

Trophic Structure of Montane Meadows and a Testing of Constant Food Web Connectance in Space.

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Abstract: Food webs of four montane meadow plots at Rocky Mountain Biological Laboratory were constructed and z-values were determined using the concept of commonality usually used in determining species area relationships. There was little correlation between commonality of plots and distance, possibly due to insufficient data, so data on three of the four plots from summer 2000 was used in the rest of the analysis. Link-Area Relationship study on three plots from 2000 yielded a z-value of 0.168. The Constant Connectance in Space model was tested on these three food webs, using known Species-Area curves and basic properties of food webs (species richness, number of links and connectance) to determine Link-Area Relationships. The model predicted a z-value of 0.135, within two confidence intervals of the observed data. The CCS model may be one of the first quantitative theories to accurately predict spatial variation of food-web structure. Predator and Prey overlap graphs were studied for the three 2000 plots as well. The z-values for predator and prey overlap graphs were found to be 0.923 and 0.144, respectively. The large LAR z-values suggest they may be the object of more statistically powerful tests.

Introduction

Food webs can tell us a lot about the ecosystem that they are describing. They can give us information about the interdependence of organisms in a particular ecosystem. Given a data set of species and their trophic interaction, there are a few types of webs that can be constructed. A trophic food web has for nodes species or trophic species, and for links, trophic links (Figure 1). A trophic species is a group of organisms that share identical sets of predator and prey. Trophic links are defined when one trophic species feeds on another or the same (cannibalism) species (Martinez 1992). Aggregation of individual species into trophic species simplifies the web without changing the general composition of the web (Pimm et. al, 1991). This type of web is known as bipartite (Strogatz, 2001), where predator and prey are treated as distinct kinds of nodes, and links are directional (ie, a predator eats a prey, not the other way around and the graph must be oriented to understand this). An important property of trophic food webs is connectance (C), defined as the number of existing links divided by the number of possible links, or

$C=L/S^2$. These trophic webs can be rearranged into two types of unipartite graphs, (Strogatz 2001) where each node is the same (ie, either prey or predator). A predator overlap graph has predators as nodes, and nodes are connected by links if they share one or more prey species in their diets (Figure 2). Similarly, a prey overlap graph may be constructed where each node is a prey species, and they share a link only if they are being eaten by a species in common (Figure 3).

Species Area Relationships (SAR) tell us that the number of species (S) found in a census plot of area A is related by a constant power of A: $S=cA^z$. The exponent, z, is an indicator of the distribution of species in the area. A high z-value indicates a small range for a species, while a low z-value indicates that the species resides in a large range. The z-value can be found as the slope found when plotting $\ln(S)$ against $\ln(A)$.

This is often impractical regarding large regions, however. A practical alternative is determining the number of species in a large area by finding the commonality of species from which we can determine the z-slope (Harte et. al 1999). Species commonality (χ_s) for two plots is defined as the number of species in common between (S_C) the two patches divided by the average number of species in the two patches. A z-value can be found for both the plots together (though they are separated by a distance D) by finding the slope of a graph of $\ln(D)$ vs. $\ln(\chi_s)$. From the species area law, we can determine the number of species that will likely be found in the large area between the plots.

Link Area Relationships (LAR) can be studied in a similar way as SAR. The number of links L in area A can be found from the equation $L=cA^z$. It is possible to find a z-value for the number of links in a community in a meadow plot by comparing the link commonality found between the two plots. A high LAR z-value denotes a high geographic

variability of trophic links within the plot, while a low z-value denotes low variability of links. A z-slope may also be found for predator and prey overlap graphs. A high LAR z-value for a predator graph coupled with a low z-value for the SAR signifies that the predators vary greatly in the types of prey they consume in different areas. However, a high SAR z-value may cause a high predator LAR z-value since the variance of species forces trophic links to change over space. Similarly, a high z-value (coupled with a low SAR z-value) for prey overlap graphs denotes that the species that attack the prey will vary as the composition of the food web changes.

Link Area Relationships have not been studied in great detail before, and it may lead to valuable information regarding complexity of food webs in various ecosystems. This may also give us a way to estimate the effect of removal of species may have on the entire trophic community. Better understanding of food webs can help to predict effects of concentrations of toxins, pollutants, and pesticides. We can know more about pest management, control of disease, and wildlife management. (Cohen et. al 1993).

A well supported model in the study of food webs is the Niche Model (Figure 4), developed by R. Williams and N. Martinez. This model constructs an actual food web given the number of species S , and the desired connectance C . It assigns to each species i a “niche value” (n_i) in the interval $[0,1]$. A beta function is used to assign a range r_i to each species while keeping the desired connectance. A center c_i for the range is randomly drawn from $[r_i/2, n_i]$. Species i consumes all species lying in the range. The niche model has shown to be more accurate for generating food webs, than other models such as the random model and the cascade model (Williams, Martinez 2000).

This year we developed the Constant Connectance in Space (CCS) Model to determine LARs based on SAR and simple properties (S, L, and C) for each web. First we used known SAR (z-value) to predict the commonality (χ_s) of the species in two plots (separated by distance D) using equation 1.

$$\chi_s = [2 \cdot 2^z][A/D^2]^z \quad (1)$$

By the definition of connectance, an equation for the number of links can be derived: $L = S^2 C$. (2)

The number of species in common is equal to a fraction (χ_s) of the mean species.

$$S_{ave} = (S_A + S_B)/2 \quad (3)$$

$$S_C = \chi_s S_{ave} \quad (4)$$

Assuming that the connectance of the two plots are roughly equal, ie. $C_A = C_B \cong C$, the number of links in common can be written as

$$L_C = C (S_C)^2 = C (\chi_s S_{ave})^2 = C (\chi_s)^2 (S_{ave})^2 \quad (5)$$

As illustrated, the number of links in common between two plots is a simple function of species commonality and basic properties of the webs in the two plots. From L_C , we can calculate χ_L , and from that the LAR z-value can be derived by plotting $\ln(\chi_s)$ vs $\ln(D)$ and examining the slope.

Prior work has been done within the time span of a summer with montane meadow food webs. While it is often thought that it takes many months to construct a

food web in detail, an entire food web of a montane meadow plot was constructed as part of a 1998 REU project (Garcia 1998). The next year the project expanded to food webs on 3 plant species in 3 plots (Buckley 1999). In summer 2000, food webs were constructed for each of 3 meadow plots. Analysis of link-area relationships determined the z-value to be 0.169 (Ignace 2000).

If Link-Area Relationships behave similarly to Species Area Relationships, the slope of a $\ln(\chi_L)$ vs $\ln(D)$ will be less than zero, signifying that link commonality between two plots will decrease at a particular rate as the distance between the plots increases. The Constant Connectance in Space (CCS) model will predict within two confidence intervals the LAR z-value that I observe for the plots. If year to year variation of webs is minimal, 2001 data should yield an LAR z-value of about 0.17, based on observations of these plots in 2000. If Link-Area Relationship theory holds for predator and prey overlap graphs, they will have an LAR z-value slightly greater than zero, signifying that predators and prey have variable respective food sources and threats depending on the makeup of the species in the area (link commonality of predator and prey overlap graphs between two plots decreases as the distance between the plots increases).

Methods and materials:

I observed trophic interactions between organisms in four montane meadow plots. The organisms were most commonly plants and insects. Four study sites were chosen at the Harte Lab upper site (Plot A), a plot in the southern area of the research meadow (Plot

B), a plot near the warming meadow (Plot C) and the Harte Lab middle site (Plot D). All sites have similar aspects, and all face south. I collected data by recording observations of possible trophic interactions, including degree of interaction (ie. the certainty of a trophic link). I encased plants that had an apparent egg sack or larvae on it with stocking, to determine if the insect uses the plant as a food source. I "grew" galls in stems by placing them in a plastic bag with a source of moisture. Each day I studied two sites for 1.75 hours at one of four times: early morning (6am), mid morning (between 8-12am), afternoon (between 1-5pm) and evening(7pm). Each site was visited 5 times each for morning and afternoon hours, and one time each for early morning and evening. I scheduled these on a rotating basis so that all sites had been visited equally with respect to time of observation, as well as spread throughout the summer. I conducted this study for a period of about five weeks, from June 27 until August 6. I missed three days of observation June 16- 18.

From the data that I collected from each plot, I constructed a trophic species web. I compared the composition of the observed webs to those generated by the niche model, given observed trophic species and connectance. This was done by 100 iterations of a program that creates webs using the niche model. Using all four webs, I calculated a LAR z-value. I then used the CCS model as described above to determine a predicted z-value based on known species area curves, and simple properties for each web such as species richness (S) and connectance (C). I constructed Predator and Prey overlap graphs for each plot, and calculated and LAR z-value in the same way as for trophic webs.

Results:

Statistics for the four webs I analyzed can be found in Table 1. I found 91 species at plot A, 113 species each at plots B and C and 95 species at plot D. A list of trophic interactions can be found in Table 2. I found 122 links at Plot A, 170 links at Plot B, 166 links at Plot C and 131 links at Plot D. The connectance for all plots was roughly similar, at about 0.013. Aggregation of these webs typically halved the number of species and doubled the connectance (Table 3). These webs were compared with those generated by the niche model to have the same values of S and C. These comparisons can be found in Table 4.

When link-commonality of these plots was plotted against distance on a log-log scale, we found very little correlation (Figure 5). We found that plots A and D had the highest commonality (27 links in common) even though they were the two farthest plots among the set (1800m apart). Plots A and B shared only 9 links, while plots A and C, which were farther apart, shared 21 links (See Table 5). Since the 2001 data set does not corroborate LAR theory, I tested the CCS model using data from summer 2000. Statistics for these webs can be found in Table 6. Last year three of the four plots were sampled, and a strong correlation ($R^2=0.98$) was found between $\ln(D)$ and $\ln(\chi_L)$, giving a LAR z-value of 0.168 (Ignace 2000).

When we used the CCS model on last years data, we found corroborative results (Figure 6). We used a SAR z-value of 0.08 based on data collected by the Harte Lab for the area surrounding my plots (Harte et. al. 1999). Using equations 1 through 5, a predicted LAR z-value was found at 0.136, with a standard deviation for the slope at 0.06. This is within two confidence intervals of the 2000 observed value of 0.168.

The predator and prey overlap graphs had about twice as many links as did the trophic species webs (Table 8). Link commonality for these graphs were similar to link commonality of trophic webs. The prey overlap LAR (Figure 7) correlated very strongly ($R^2=1$) creating a z-value of 0.144 for the 2000 data. The Predator overlap graph LAR showed a z-value of 0.923, though the correlation was not as strong ($R^2=0.6801$)

Discussion

Data collected in 2001 did not corroborate the LAR theory. However, the CCS model used on data from 2000 predicted the observed LARs within two confidence intervals. In addition, predator and prey overlap graphs for plots based on the 2000 data showed very high LAR z-values, signifying that they may be the object of more statistically significant tests.

The data for 2001 may have failed to support the LAR theory because of insufficient effort. In 2000, three plots were sampled by 2 researchers, and in 2001, four plots were sampled by 1 researcher. Three observation days were missed from July 16 to 18, which may result in missed data on species that shifted to a higher elevation during that time. There may be year to year variation so that in 2000, data fit the LAR model closely, but simply by variation, 2001 data did not. Another possibility is that last year's data simply fit the model by chance. In other words, last years observations may have unusually low variation which allowed researchers to luckily observe a significant LAR. Another possibility is that our LAR theory is incorrect and last years data failed to illustrate the inconsistency.

The program that I used to test the niche model only works well with webs with high connectance. Because of this I was only able to generate predicted webs for plots A and D (2001 data), whose trophic species webs connectance values were high enough for the niche model program to run efficiently. The niche model predicted percent top species (those species with no predators), percent intermediate species (species with both predator and prey), percent basal species (those species with no prey, namely plants), percent herbivores. In both cases, the observed values for percent top predators were much higher than the values offered by the model. This can be explained by my methods and the focus of my food web. My methods allowed me to observe mainly insects feeding on plants. In the actual communities surrounding my plots, the insects are eaten by other species, particularly vertebrates such as birds, snakes and chipmunks. My presence around the plot may have prevented vertebrates from feeding on species in the plot. Hence many insect species were represented as having no predators and treated as top species. For the same reason, the observed values of intermediate species are much lower than that predicted by the model. Almost all herbivorous insects are treated as top predators in the observed food webs, while in actual and model generated food webs they would be intermediate. Percent herbivory was observed at higher than predicted values because my methods allowed for few observations of carnivory.

The CCS model predicts the LAR z-values within two confidence intervals, based on 2000 data. If Link Area Relationships do behave as Species Area Relationships, the CCS model does a good job predicting them. However, we are not sure that LAR theory is legitimate, partly because the 2000 data only had three points, and partly because LAR theory is still in it's infancy. The Predator and Prey overlap graphs LAR z-values signify

that as two plots are separated by an increasing distance, the species on which a predator will feed varies. The large LAR z -values for overlap graphs suggest they may be the object of more statistically powerful tests.

Conclusion

A sample effort threshold of food webs construction may not have been attained and four webs may be much for one person in one summer. Further research could resolve this issue by repeating this experiment with more manpower (or woman power). Finding LAR's with four webs is twice as effective as finding them with three webs because three more comparisons can be made, yielding six data points rather than three. The niche model reasonably estimates basal fraction, but due to the sampling methods used in this study, percent top and intermediate species, as well as percent herbivores is not predicted well. If LAR theory holds the CCS model may be one of the first quantitative theories to accurately predict spatial variation of food-web structure.

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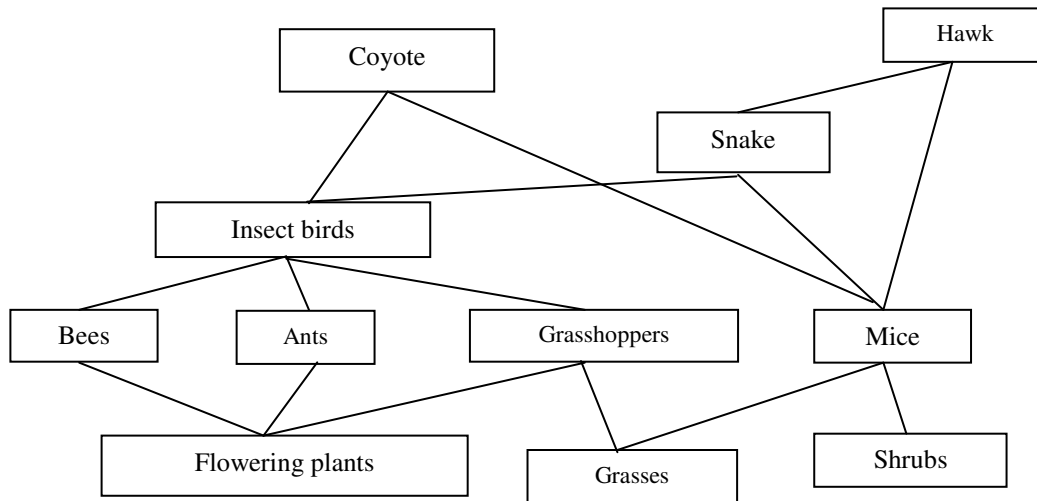


Figure 1: Trophic food web. Nodes are species. Links are trophic links, representing the trophic interaction between two species. In this case, Bees and Ants are trophic species, since they share the same predator and prey. Aggregation of individual species into trophic species simplifies the web without changing the composition of the web. This bipartite graph has two distinct kinds of nodes: predator and prey. Links are directional, since a predator eats a prey.

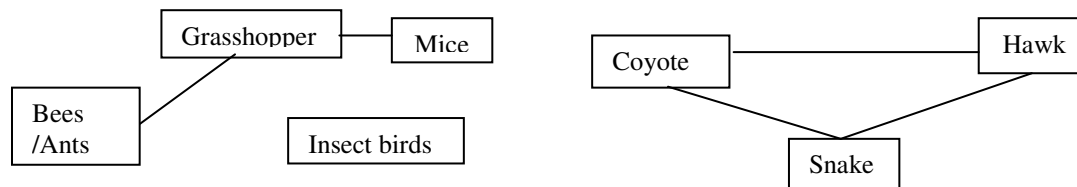


Figure 2: Predator Overlap graph for trophic food web of Figure 1. Nodes are predators, and are connected if they share any prey species in common.

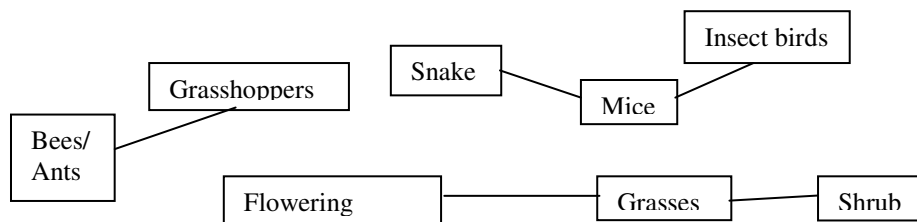


Figure 3: Prey overlap graph for trophic food web in Figure 1. Nodes are prey and are linked if they share any predators.

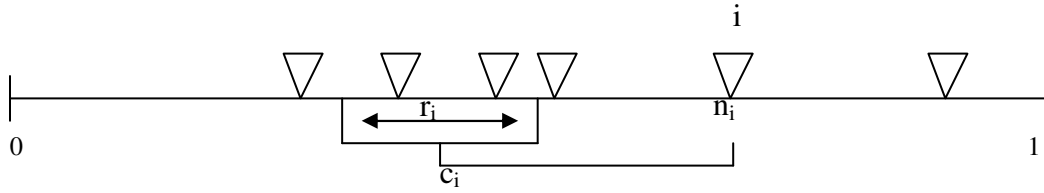


Figure 4: Niche Model: Given a number of species, desired connectance and desired error, the niche model will generate a web that satisfies the conditions. Each species i is given a randomly assigned niche value (n_i), and a predation range (r_i) derived by a beta function to keep desired connectance. The center of the range (c_i) is randomly drawn from $[r_i/2, n]$. Species i consumes every species falling in the range.

Table 1: Properties of food webs in 4 plots 2001			
Plot	Species	Links	Connectance
A	90	122	0.01506173
B	113	170	0.01331349
C	113	166	0.01300023
D	95	131	0.01451524

Table 3: Effects of trophic aggregation on food webs. Original food webs are based on morphic species. I then aggregated these species into trophic species and constructed trophic species webs.

Plot	Species	Links	Connectance
Original A	90	122	0.015
Trophic A	40	74	0.046
Original B	113	170	0.013
Trophic B	74	129	0.023
Original C	113	166	0.013
Trophic C	67	121	0.027
Original D	95	131	0.015
Trophic D	53	88	0.031

Table 4: Comparison of Empirically Observed properties of trophic species webs with niche-model generated means

	PlotA obs	PlotA model	S.D	PlotD obs	PlotD model	S.D
%Top	67.5	16.825	6.989	64.1509	18.49	7.499
%Inter	7.5	53.575	7.413	9.43396	50.03	8.268
%Basal	25	29.6	4.764	26.4151	31.4717	4.222
%Herbivore	55	20.025	6.391	56.6038	22.81	4.938

Table 4 Comments: The niche model can calculate four parameters given a web. Top species are those with no predators. Intermediate species have both predator and prey, and basal species have no prey, usually plants.

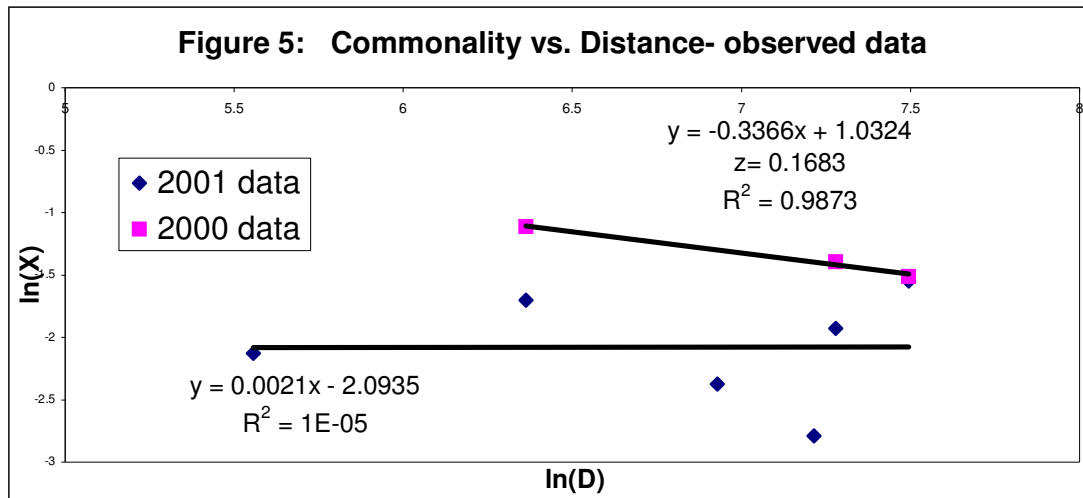


Figure 5. A z value of 0.00105 was found for data collected in 2001. However, given that $R^2=1E-05$, this figure cannot be considered significant.

Table 5 : Data and Calculations for LAR									
Plot 1	Plot 2	# Links 1	# Links 2	Lc	χ_L	D	$\ln(\chi_L)$	$\ln(D)$	
2001 Data									
A	B	123	170	9	0.061433447	1360	-2.7898	7.2152	
A	C	123	166	21	0.14532872	1450	-1.92876	7.2793	
A	D	123	131	27	0.212598425	1800	-1.54835	7.4955	
B	C	170	166	20	0.119047619	259	-2.12823	5.5568	
B	D	170	131	14	0.093023256	1021	-2.37491	6.9285	
C	D	166	131	27	0.181818182	580	-1.70475	6.363	
2000 Data									
C	D	163	154	52	0.32807571	580	-1.11451	6.363	
C	A	163	127	36	0.248275862	1450	-1.39321	7.2793	
A	D	127	154	31	0.220640569	1800	-1.51122	7.4955	

Table 6 Statistics for 3 plots 2000				
Plot	Species	Links	Connectance	
A	84	127	0.0179	
C	95	163	0.0180	
D	92	154	0.0181	

Table 8: Comparative Statistics of Trophic webs and predator and prey overlap graphs				
Web	Species	Links	Connectance	
PlotA	70	111	0.022	
PlotAPred	29	169	0.2	
PlotAPrey	44	219	0.113	
PlotC	76	146	0.0252	
PlotCPred	30	179	0.198	
PlotCPrey	51	333	0.128	
PlotD	80	113	0.017	
PlotDPred	29	104	0.123	
PlotDPrey	57	296	0.091	