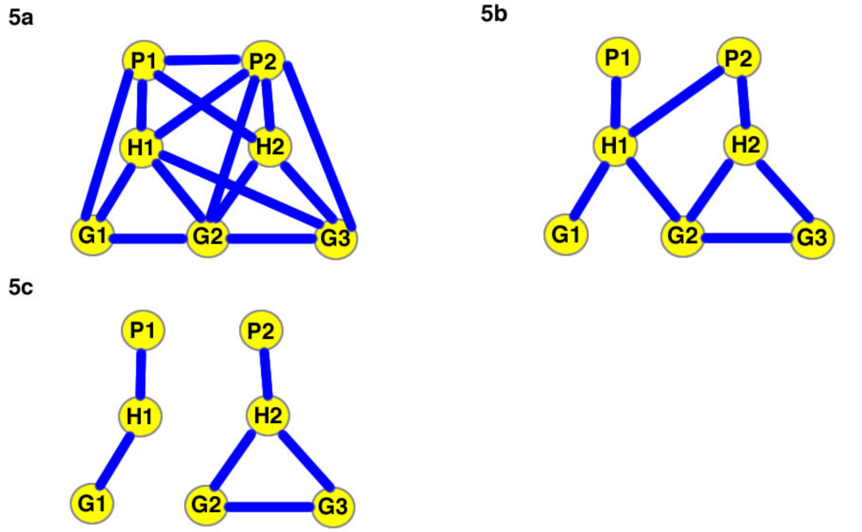

Figure 5 Range of connectivity. A is over-connected or crystalline, B is intermediate and C is under-connected or fragmented.

7.7 Resilience of a food web

The ball and cup metaphor for resilience (Figure 2) illustrates that idea that there are multiple basins of attraction and with enough sloshing around (stress) the ball can end up in the other basin. The amount of stress is the resilience for that particular basin.

Figure 6 illustrates two related network structures that can shift depending on conditions that lead to the health of the top predators. In one case (Figure 6a) Predator 1 is very strong and is able to eat all of the herbivore prey and even some of the plants directly. An example might be conditions that favor a black bear population that can dominate their foraging range and eat plants and many animals. Such a dominant predator will help define the behavior of a food web. The alternate structure is when that predator is not doing well and can only exist by relying on a single prey over a narrow range. The switch allows the competing predator to dominate. This hypothetical example illustrates the concept of resilience. These alternate food webs can flip back and forth depending on the conditions for Predator 1. If the food web is in state "a" but the conditions change enough, then it shifts to state "b". In some cases the two states would be very different and one maybe a healthy and complex set of interactions and the alternative state maybe degraded or simplified. An example of a switch to alternative stable states is when lakes become polluted. These lakes can shift from having a wide range of algal species, emergent plants and fish in the un-polluted state to a lake with a few dominant algal species and fish that stir up the mud. The diverse state may have a high degree of resilience and able to absorb high amounts of stress (pollution) before it flips to the degraded state, but once it flips, the degraded state may also have strong resilience. Many degraded lakes are extremely difficult to restore to their pre-polluted state even if the sources of pollution are removed. We are interested in preserving the resilience and health of natural and healthy ecosystems in part because it may be so difficult to overcome the resilience of the degraded systems.

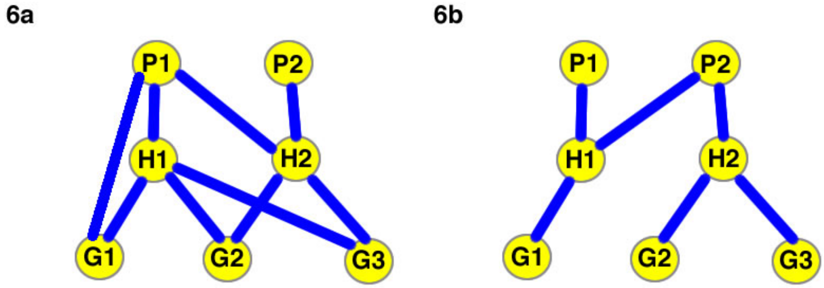

Figure 6. Two related networks that can shift back and forth depending on the health of the top predators. a) Predator P1 is very robust, is able to eat both herbivores (H1 and H2) and has taken on some omnivory (of G1). b) Predator P1 is weak and relies on H1. P2 is able to compete successfully with P2 for H1.

7.8 List of the characteristics of the node and arrow network view of food webs

A food web network has the following characteristics that can be used to understand and describe its behavior:

1. Each link between two species represents specific activities such as predatory prey interactions.

2. Each node should only have several links. More links represent generalist species and fewer links represent specialist species.

3. Resilient food webs will have an intermediate level of connectedness, not too connected and not too independent.

4. A single perturbation will cause an immediate reaction and then several levels of response from the full network, depending on the connectedness. This allows the entire network to share in compensation for that individual change.

5. Continued variability in the environment and the response of individual species can result in a highly complex variation in all of the species all the time. Even though there is continuous or intermediate variability, this can lead to a dynamic yet stable state of the network.

6. Individual perturbations or environmental fluctuations can cause changes in the network that are temporary, with the food web returning to a stable state. If individual or environmental perturbations are too large, the food web network could flip to an entirely different stable state. The amount of perturbation that it takes to just reach the border for a network transition is called the resilience.

7. Healthy natural networks have a high threshold of resilience.

7.9 Connectivity in spatial networks

In the previous section, we discussed the connectivity of a food web network. The conclusion was that an intermediate level of connectivity is important for stability and resilience of the food web; too much connectivity leads to the entire system acting as a single unit and too little connectivity leads the system susceptible to breaking into separate pieces. In the food web networks that we examined there were usually only several links per node, leading to very low fractional connectivities. Here, we are going to take a network view of region as a lattice of patches that are geographically connected. In this treatment, connectivity is crucial because it keeps the system whole and avoids fragmentation. A loss of connectivity between the small patches leads to smaller and smaller contiguous areas, smaller maximum habitat size within the overall region. Loss of connectivity that leads to fragmentation is bad for the region because it can cause isolation of sub-populations that are too small to function properly.

Side Bar: Spatial network vocabulary

Lattice - a grid of squares that represents the landscape of an ecosystem.

Maximum habitat size - the biggest area of connected grid elements within the lattice

Fragmented - several to many parts of the lattice are not connected

An overly mechanistic, but motivational, metaphor for the ecosystem region is to imagine that it is an airplane. You are going to ride on this plane, but the ground crew needs to remove a few rivets. You're thinking "certainly the plane can fly safely without one of the thousands of rivets". But each time you fly they take out another rivet. Of course, this metaphorical airline still has first class, but that's another story. When would you stop flying on this airline?

7.10 Fragmentation - how many patches can you disconnect?

We will use a simple model for an ecological region that is a lattice of square patches. Each patch can connect to its four closest neighboring patches (N,E,S and W but not diagonally). In this model, habitat destruction happens in random patches (rather than along roads or any particular shape). As the individual patches are destroyed, the overall habitat looses connectedness. Continuing destruction of the patches leads to smaller and smaller maximum habitat size, the area of the maximum number of connected patches. Further destruction, in this spatial lattice model, reaches a critical point where the maximum habitat size drops dramatically. Figure 7 shows this general pattern, with an example of the ecosystem region and patches. Figure 8 shows the shape of the curve for largest habitat size.

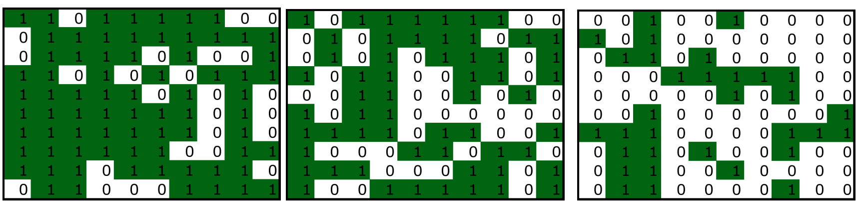

Figure 7. An ecosystem region that is divided up into patches. Each patch is connected to its four nearest neighbors. Different levels of random patch destruction are illustrated, a- minimal (30% loss), b-critical (41% loss), c-overcritical (60% loss). This figure was adapted from Sole and Goodwin 2000.

An important point about this pattern is that as the system reaches a critical level of patch destruction there can be a precipitous drop in the maximum habitat size within that region. This has major implications for management of these reserves and protection from fragmentation. This spatial lattice approach presents a different view of habitat fragmentation than other models. Another model predicts that the largest habitat size would decrease linearly with

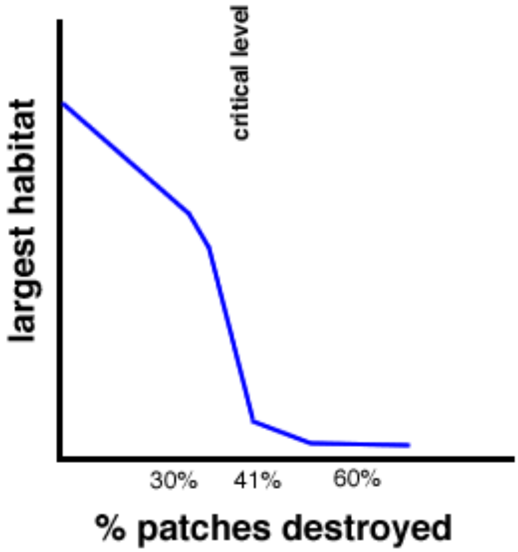

Figure 8. A graph of maximum habitat size against the proportion of patches that have been destroyed. Notice the critical level that is associated with a rapid loss of habitat size.

the % patch destruction reaching a maximum when about 50% of the patches have been destroyed. These two different models would have dramatically different consequences as you approach the critical level. In the linear model, the next patch destroyed will contribute the same degree of loss in habitat as a percent loss at any other level. In the spatial lattice model, a percent loss in critical region could result in a potentially irreversible degradation of the habitat.

Habitat destruction and fragmentation may also result in simplification or impoverishment of food web networks. As the areas get smaller, there may be to little diversity of plants, herbivores and predators to meet all their needs in a variable environment. This can eliminate competitors and decrease the health of the entire system.

7.11 Patch state diversity

In the above treatment we only dealt with patch destruction; removing the patch from the network permanently. Such destruction is obviously detrimental to the larger habitat and species diversity that can be maintained. Diversity of the successional state of a patch and variation in the level of connectedness between patches can create dynamic situations that foster biological diversity. A mosaic of habitat, microclimates and communities with multitudes of transitions between them is a very rich environment.

The metaphor/example for a habitat mosaic is the forest that is kept in a dynamic state by the continual, but intermediate level, of natural disturbances. For example, you might observe the following states of patches within the "forest":

Bare ground following a fire
Grasses and other pioneer species
Tree seedlings
Immature deciduous trees
Deciduous trees
Coniferous trees

There are a multitude of small disturbances including localized fires, blow downs, river course changes, and other events. These events don't propagate across the entire landscape because of the terrain and because previous small disturbances have yet to finish playing out. For example, a patch of forest only burns up to the border of a recent fire. Intermediate disturbances such as these can lead to higher biodiversity and a healthier and resilient ecosystem.

7.12 List of spatial behaviors

Destruction of patches will decrease the largest habitat size within an ecoregion.

There is a critical level of patch destruction that leads to a precipitous drop in the habitat size.

Patch disturbance, rather than destruction, at an intermediate level can lead to increased biodiversity in the region.

7.13 Case Study: Biodiversity and stability of natural grasslands

There are many reasons to conserve biodiversity ranging from a moral obligation to protect the Earth's resources to more pragmatic and utilitarian reasons that serve humans. The issue of preserving biodiversity has usually been framed in the context of saving individual species, especially threatened or endangered species, before they become extinct. Another view of saving biodiversity is to save or restore communities that provide essential ecosystem services for humans.

One crucial question is whether more complex communities perform better than simple communities. This question has two important parts; what do we mean by "simple" and "complex" and what do we use as a basis to judge what is "better"? For our purposes the complexity of a food web will be related to the number of species and the connectivity. The complexity of these systems will increase with the more ways that the species can interact. More complex systems will also have an intermediate level of connectivity, every species will be connected to several other species. Better performance does not mean simply more efficient production. In natural communities, better performance is related to the ability of the entire community to survive disturbances. A "better" community structure would bounce back from small disturbances very quickly and would have to be very severely disturbed not to recover. The degree of the stress that a community can withstand and still recover is the resilience.

Researchers have taken several approaches to address the relationship between species richness and the productivity of community. One approach is to construct artificial communities in well-controlled experimental chambers and another approach is to compare natural communities that have different species richness. Each approach has its benefits and drawbacks.

In a study conducted in artificial and highly controlled chambers, communities with nine, fifteen and thirty-one species were compared. All three communities consisted of decomposers, primary producers, primary and secondary consumers. The results were that the productivity (measured as total plant biomass increase over time) was higher with more diversity. The most diverse community had almost twice as much production as the species-poor community. The species-poor community was also more variable, indicating that it was not as stable as the more diverse communities.

Another study conducted in the field demonstrated that species-rich plots of grassland were more resistant to drought events than species-poor plots. These species-plots were both more resistance to drought and they recovered more rapidly after drought stress. More diversity seemed to help the communities use the resources more effectively and thus increase both productivity and resilience.

We have to be cautious when interpreting these studies and attempting to extrapolate from controlled and small-scale experiments to the ecosystem level. There are many methodological and statistical problems that could weaken the impact of these findings. These studies, however, are an important demonstration of the value of diverse communities. The more complex networks in diverse communities are able to utilize the available resources in flexible ways that can lead to their ability to resist stress in the first place and recover more swiftly afterwards.

A more complete story

Please see these references for a more complete description of this problem.

Chapin et al. (1998). Ecosystem consequences of changing biodiversity. Bioscience ???:45 - ??/ (January)

Tilman, David & John A. Downing. 1994. Biodiversity and stability in grasslands. Nature 367: 363-365. (27 Jan)

Tilman, David, Peter B. Reich, & Johannes M. H. Knops (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441:629-632 (June 1)

Tilman, David, David Wedin & Johannes Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718-720. (22 Feb)

Or you can search for "drought", "biodiversity", and "grasslands" to find other references.

Salient features

The focus of this case study makes it ideal to examine some of the points from a network perspective. The proposed reasons for increased stability of the diverse grassland include compensatory interactions between species. The weak positive and negative influences that these species have on each other can be described as linkages (rather than flows and stocks that we would have to use with our simple system viewer). Another feature is that they are looking for resilience and stability under conditions of disturbance or perturbations by the weather (i.e. drought).

to be added: a list and simple description of the species-species interactions and microhabitat-species interactions that were observed.

7.14 Summary

We can describe the structure of ecosystems or other functional networks and use metrics (such as link density or connectivity) to examine the function. Some networks, such as food webs, can be represented with node and link diagrams and others, such as forest surface cover, can be better represented with a lattice and fixed squares. In both types of representations, the concept of "intermediate level of connectivity" is important relative the health and resilience.

