Notes

Major dimensions in food-web structure properties

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Abstract. The covariance among a range of 20 network structural properties of food webs plus net primary productivity was assessed for 14 published food webs using principal components analysis. Three primary components explained 84% of the variability in the data sets, suggesting substantial covariance among the properties employed in the literature. The first dimension explained 48% of the variance and could be ascribed to connectance, covarying significantly with the proportion of intermediate species and characteristic path length. The second dimension explained 19% and was related to trophic species richness. The third axis explained 17% and was related to ecosystem net primary productivity. A distinct opposite clustering of connectance, the proportion of intermediate species, and mean trophic level vs. the proportion of top and basal species and path length suggests a dichotomy in food-web structure. Food webs appear either clustered and highly interconnected or elongated with fewer links.

Key words: connectance; food-web properties; network topology; principal components; trophic species.

Introduction

An increasingly wide variety of properties is employed to describe and analyze food-web network structure (Warren 1994, Williams and Martinez 2000). Analysis of the empirical values of these properties has played a central role in the search for generalities of food-web structure (Briand and Cohen 1984, Hall and Raffaelli 1991, Martinez 1991, Bengtsson 1994, Williams and Martinez 2000, Dunne et al. 2002*a*).

With the advent of more detailed, highly resolved data sets it has become apparent that many food-web properties are "scale dependent" with the number of trophic species S (Martinez 1991, 1994, Bengtsson 1994) or connectance C (Williams et al. 2002). S and C themselves appear to covary negatively, particularly at low S for food webs from different communities (Beckerman et al. 2006). However they appear independent across food webs from the same community (Warren 1994) or community type (Martinez 1992). S and C have been usefully applied as the only parameters in simple models of food-web structure (Williams and Martinez 2000, Cattin et al. 2004, Stouffer et al. 2005). However, there has yet to be a study that looks

systematically at the interdependencies of the wide range of network properties and food webs currently used in modeling and analysis, and to what degree these properties covary with S and C. We address this issue by using a standard principal components analysis and examine the following questions: (1) Can the multidimensionality implied by a wide range of network properties be reduced to fewer major dimensions? (2) If so, how can we characterize these major dimensions? and (3) What can we extrapolate from this about drivers of food-web network structure? If it is possible to identify a few orthogonal dimensions, future work, both practical and conceptual, could focus on understanding just these dimensions and associated drivers. Covariance patterns suggesting causal links could be verified experimentally.

Materials and Methods

We selected 14 food webs for analysis from a larger set described in Dunne et al. (2002*b*, 2004). These include three terrestrial webs (Coachella Valley, El Verde Rainforest, the island of St. Martin), five freshwater lake, pond, or stream webs (Bridgebrook Lake, Little Rock Lake, Lake Tahoe, Skipwith Pond, Stony Stream), three estuary webs (Chesapeake Bay, St. Marks Estuary, Ythan Estuary including parasites; see Plate 1), and three marine webs (Benguela, small Caribbean Reef, and
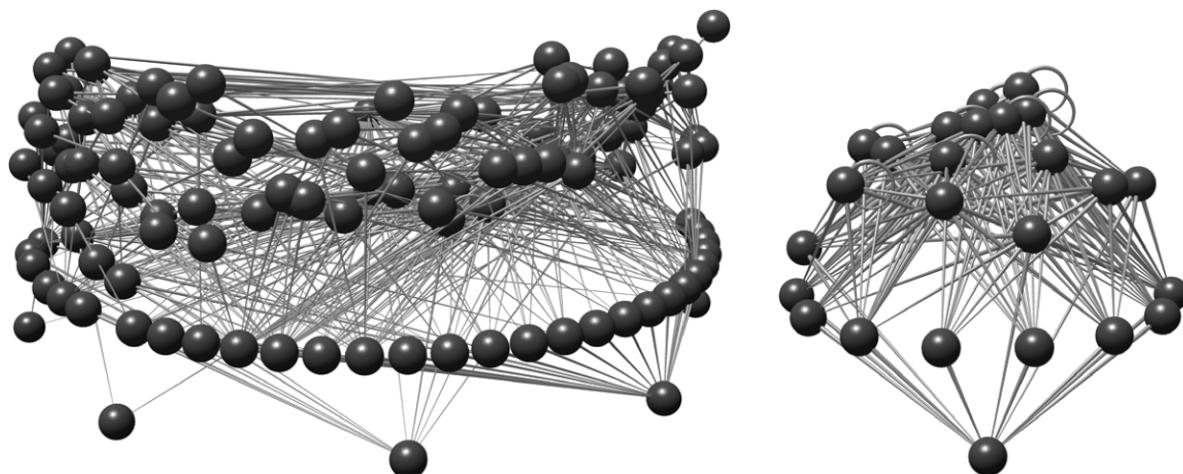
PLATE 1.　The two most contrasting food webs in terms of connectance and path length (cf. Fig. 2a): (left) the Ythan Estuary with parasites and (right) Skipwith Pond. Graphics prepared by J. A. Dunne.

northeastern U.S. Shelf; for a brief description of these webs see Appendix). We excluded source webs as well as smaller webs from studies that generated multiple webs for the same or highly similar habitats. For each web we calculated the values for a set of 20 network structure properties, described in Table 1. In addition, for each food web an estimate of net primary productivity (NPP) was taken from Field et al. (1998), a recent attempt to estimate terrestrial and aquatic production consistently.

We applied principal components analysis and multiple analysis of variance.

RESULTS AND DISCUSSION

Three major principal components explained 88% of the total variation, and most of the examined food-web properties covaried significantly with at least one of these axes (Fig. 1, Table 2). The first axis explained almost one-half of the total variation and correlated

TABLE 1.　Food-web properties applied and abbreviated labels.

Label	Definition
Bas	percentage of basal taxa (taxa without resources)
C	connectance (L/S^2), S^2 is the maximum number of links possible in a matrix of S species
Can	percentage of cannibals
ChLen	mean food chain length, averaged over all species
ChSD	standard deviation of ChLen
ChNum	log number of food chains
Clust	mean clustering coefficient (probability that two taxa linked to the same taxon are also linked)
GenSD	normalized standard deviation of generality (number of resources per taxon), or the number of prey of a taxon standardized by L/S
Herb	percentage of herbivores plus detritivores (taxa that feed on basal taxa)
Int	percentage of intermediate taxa (with both consumers and resources)
LinkSD	normalized standard deviation of links (number of consumers plus resources per taxon)
Loop	percentage of taxa in loops (food chains in which a taxon occurs twice)
L/S	links per species
MaxSim	mean of the maximum trophic similarity of each taxon to other taxa, the number of predators and prey shared by a pair of species divided by their total number of predators and prey
NPP	net primary productivity (g C·m^{-2}·yr^{-1})
Omn	percentage of omnivores (taxa that feed on ≥ 2 taxa with different trophic levels)
Path	characteristic path length, the mean shortest food chain length between species pairs
S	number of trophic species, or taxa, referring to the number of compartments in the original food web, or functional groups of taxa that share the same predators and prey
TL	short-weighted trophic level averaged across taxa
Top	percentage of top taxa (taxa without consumers)
VulSD	normalized standard deviation of vulnerability (number of consumers per taxon), or the number of predators of a taxon standardized by L/S

　　Notes: L is the number of links a species has with other species in the web. Properties are explained in detail in Williams and Martinez (2000, 2004).
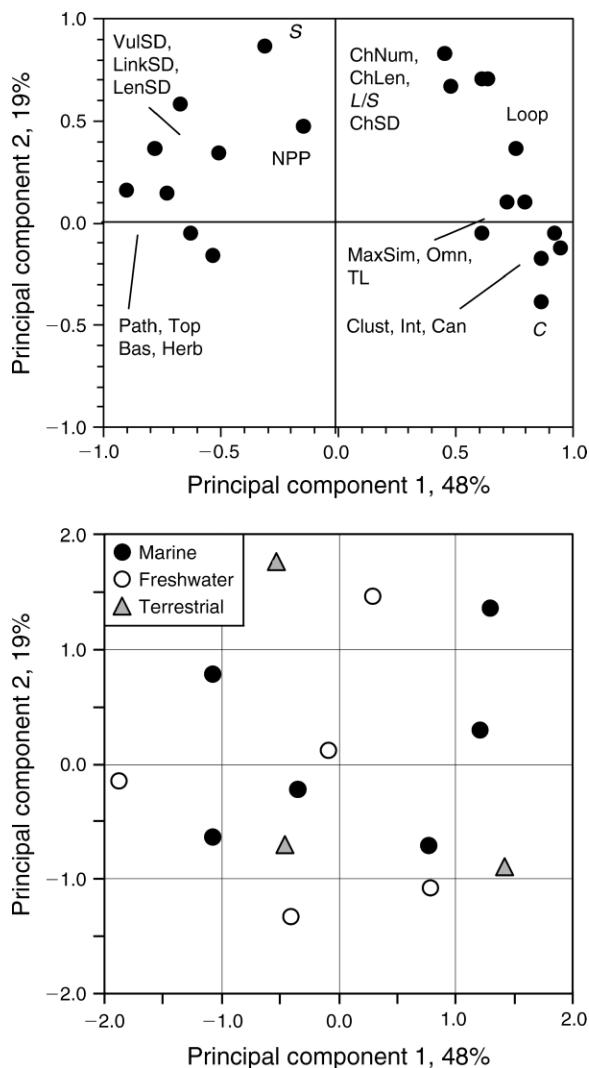
negatively with NPP ($r = -0.63$). This axis also covaried positively with Bas and GenSD reflecting food item diversity), and negatively with TL, Top, and Omn. Herb was the only property that did not covary significantly with the first three axes, and was also the only one that covaried significantly with a fourth axis (explaining only little additional variation, Table 2). No properties significantly covaried with all three principal components (Table 2), and most (11) highly significant correlations ($P < 0.01$) were with the first principal component. The second principal component had four and the third only one.

These results suggest that variability in ecological network structure can be compressed largely along three major dimensions. The first dimension can be interpreted to correspond with C and the second dimension with S. The third dimension appears to correspond to NPP and also covaries with the proportion of basal species, which suggests that some of the variability in observed food-web structure is attributable to habitat productivity. The apparent orthogonality of S and C implies that both species-rich and species-poor food webs can be equally well-connected (Warren 1989, Martinez 1993).

The current analysis highlights which other properties are likely to correlate with S and C. For example, as

FIG. 1. (a) Principal component analysis of food-web properties. Together the three components explained 84% of the variance. Displayed are correlations with the first and second principal components; hence vertical and horizontal axes are constrained between −1 and +1, corresponding to perfect negative or positive correlation. Component 1 is interpreted as reflecting the distribution of species over trophic levels, component 2 as taxonomic species richness, and component 3 as general ecosystem productivity. Properties are identified in Table 1; all correlation coefficients are presented in Table 2. (b) Breakdown of the 14 studied food webs into terrestrial, freshwater, and marine categories plotted against the first two principal components of the PCA.

TABLE 2. Correlation of 21 food-web properties to the first three principal components.

	Principal component†		
Property label	1 (48%)	2 (19%)	3 (16%)
S	−0.32	*0.86*	0.27
C	*0.86*	−0.39	0.12
L/S	0.48	*0.66*	0.50
Top	*−0.73*	0.14	**−0.55**
Int	*0.92*	−0.05	−0.09
Bas	*−0.62*	−0.05	**0.61**
Herb	**−0.53**	−0.16	0.44
Can	*0.87*	−0.18	0.06
Omn	*0.80*	0.10	**−0.56**
Loop	*0.76*	0.36	0.11
ChLen	*0.64*	*0.70*	0.03
ChSD	*0.61*	*0.70*	−0.22
ChNum	0.46	*0.82*	0.26
TL	*0.72*	0.10	**−0.58**
MaxSim	*0.61*	−0.05	*0.69*
GenSD	**−0.51**	0.34	**0.62**
VulSD	*−0.78*	0.36	−0.35
LinkSD	*−0.67*	**0.58**	−0.19
Path	*−0.88*	0.15	−0.24
Clust	*0.95*	−0.13	0.01
NPP	−0.15	0.47	**−0.63**

Notes: Property labels are as in Table 1. Correlations over 0.53 are significant at $P = 0.05$ (bold) and those over 0.66 at $P = 0.01$ (bold and italic). Inclusion of size class (annexe 1, indicating areal extent of the food web) did not greatly alter the covariance pattern in this PCA, and size class itself was not correlated significantly to any of the first three principal components in that analysis.

† The proportion of variance explained by a component is in parentheses. A fourth component added another 5% and was correlated significantly only to Herb.
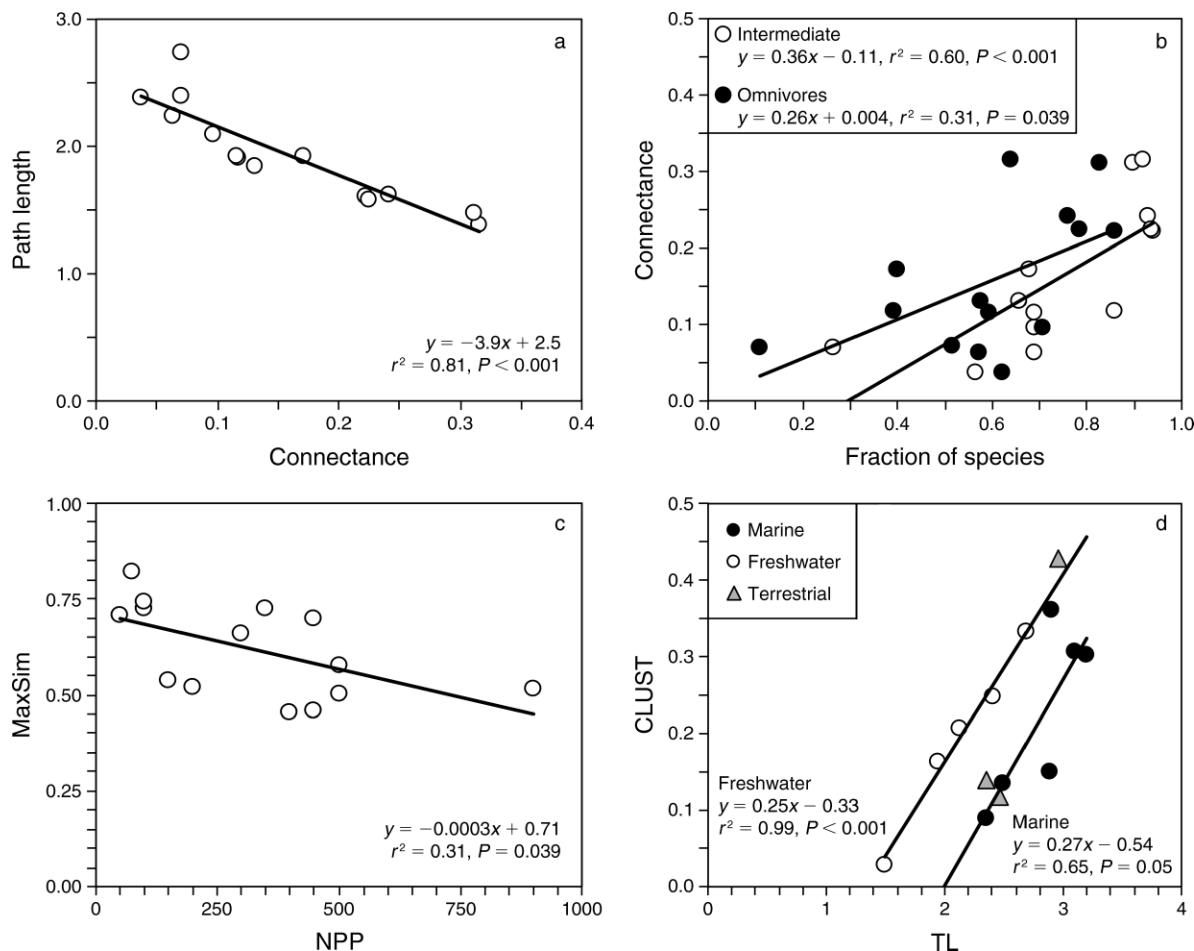
highly significantly ($P = 0.01$) and positively with Clust, Int, C, Can, Omn, Loop, and TL ($r = 0.72$–0.95), and negatively with Path, VulSD, Top, and LinkSD ($r = -0.67$ to -0.88). The second axis correlated highly significantly and positively with S, ChNum, L/S, and ChLen ($r = 0.66$–0.88). The third axis covaried highly significantly and positively with MaxSim ($r = 0.69$), and

FIG. 2. Variability among selected properties of 14 well studied food webs: (a) Path length vs. C (connectance), (b) C vs. Int (intermediate taxa, open symbols) and C vs. Omn (omnivores, solid symbols); (c) MaxSim (maximum trophic similarity) vs. NPP (net primary productivity); (d) CLUST (clustering coefficient, fraction of species pairs connected to the same species that are connected to each other) vs. TL (mean trophic level) broken down for terrestrial, marine, and freshwater food webs.

reported in Williams et al. (2002), Path covaried with axis 1 and was negatively correlated with C (Fig. 2a). Contrary to what was reported in Dunne et al. (2002b), the proportion of omnivores also covaried with axis 1 and was positively correlated with C ($r = 0.56$, $P < 0.04$; Fig. 2b). The proportion of intermediate species also positively correlated with C. The negative correlation of MaxSim with NPP (Fig. 2c) suggests that taxa in food webs become trophically less similar, hence more diverse, with increasing productivity. Because this was only apparent as a third dimension in the overall variability, it suggests that the search for productivity–diversity generalizations may well be hampered by the stronger signals of other principal components. The distinct opposite clustering along the first axis of connectance, the proportion of intermediate species and mean trophic level on the one hand, and the proportion of top and basal species and path length on the other suggests a dichotomy in web structure: food

webs are either clustered and highly interconnected or elongated with few links.

A comparison among freshwater, marine, and terrestrial food webs is hampered by the unequal distribution over these categories and the limited size of our data set. A MANOVA was carried out comparing these three with connectance (C) and trophic species (S) as covariables to look for pattern over-and-above that spanned by the first two principal components. A significant difference among the three types was only found for the proportion of herbivores, which includes detritivores ($P = 0.018$), for omnivores ($P = 0.001$), mean trophic level (TL, $P = 0.002$), and GenSD ($P = 0.045$). Freshwater systems had a higher proportion of herbivores and a lower mean trophic level. Possibly, the freshwater food webs had a higher proportion of plant and detritus eaters because the micro-algal diversity in benthos and plankton is high. A high diversity in herbivores follows, and also of Int, but not of higher

trophic level predators. This appears consistent with the higher clustering in freshwater food webs for the same mean trophic length (Fig. 2d).

While underpinning the importance of C and S in the modeling of food-web network structure, this analysis also provides a cautionary note. Given the high degree of covariance among food-web properties that sort along a few major dimensions, a goal for future research is to move from the statistical study of many specific covarying properties (e.g., Williams and Martinez 2000, Dunne et al. 2004) to more robust ways of evaluating the fit of alternative, mechanistic network models to data (cf. Beckerman et al. 2006). This needs to be accompanied by a systematic compilation of new, taxonomically well-resolved food-web data as in Martinez (1991), Havens (1992), Townsend et al. (1998), Martinez et al. (1999), and Lafferty et al. (2006). Beyond methodological reservations (e.g., Townsend et al. 1998, Winemiller et al. 2001), our analysis justifies a search for factors that cause richness in intermediate species because this appears related to high connectance and hence robustness (Dunne et al. 2002a, b).

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APPENDIX

Characterization of the 14 studied food webs (*Ecological Archives* E090-018-A1).