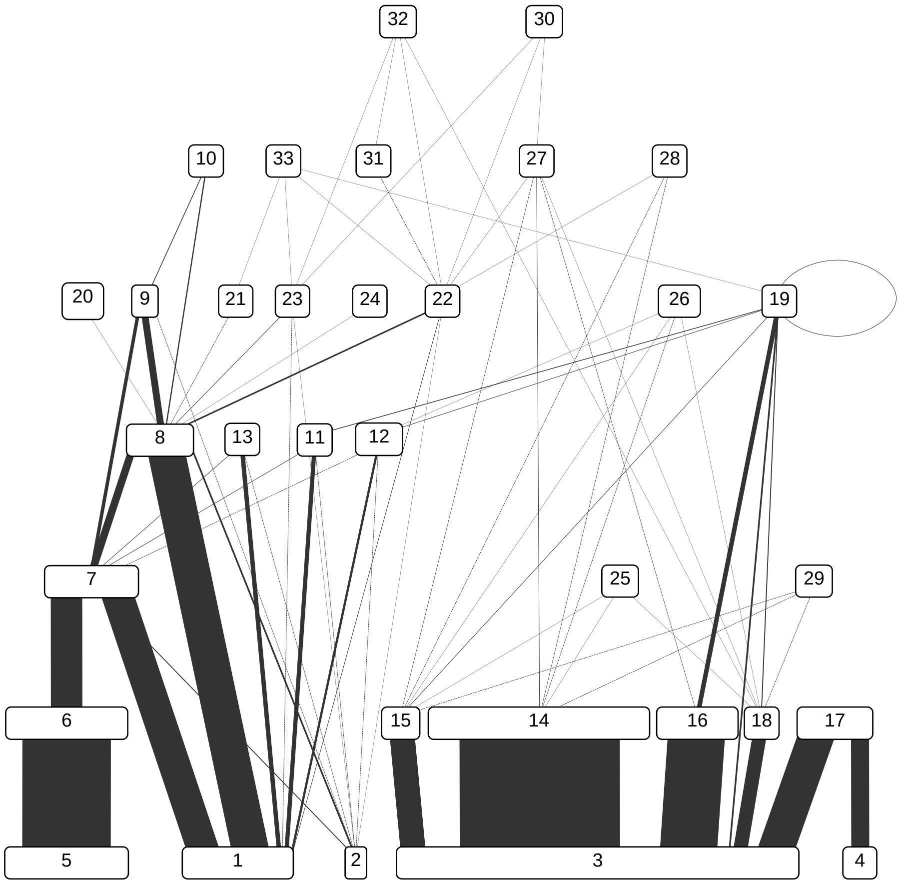
Quantitative descriptors and their perspectives for food-web ecology



par

Carolin Banašek-Richter

Thèse présentée à la Faculté des Sciences de l'Université de Neuchâtel pour l'obtention du grade de Docteur ès Science

2004

IMPRIMATUR POUR LA THESE

Quantitative descriptors and their perspectives for food web ecology

Mme Carolin BANASEK-RICHTER

UNIVERSITE DE NEUCHATEL

FACULTE DES SCIENCES

La Faculté des sciences de l'Université de
Neuchâtel, sur le rapport des membres du jury

Mme M. Rahier, MM. C. Mermod (directeur de thèse),
L.-F. Bersier (co-directeur de thèse),
J.-P. Gabriel (Fribourg) et
R. Ulanowicz (Solomons USA)

autorise l'impression de la présente thèse.

Neuchâtel, le 12 juillet 2004 La doyenne:

M Ra

Martine Rahier

Foreword

The present PhD thesis of Carolin Banašek-Richter is part of a larger research project entitled *A quantitative approach to food web ecology*. This project was funded by the Swiss National Science Foundation. Two PhD students, Carolin and Marie-France Cattin Blandenier, were involved in this enterprise.

What is not apparent in the present thesis is that Carolin also contributed to the part of the project dedicated to the empirical description and analysis of food webs in wet meadows of the Grande Cariçaie (South shore of the Lake Neuchâtel, Switzerland). Carolin participated actively in data collection and in the identification of many taxonomic groups. The description of the field methods, the species list, and the food-web matrices can be found in the PhD thesis of Marie-France, entitled *Food web ecology: models and application to conservation*. The quantitative analysis of the food webs of the Grande Cariçaie are exposed in chapters 4, 5, and 6 of the present thesis. Carolin is co-author of two works that tackled the effect of mowing on the spider communities in the wet meadows (Cattin, M.-F., Blandenier, G., Banašek-Richter C. and Bersier L.-F. 2003. Effects of mowing on the spider (Araneae) community as management practice in wet meadows. *Biological Conservation*, **113**: 179-188.), and on the global structure of the food-webs (Cattin M.-F., Bersier L.-F. and Banašek-Richter C. Conservation of wet meadows by mowing: a food web approach. In prep.). She also participated to the discussions on the elaboration of a model aimed at describing the static structure of food webs (Cattin M.-F., Bersier L.-F., Banašek-Richter C., Baltensperger R. and Gabriel, J.-P. 2004. Phylogenetic constraints and adaptation explain food web structure. *Nature*, **427**: 835-839).

Finally, Carolin also took part to the experimental part of the research project. The aim was to test the hypothesis that the occurrence of trophic cascades is triggered by the edibility of plants. We took advantage of the fact that the wet meadows of the Grande Cariçaie are dominated by two unpalatable plants (Schoenus nigricans and Cladium mariscus). We used the palatable *Lolium perenne* to test this hypothesis. *Lolium* were planted in 24 pots (50 cm of diameter), cultivated in Neuchâtel's Botanical garden, and brought to our field site in the Grande Cariçaie. We manipulated the edibility of *Lolium* with jasmonate. We used a two factorial design with edibility of plants (edible vs. less edible) and density of spiders (high vs. low) as the controlled variables. The expected herbivores were crickets, and we had to protect the pots against roe-deer with wire netting. Unfortunately, we failed to protect the pots against voles... This huge amount of work was annihilated in a few nights by voles, which much appreciated our experiment.

Louis-Félix Bersier

CONTENTS

I GENERAL INTRODUCTION

A food web describes the trophic interactions between all species comprising a biological community. The first ecologist to acknowledge the scientific significance of food webs was Charles Elton in 1927 (Lawton 1989). He coined the terms "food chain", understood as a chain of animals that feed on one another, ultimately depending on green plants, and "food cycle", as the sum of food chains in a community. The latter is referred to as a food web in more recent literature.

Suites of characteristic features make up the structure of a food web. The first step towards understanding this structure lies in the collection of data. This data can be analysed in an attempt to find regularities that prove valid over a wide range of data collected from different communities. The search for regularities is a point of much controversy among food web ecologists: are the alleged regularities that have been postulated in the past really regularities or merely artifacts of inadequate methods of data analysis? If regularities do exist they can be used to derive models of food webs, which in a last step must be validated. Unfortunately, validation often fails, thus inducing the necessity to retrace the afore taken steps. The focus of this thesis lies on the aspect of data analysis in an attempt to resolve some of the controversy about finding regularities in food web structure.

Conventionally, descriptions of food webs are based on binary matrices (**a** in Fig. 1). That is a square matrix, with species in their function as predators listed column-wise (*j*) and the same species in their function as prey row-wise (*i*). A 1 would designate that the species of column *j* is feeding on the species of row *i*, a 0 if there is no such link between *j* and *i*. As a means of uniformly describing different food webs, qualitative properties have been derived from this matrix. E.g. the ratio of prey to predators (N:P), the proportion of top species (species having no predators, %T), the proportion of intermediate species (species which have prey and are preyed upon, %I), the proportion of basal species (species which only serve as prey), or link density (LD), understood as the average number of links (*L*) per species (*S*) in the web. While approximately 20 properties have been postulated in this fashion, this thesis concentrates to some extent on link density because of its role as a fundamental descriptor of complexity (May 1972).

Since Elton, the interest in food webs has advanced far beyond a mere description of feeding interactions. For one, food webs have played a major role in exploring the relationship between complexity and stability in natural communities (e.g. MacArthur 1955, Elton 1958, Gardner & Ashby 1970, May 1972, 1973, Pimm 1984). To understand the structure and functioning

a

$$\begin{array}{c|cccccc|} & \multicolumn{6}{c}{\text{predators } (j)} \\ & n_1 & n_2 & n_3 & \ldots & n_{S-1} & n_S \\ \hline n_1 & 0 & 0 & 1 & \ldots & 0 & 1 \\ n_2 & 0 & 1 & 0 & \ldots & 1 & 1 \\ n_3 & 0 & 0 & 1 & \ldots & 1 & 1 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ n_{S-1} & 0 & 1 & 0 & \ldots & 1 & 0 \\ n_S & 0 & 0 & 0 & \ldots & 0 & 0 \\ \hline \end{array}$$

b

$$\begin{array}{c|cccccc|} & \multicolumn{6}{c}{\text{predators } (j)} \\ & n_1 & n_2 & n_3 & \ldots & n_{S-1} & n_S \\ \hline n_1 & 0 & 0 & 13 & \ldots & 0 & 54 \\ n_2 & 0 & 2 & 0 & \ldots & 33 & 4 \\ n_3 & 0 & 0 & 1 & \ldots & 16 & 5 \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\ n_{S-1} & 0 & 40 & 0 & \ldots & 31 & 0 \\ n_S & 0 & 0 & 0 & \ldots & 0 & 0 \\ \hline \end{array}$$

Fig. 1 Representation of an arbitrary food web qualitatively (**a**) and quantitatively (**b**). Species (n) are listed column wise in their function as predators ($n_1 \leq j \geq n_s$) and row wise in their function as prey ($n_1 \leq i \geq n_s$). For matrix **a**, a 1 designates a link, a 0 the absence of a link. Matrix **b** includes the biomass flux associated with the non-zero elements of **a** (e.g. in kg * m^{-2} * $year^{-1}$).

---

of these communities, the recognition of regularities in natural food webs became of increasing interest (e.g. Cohen 1978, Pimm 1982, Winemiller 1990). Regularities can only be perceived if a means of comparing web structure across different communities exists. This necessitates the application of universal food web descriptors like the ones mentioned above. The search for general patterns based on such properties or descriptors and their explanation has a long tradition in ecology (e.g. Gallopin 1972, Cohen 1978, Pimm 1982, Briand & Cohen 1984, 1987, Paine 1988, Lawton 1989). By and large, generalizations focus on how food-web structure changes with an increase in the number of species comprising the web. This approach brought forth a number of intriguing hypotheses like a universally constant predator-prey ratio (Evans & Murdoch 1968, Arnold 1972, Cameron 1972, Moran & Southwood 1982, Jeffries & Lawton 1985), or scale-invariance for the proportion of top, intermediate, and basal species, as well as for the proportion of feeding links between any two of these trophic categories (i.e. %TI, %TB, %II, %IB, Briand & Cohen 1984, Cohen & Briand 1984). In this context, scale stands for species richness, or the number of species comprising the web (S).

One of the first analysis of a collection of food webs in terms of link density's behaviour with variable species richness was undertaken by Sugihara et al. (1989) for a compilation of 60 invertebrate-dominated community food webs. They found link density to be independent of the number of species comprising the web. As data became more highly resolved however, this conviction was upset in favour of scale-dependent link density (e.g. Winemiller 1990, Havens 1992, Martinez 1992, Deb 1995). The same controversy exists for a number of other food web properties, predicted as scale-invariant in early analyses but soon found to depend on scale on the basis of more extensive data material (Schoener 1989, Warren 1989, 1990, Winemiller 1989, Winemiller et al. 2001). Moreover, the propagated generalizations were criticized as being premature or artificial as they were derived from food web data not necessarily collected with the intent of being used in among-web comparisons and thus effectively unsuitable (e.g. due to low or variable taxonomic resolution, lumping, idiosyncratic representations, Pimm 1982, Paine 1988, Lawton 1989, Pimm et al. 1991). Cohen for example advocated the use of yield/effort graphs that set the number of observed links in relation to observational (or sampling) effort and thus enable a sensible estimate of how complete a reported food web is (Cohen 1978).

In an attempt to resolve the apparent controversy with respect to the scaling-behaviour of conventionally employed food web descriptors, Goldwasser and Roughgarden (1997) simulated the process of data assemblage. They found qualitative properties to be highly sensitive to variable sampling effort and to demand extensive sampling to reach original values. For the collection of data in the field, high sampling effort translates to a high number of sampling replicates and a high likelihood that the collected data will match the true situation in the studied area. The completeness of an assembled food web is therefore always a function of the extent of sampling exerted in its compilation. Ideally, descriptors employed to compare webs of differing or unknown levels of sampling effort should show little sensitivity to sampling effort (Goldwasser & Roughgarden). Otherwise, the theories derived from this data may be explaining patterns that do not occur in nature (Lawton and Warren 1988). Yet Goldwasser and Roughgarden's results quite impressively demonstrated that conventional qualitative food web properties will not do in this respect, leading them as far as to suggest that such properties may be too sensitive to serve as guides to ecological function (s. also Hall & Raffaelli 1991). Addressing this apprehension, one aim of this work was to find descriptors that prove less sensitive to sampling effort.

On the example of link density, it has been shown that a property's sensitivity to sampling effort can essentially affect its scaling-behavior in the sense that an intrinsically scale-dependent system will exhibit scale-invariance if sampled at low intensity (Bersier et al. 1999). This finding implies that scale-invariant link density may be a product of low sampling effort, while scale-invariance can only be observed when webs are sampled extensively, and thus reconciles the aforementioned opposing results on link density's scaling behaviour.

Evidently some problems are related with the use of qualitative food web descriptors. Considering that they are based on binary information, an approach that does not account for the sometimes vast differences in interaction strength between links, this may not be surprising. The inherent problem with binary data – and probably the culprit of much of the controversy about finding regularities – is that every link is given the same weight, irrespective of its importance: weak links count just as much as strong ones do. To overcome these limitations, several authors have emphasized the necessity for food webs derived from quantitative information on feeding interactions (Pimm & Kitching 1988, Lawton 1989, Winemiller 1990). During the last decade, extensive assemblages of food webs that depict feeding interactions quantitatively became available (e.g. Tavares-Cromar & Williams 1996, deRuiter et al. 1995, 1998, Cattin 2004). In the corresponding matrix (**b** in Fig. 1) the value of any matrix-element is equivalent to the amount of biomass flux from the species in row *i* to the species in column *j* (it tells us to what extent *j* feeds on *i*). To adequately incorporate this information in among-web comparisons with the aim of deducing concurrent trends or in order to explain food-web structure in terms of biomass flux, quantitative food web descriptors are needed. This prompted the conception of quantitative counterparts for conventionally employed food web properties (Bersier et al. 2002). The new descriptors were derived from the diversity index of Shannon and Wiener, thus taking the disequitability between links with respect to the magnitude of biomass flux into account. Applying this index leads to the postulation of new quantitative formulas for the conventionally employed descriptors: an unweighted version where each species is given the same weight and a weighted one, which takes the total amount of in- and outflow per species into account. In the course of this thesis the work of Bersier et al. is repeatedly referred to and is thus presented in Chapter II as a theoretical basis.

It will be of interest to see how quantitative descriptors perform in relation to their qualitative counterparts. Given that the latter's sensitivity to the incompleteness of existing data has been severely criticized, this comparison pertains especially to the properties' sensitivity regarding the effects of variable sampling effort – an aspect which will be considered in detail in Chapter III.

Since the quantitative properties analyzed prove to be more robust against the effects of variable sampling effort as well as more adequately incorporating the information inherent to quantitative food webs, they can be regarded as more reliable for between-web comparisons than their qualitative counterparts. With these quantitative descriptors it is thus possible to move from data analysis one step further to a comparison of webs with the aim of discerning regularities that manifest themselves quantitatively. The search for regularities most often relies on the analysis of a property's behaviour with increasing scale or species richness. Compliant with this practice link density's scaling behavior will be scrutinized qualitatively and quantitatively in Chapter IV on the example of seven discrete collections spanning 5 to 13 webs, based on the environment from which the collections stem and the division into community and partial webs. The results are related to considerations on stability and complexity, an approach derived from the work of Ulanowicz (2002) and May (1972), and bridges the gap between static descriptions of food webs and dynamical analysis.

Chapter V extends the within-collection analysis of link density to a comparison between collections for the 13 other qualitative properties and their quantitative counterparts, which were already considered in respect to sampling effort (Chapter III). The objective is to confirm or refute the results obtained in the foregoing chapter, and to discern features of quantitative food-web structure.

While quantitative properties were proven to be more robust to sampling effort than their qualitative counterparts this may be at the cost of being less sensitive in detecting differences between systems. A final analysis thus explores differences between community webs from aquatic and terrestrial environments (Chapter V). Following Bengtsson (1994) this analysis takes the scale-dependence of most food-web descriptors into account and excludes the effect of scale when comparing food web descriptors between webs.

To conclude, Chapter VI serves as a synthesis of the preceding chapters, highlighting especially the findings on link density's scaling behaviour on the example of a collection of food webs from Lake Neuchâtel.

REFERENCES

Arnold, S.J., 1972. Species densities of predators and their prey. American Naturalist 106: 220-236.

Bengtsson, J., 1994. Confounding variables and independent observations in comparative analyses of food webs. Ecology 75, 1282-1288.

Bersier, L.F., Dixon, P., Sugihara, G., 1999. Scale-invariant or scale-dependent behavior of the link density property in food webs: A matter of sampling effort? American Naturalist 153: 676-682.

Bersier, L.F., Banašek-Richter, C., Cattin, M.F., 2002. Quantitative descriptors of food-web matrices. Ecology 83: 2394-2407.

Briand, F., Cohen, J.E., 1984. Community food webs have scale-invariant structure. Nature 307: 264-267.

——— 1987. Environmental correlates of food chain length. Science 238: 956-960.

Cameron, G.N., 1972. Analysis of insect trophic diversity in two salt marsh communities. Ecology 53: 58-73.

Cohen, J.E., 1978. Food webs and niche space. Princeton University Press, Princeton, New Jersey.

Cohen, J.E., Briand, F., 1984. Trophic links of community food webs. Proceedings of the National Academy of Sciences of the United States of America 81: 4105-4109.

Deb, D., 1995. Scale-dependence of food web structures : Tropical ponds a paradigm. Oikos 72:245-262.

de Ruiter, P.C., Neutel, A.M., Moore, J.C., 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269: 1257-1260.

——— 1998. Biodiversity in soil ecosystems: the role of energy flow and community stability. Applied Soil Ecology 10: 217-228.

Elton, C.S., 1927. Animal ecology. Sidgwick & Jackson, London.

——— 1958. The ecology of invasions by animals and plants. Chapman & Hall, London.

Evans, F.C., Murdoch, W.W., 1968. Taxonomic composition, trophic structure, and seasonal occurrence in a grassland insect community. Journal of Animal Ecology, 37: 259-273.

Gallopin, G.C., 1972. Structural properties of food webs, in: Patten, B.C. (Ed.), Systems Analysis and Simulation in Ecology, Vol. 2. Academic Press, New York, pp. 241-282.

Gardner, M.R., Ashby, W.R., 1970. Connectance of large dynamic (cybernetic) systems: Critical values for stability. Nature 228: 784.

Goldwasser, L., Roughgarden, J., 1997. Sampling effects and the estimation of food-web properties. Ecology 78: 41-54.

Havens, K.E., 1992. Scale and structure in natural food webs. Science 257: 1107-1109.

Jeffries, M.J., Lawton, J.H., 1985. Predator-prey ratios in communities of freshwater invertebrates: the role of enemy free space. Freshwater Biology 15: 105-112.

Lawton, J.H., 1989. Food webs, in: Cherrett, J.M. (Ed.), Ecological concepts. Blackwell Scientific, Oxford, pp. 43-78.

Lawton, J.H., Warren, P.H. 1988. Static and dynamic explanations for patterns in food webs. Trends in Ecology and Evolution 3(9): 242-245.

MacArthur, R.H., 1955. Fluctuations of animal populations, and a measure of community stability. Ecology 36: 533-536.

Martinez, N. D., 1992. Constant connectance in community food webs. American Naturalist 139:1208-1218.

Martinez, N.D., Hawkins, B.A., Dawah, H.A., Feifarek. B.P., 1999. Effects of sampling effort on characterization of food-web structure. Ecology 80: 1044-1055.

May, R.M., 1972. Will a large complex system be stable? Nature 238: 413-414.

——— 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton.

Moran, V.C., Southwood, T.R.E., 1982. The guild composition of arthropod communities in trees. Journal of Animal Ecology 51: 289-306.

Paine, R.T., 1988. Food web: Road maps of interactions or grist for theoretical development? Ecology 69: 1648-1654.

Pimm, S.L., 1982. Food webs. Chapman and Hall, London.

Pimm, S.L., Kitching R.L., 1988. Food web patterns: Trivial flaws or the basis of an active research program? Ecology 69: 1669-1672.

Pimm, S.L., Lawton, J.H., Cohen, J.E., 1991. Food web patterns and their consequences. Nature 350: 669-674.

Schoener, T.W., 1989. Food webs from the small to the large. Ecology 70: 1559-1589.

Tavares-Cromar, A.F., Williams, D.D., 1996. The importance of temporal resolution in food web analysis: Evidence for a detritus-based stream. Ecological Monographs 66: 91-113.

Warren, P. H., 1989. Spatial and temporal variation in the structure of a freshwater food web. Oikos 55:299-311.

——— 1990. Variation in food-web structure: The determinants of connectance. American Naturalist 136, 689-700.

Winemiller, K.O., 1989. Must connectance decrease with species richness. American Naturalist 134: 960-968.

Winemiller, K.O., 1990. Spatial and temporal variation in tropical fish trophic networks. Ecological Monographs 60: 331-367.

Winemiller, K.O., Pianka, E.R., Vitt, L.J., Joern, A., 2001. Food web laws or niche theory? Six independent empirical tests. American Naturalist 158:193-199.

ACKNOWLEDGEMENTS

I am greatly indebted to a number of people for their enormous support. Without them this thesis would not have been possible.

I wish to thank my "boss" Dr. Louis-Félix Bersier who initiated this work and who guided and advised me through all aspects of food web ecology during the last 5 years. His brilliant mind and patient counseling were essential in accomplishing this thesis. I am extremely grateful for the opportunity to work with him and to profit from his knowledge.

Merci beaucoup to my colleague Marie-France Cattin Blandenier for putting up with my bad French, for the collaboration in the field, the lab, and the office, and for assembling the "Chabrey" food webs on which many of my analyses are based.

Prof. Claude Mermod was kind enough to provide the possibility to work in his lab as the official "directeur de thèse". I regret that there were not more connections to his research on vertebrate eco-ethology and thank him for serving as reviewer and jury member nevertheless.

Thank you very much to Dr. Richard Baltensperger and Prof. Jean-Pierre Gabriel from the University of Fribourg for their mathematical expertise. The latter also reviewed this work and was one of the jury members.

As was Prof. Martine Rahier, dean of the science faculty at the University of Neuchâtel – thank you very much for accepting this task.

Prof. Robert Ulanowicz from the University of Maryland was external reader of my thesis. I wish to thank him especially for his generous evaluation, which was a great encouragement to me.

A number of people helped with the work in the field, making life a great deal easier for Louis-Félix, Marie-France, and myself. Merci beaucoup and grazie mille to Gilles Blandenier, Yves-Olivier Gasser, Laurent Juillerat, Sergio Rasman, and

Antoine Schnegg. Many thanks also to Grégoire Desmeules, Yves Merz, and Jean-Pierre Tutrone for helping assemble the "Chabrey" food webs.

Un grand merci to Natacha Schneiter and Brigitte Cattin for handling all our administrative concerns with supreme ease and friendliness.

For accommodating me with astonishing hospitality during several trips to Neuchâtel, many thanks to Dr. Bernd Eilrich, Dr. Attila Kovacs, Adrienne, Kathrin Meyer, and to the family Ernst.

Finally, there is my family, who I wish to thank for their unconditional support and their persistent interest in my work.

In particular, Dorothee (Dota) Richter was an extremely great help during the last crucial days before my "défense". Muchas gracias!

Many thanks also to my mother-in-law for her great sympathy and for acknowledging this achievement the way she did.

I am extremely grateful to my parents for giving me the opportunity to study Biology, for their tremendous support in every possible situation, and for their unreserved and irrefutable belief in me.

Last, but far from least, I thank Karl, who patiently stood through all of this with me, for his faithful encouragement, his admiration for the mathematical formulas in the text, and all the rest ..., and I thank Amelie for being her marvelous, delightful self.

This work was supported by the Swiss NSF grant 31-52566.97.

* * *

I dedicate my Ph.D. thesis to my grandmother, Anna Marie Richter, who would have been very proud to know that it is finally completed.

II QUANTITATIVE DESCRIPTORS OF FOOD WEB MATRICES[1]

Introduction

A community food web describes the feeding relationships among the taxa comprising a community. Analyses of initial collections of community food webs have identified a suite of intriguing regularities; some web properties (among others, the fractions of top, intermediate, and basal taxa, the number of links per taxa, rigid circuits) were found to be scale invariant : they stay roughly constant across a variety of webs spanning a wide range in the number of taxa they contain (e.g. Cohen 1977, 1989, Pimm 1982, Briand and Cohen 1984, Sugihara, Schoenly and Trombla 1989, Lawton 1989, Pimm, Lawton and Cohen 1991, Havens 1992). These findings fostered the formulation of models explaining the structure of these biological networks (Sugihara 1984, Cohen and Newman 1985). However, the quality of the data set, which had been gathered from the literature, was rightfully criticized (e.g., May 1983, Paine 1988). Subsequently compiled food webs, aimed specifically at documenting the feeding relationships in communities, did not uphold the initially found regularities (Warren 1989, Winemiller 1990, Polis 1991, Martinez 1991, Carney, Havens and Bersier 1997, Deb 1995), and new hypotheses about the structure of communities have been proposed (Martinez 1992, Polis and Strong 1996, Solow and Beet 1998, Williams and Martinez 2000). In all these studies, food webs have been analyzed with qualitative descriptors, and it has been shown that most of these indices are extremely sensitive to different levels of sampling effort (Goldwasser and Roughgarden 1997, Martinez et al. 1999). In the same vein, Bersier, Dixon and Sugihara (1999) showed that the scaling behavior of the link density property was affected by varying levels of sampling effort : using two models and empirical data, they found that low sampling effort tends to produce the appearance of scale invariance in intrinsically scale dependent systems.

These sampling effects highlight the following problem inherent to qualitative food webs. The distribution of link importance in highly resolved food webs is likely to be strongly uneven (see e.g., Goldwasser and Roughgarden 1993). In qualitative food webs, the same weight is given to all links, which distorts the true picture of the structure of the food webs (Kenny and Loehle 1991). This points to the need for quantitative data on link importance, which allows a more sensible approach to food web structure (e.g., May 1983, Kenny and Loehle 1991, Pimm et al. 1991, Cohen et al. 1993, Bersier et al. 1999). To make use of such data, we must think of alternative ways of defining food web properties that take the disequitability in the distribution of link importance into account. Quantitative descriptors have already been proposed, but

---

[1] Chapter published: Bersier L.-F., Banašek-Richter C. & Cattin M.-F. 2002. *Ecology* **83**: 2394-2407

generally with aims that differ from those of classical food web properties. For example, ascendancy (Ulanowicz 1986) and mutual information (Hirata 1995) are used as macro-descriptors of complex systems; they are typically applied to large ecosystems, whose compartments are highly aggregated, and aim at expressing the phenomenology of growth and development of these systems (Ulanowicz 1997).

In this paper, we propose a suite of descriptors that can be applied to quantitative food webs. We chose to derive our descriptors from information theory, and tried to propose indices having a similar meaning as those customarily used to describe qualitative food webs. The computation of each property is exemplified by the use of a published quantitative food web, the Chesapeake Bay mesohaline ecosystem (Baird and Ulanowicz 1989).

The food web matrix

A qualitative food web composed of s taxa, can be represented by an s-by-s predation matrix $\mathbf{a} = [a_{ij}]$, with

$$a_{ij} = \begin{cases} 1 & \text{if taxon } j \text{ preys on taxon } i \\ 0 & \text{otherwise} \end{cases} \tag{1}$$

and $a_{i\cdot}$ the sum of row i, $a_{\cdot j}$ the sum of column j, and $a_{\cdot\cdot}$ the sum of $\mathbf{a}$. This matrix can be represented graphically as a connected directed graph whose vertices are the taxa, and the edges the trophic interactions (Fig. 1). In a quantitative food web, it is necessary to assign a unit to a_{ij}. The quantitative descriptors presented here are suited for quantitative measures whose units are comparable row- and column-wise, for example for flow of carbon (e.g., milligram of carbon per day and square meter). In the following, we will use the general term “flow of biomass” when referring to these quantitative measures. To avoid confusion, we will call such a matrix $\mathbf{b}$, with elements b_{ij} :

$$b_{ij} = \quad \text{biomass passing from taxon } i \text{ to taxon } j \text{ per unit surface area and time.} \tag{2}$$

The Chesapeake Bay ecosystem (Baird and Ulanowicz 1989) depicted in the Appendix and Figure 1 is an example of a quantitative food web. This data set was recently included in an analysis by Williams and Martinez (2000) as one of the largest and highest-quality empirical food webs. Still, however, lower taxa are highly aggregated.

Qualitative descriptors

Food web matrices are complex objects, and descriptors have been devised to extract ecologically meaningful information from these entities. The qualitative descriptors for which we propose quantitative counterparts can be classified into different groups :

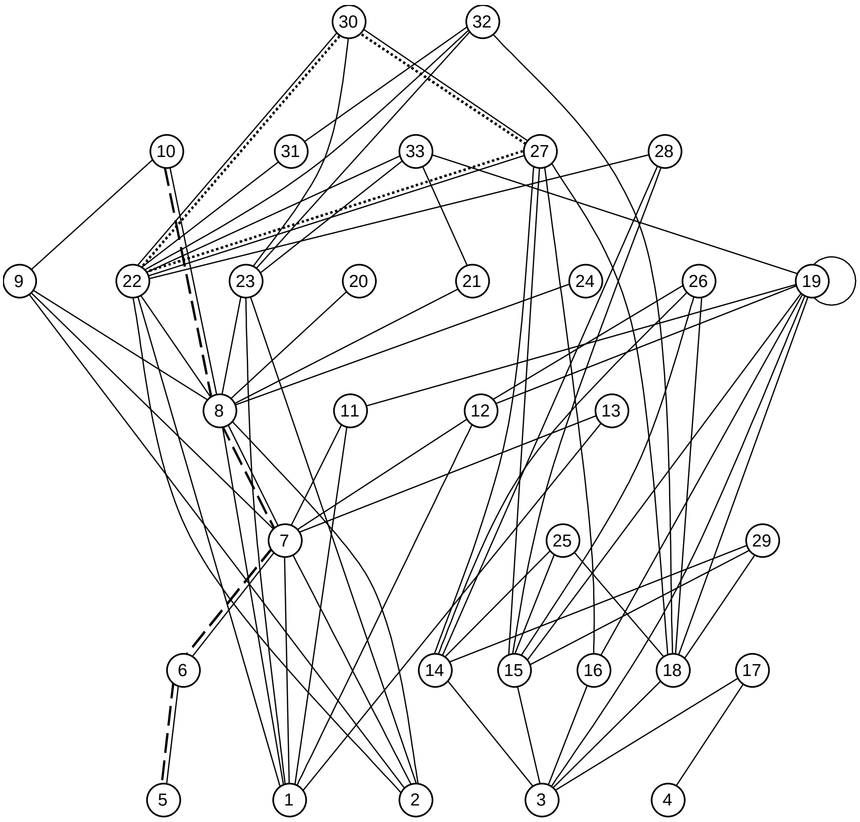


Figure 1. Connected directed graph representing the trophic interactions among the 33 major taxa of the Chesapeake mesohaline ecosystem (Baird and Ulanowicz 1989). Data and list of taxa are in the Appendix. Taxa are arranged according to their trophic level (consumers are always above their prey). Dashed line : example of a maximal food chain; dotted line : example of a closed omnivorous link.

Species properties – In a food web, a taxon (k) is top if it has prey but no consumers, intermediate if it has prey and consumers, and basal if it only has consumers. Four properties have been built on account of these categories : the ratio of prey to consumers ($N:P$), the proportion of top ($\%T$), of intermediate ($\%I$), and of basal species ($\%B$). Note that these are not independent measures as $\%T + \%I + \%B = 1$, and $N:P = (\%B + \%I) / (\%I + \%T)$. The ratio of consumers to prey has been found to cluster about 1 in collections of food webs, which means that, on average, taxa have the same number of prey as of consumers. This pattern has been criticized as a mathematical inevitability in large webs (Closs et al. 1995), which all have a large proportion of intermediate taxa (Martinez and Lawton 1995).

Link properties – This category includes the link density (LD) and the various measures of connectance (see Warren 1994 for a list of definitions), which are all based on the total number of trophic links (l) and on the number of taxa in food web (s). They play a key role in community ecology because they lay at the heart of many theories on community stability (May 1974, Pimm 1984) and structure (Martinez 1992, Solow and Beet 1998). The link density is measured simply as l/s; a widely used measure of connectance is l/s^2, called directed connectance (C), which corresponds to the number of actual links over the number of possible links, including cannibalistic loops (Martinez 1992). The proportions of links between the three categories of taxa also fall in this category, i.e., between top and intermediate ($\%TI$), top and basal ($\%TB$), intermediate and intermediate ($\%II$), and intermediate and basal taxa ($\%IB$). Again, these four proportions are not independent as their sum equals 1.

Chain properties – A food chain is a distinct path within the food web matrix from any taxon down to a basal taxon. A chain linking a top and a basal taxon is called a maximal food chain (Fig. 1). Several measures using food chains capture the complexity of the food web : the number of maximal food chains (n_f), the mean (M_{cl}), median (MD_{cl}), standard deviation (SD_{cl}), and maximum (MAX_{cl}) of the lengths of maximal food chains. However, the presence of loops (e.g., A eats B and B eats A) can render the computation of properties based on maximal chain length problematic, because it is possible to have no top taxon. Therefore an approach that avoids this difficulty is to calculate chain properties including all food chains, rather than just maximal chains (e.g., Williams and Martinez 2000).

Omnivory properties – A taxon is omnivorous if it consumes prey belonging to different trophic levels. There are several ways of defining the trophic level of a taxon (Yodzis 1989); the characterization we adopt here is one plus the length of the longest chain from the focal taxon to a basal taxon. The degree of omnivory can be measured simply as the proportion of taxa that consume prey from more than one trophic level ($\%O$). At least two other measures of omnivory have been proposed in the literature. The first one is the number of closed omnivorous links divided by the number of top taxa (Sprules and Bowerman 1988, Hall and Raffaelli 1991). A closed omnivorous link is a loop starting from the consumer to a prey more than one trophic level away, and back to the consumer through at least one other prey located at an intermediate trophic level (see Fig. 1). The second one is the mean of the standard deviations in chain lengths over all taxa (Goldwasser and Roughgarden 1993).

Consumer-prey asymmetries – The vulnerability (V) and generality (G) properties were introduced by Schoener (1989) as the mean number of consumers per prey, and the mean number of prey per consumer, respectively. They can be computed easily as $l/(n_B+n_I)$, and $l/(n_T+n_I)$, respectively, with n_T the number of top, n_I the number of intermediate, and n_B the number of basal taxa. Williams and Martinez (2000) introduced a measure of the variability for V and G, the standard deviation of normalized generality (sd_G), and of normalized vulnerability (sd_V). For taxon k, normalized G_k and V_k are :

$$G_k = \frac{1}{l/s} \sum_{i=1}^{s} a_{ik} \qquad V_k = \frac{1}{l/s} \sum_{j=1}^{s} a_{kj} \tag{3-4}$$

which forces mean G_k and V_k to equal 1, and allows comparisons across webs of different sizes.

Several other properties, from simple to elaborate in computations, have been proposed, e.g., the proportion of intermediate links by consumers only (Goldwasser and Roughgarden

1997), the mean maximum trophic similarity of each taxon in the food web (Williams and Martinez 2000), the lumpability of a food web (Solow and Beet 1998), as well as topological properties of graphical representations of food webs, i.e., intervality (Cohen 1978) and the rigid circuit property for niche overlap graphs, and the presence of topological holes for resource graphs (Sugihara 1982, 1984). Since these descriptors are not widely used, they will not be considered here.

Quantitative descriptors

The catalyst for the formulation of the quantitative descriptors presented here is the work of Ulanowicz and Wolff (1991) on effective connectance. Like these authors, we use information theoretical indices, particularly the Shannon (Shannon 1948) measure of entropy (or uncertainty), H. The reader can refer to Ulanowicz (1997) for a didactical introduction to the concept, or to Ulanowicz (1986) for a more technical treatment. For a given number x of events, H reaches its maximum when all events occur in equal proportion ($H = \log x$); the minimum is a function of the number of cases in each event (Austin 1999). Measured in logarithms of base 2, the unit of H is bit. We will base our indices on what we will call the “reciprocal” of H, 2^H, which can be thought of as the number of events occurring in equal proportion that would produce the same value of H. This reciprocal has the desirable property of recovering the original units (the number of events), however it is now a real number. In ecological literature, an event is typically a species and a case an individual or some measure of abundance; in our context, an event usually refers to a taxon and a case to the flow of biomass to or from a taxon. We calculated quantitative properties using C++, checked the results in spreadsheets, and developed Excel functions for most properties.

Species properties – Taxa can be classified as top, intermediate and basal with quantitative information on trophic links in the same way as with qualitative data. We suggest a positional index d, which uses quantitative information about the flux of biomass to assess to what degree a taxon k is top, intermediate, or basal. For each taxon, one can measure the diversity of the biomass coming from its prey (H_N, the diversity of inflows) and of that going to its consumers (H_P, the diversity of outflows); for taxon k,

$$H_{N\,k} = -\sum_{i=1}^{s} \frac{b_{ik}}{b_{\cdot k}} \cdot \log_2 \frac{b_{ik}}{b_{\cdot k}} \qquad\qquad H_{P\,k} = -\sum_{j=1}^{s} \frac{b_{kj}}{b_{k\cdot}} \cdot \log_2 \frac{b_{kj}}{b_{k\cdot}} \qquad (5\text{-}6)$$

Column sum $b_{\cdot k}$ and row sum $b_{k\cdot}$ represent the total amount of biomass emanating from and going to taxon k, respectively. The reciprocals of $H_{N,k}$ and $H_{P,k}$ are :

$$n_{N\,k} = \begin{cases} 2^{H_{N,k}} & \\ 0 & \text{if } b_{\cdot k} = 0 \end{cases} \qquad\qquad n_{P\,k} = \begin{cases} 2^{H_{P,k}} & \\ 0 & \text{if } b_{k\cdot} = 0 \end{cases} . \qquad (7\text{-}8)$$

These equivalent numbers of prey (n_N) and consumers (n_P) are used to compute a simple positional index d'_k, which takes the disequitability in link magnitude of inflows to and outflows from taxon k into account :

$$d'_k = \frac{n_{N,k}}{n_{N,k} + n_{P,k}}. \qquad (9)$$

However, this index gives the same weight to both sets of prey and consumers, disregarding the magnitude of incoming ($b_{\cdot k}$) and outgoing flows ($b_{k\cdot}$). To better capture the functional status of a taxon in a food web, the total amount of biomass coming from the prey and going to the consumers is taken into account. Consequently, the proposed index for taxon k is :

$$d_k = \frac{b_{\cdot k} \cdot n_{N,k}}{b_{\cdot k} \cdot n_{N,k} + b_{k\cdot} \cdot n_{P,k}} \qquad (10)$$

Note that we use the apostrophe for the unweighted version of indices (here d'_k), which are those giving the same weight to each taxon irrespective of their inflows and outflows. With both indices, a taxon is top if $d_k = 1$, basal if $d_k = 0$, and intermediate otherwise. Computing the proportions of basal, intermediate, and top taxa is similar to finding the proportions of d_k values equal to 0, larger than 0 and smaller than 1, and equal to 1, respectively. However, we feel that a more sensible way of describing the positional status of the taxa in the food web would be to widen the interval of the top taxa from [1] to, e.g., [0.99,1], or more informatively to compute the frequency distribution of d_k- and d'_k -values among all taxa.

The ratio of prey to consumers (*N:P*) can be expressed quantitatively by using the equivalent numbers of prey (n_N) and consumers (n_P). The total number of consumers is the count of non zero n_N. The diversities are computed over the n_N-values, and their reciprocals correspond to the number of consumers that would populate the food web if each consumer had the same number of prey (strictly speaking, of prey equivalents n_N). The same approach is applied to the n_P-values to obtain the adjusted total number of prey. Taking the biomass of the fluxes into account requires a weighting of $n_{N,k}$ by $b_{\cdot k}$, and of $n_{P,k}$ by $b_{k\cdot}$. The two versions of the *N:P* index are consequently expressed as :

$$N{:}P'_q = \frac{2^{-\sum_{k=1}^{s} \frac{n_{P,k}}{\sum n_{P,k}} \cdot \log_2 \frac{n_{P,k}}{\sum n_{P,k}}}}{2^{-\sum_{k=1}^{s} \frac{n_{N,k}}{\sum n_{N,k}} \cdot \log_2 \frac{n_{N,k}}{\sum n_{N,k}}}} \qquad N{:}P_q = \frac{2^{-\sum_{k=1}^{s} \frac{b_{k\cdot} \cdot n_{P,k}}{\sum b_{k\cdot} \cdot n_{P,k}} \cdot \log_2 \frac{b_{k\cdot} \cdot n_{P,k}}{\sum b_{k\cdot} \cdot n_{P,k}}}}{2^{-\sum_{k=1}^{s} \frac{b_{\cdot k} \cdot n_{N,k}}{\sum b_{\cdot k} \cdot n_{N,k}} \cdot \log_2 \frac{b_{\cdot k} \cdot n_{N,k}}{\sum b_{\cdot k} \cdot n_{N,k}}}}. \qquad (11\text{-}12)$$

Link properties – First, one should note that the qualitative link density (*LD*) can be computed as the mean number of prey taxa over all species, or as the mean number of consumer taxa. We use both equivalences to devise an adequate way of expressing the link density in a quantitative manner, by computing the averages of the equivalent numbers of prey

$n_{N,k}$ and of consumers $n_{P,k}$. The unweighted index LD'_q, which gives the same weight to all taxa, is then :

$$LD'_q = \frac{1}{2}\left(\sum_{k=1}^{s}\frac{1}{s}\cdot n_{P,k} + \sum_{k=1}^{s}\frac{1}{s}\cdot n_{N,k}\right) = \frac{1}{2\cdot s}\left(\sum_{k=1}^{s} n_{P,k} + \sum_{k=1}^{s} n_{N,k}\right). \tag{13}$$

The weighted index *LD'* requires a weighting of the species by their relative outflows and inflows :

$$LD_q = \frac{1}{2}\left(\sum_{k=1}^{s}\frac{b_{k\cdot}}{b_{\cdot\cdot}}\cdot n_{P,k} + \sum_{k=1}^{s}\frac{b_{\cdot k}}{b_{\cdot\cdot}}\cdot n_{N,k}\right). \tag{14}$$

Ulanowicz and Wolff (1991) have defined the effective connectance per node *m*, which was proposed as a good candidate for a quantitative substitute of the link density property (Bersier et al. 1999). The effective connectance per node is the reciprocal of the average diversity over inputs and outputs, which can be written as :

$$m = 2^{\Phi/2} \text{ , with} \tag{15}$$

$$\Phi = \sum_{k=1}^{s}\frac{b_{k\cdot}}{b_{\cdot\cdot}}\cdot H_{P,k} + \sum_{k=1}^{s}\frac{b_{\cdot k}}{b_{\cdot\cdot}}\cdot H_{N,k} \quad . \tag{16}$$

The index Φ is the sum of the diversity of outflows weighted by the total outflows, and of the diversity of inflows weighted by the total inflows. Φ can be thought of as the average amount of choice in trophic pathways (Ulanowicz and Wolff 1991). We can expand the equation of LD_q in the following form to see that the difference to *m* resides solely in the weighting, which applies in our case not to the inflow and outflow diversities, but directly to the taxa's equivalent numbers of prey and consumers :

$$LD_q = \frac{1}{2}\left(\sum_{k=1}^{s}\frac{b_{k\cdot}}{b_{\cdot\cdot}}\cdot 2^{H_{P,k}} + \sum_{k=1}^{s}\frac{b_{\cdot k}}{b_{\cdot\cdot}}\cdot 2^{H_{N,k}}\right).$$

Ulanowicz and Wolff also defined the topological connectance per node m^*, which is the value that *m* would take on if all nonzero b_{ij} in the food web were assumed equal in magnitude; *m* is always smaller or equal to m^*. As with the topological connectance per node, one can define the "topological" equivalents LD_q^* and $LD_q'^*$, for which all links are given the same magnitude. We find that $LD_q'^*$ has the desirable feature of being equal to the qualitative link density *LD*. For a qualitative food web, directed connectance (*C*) can be computed as *LD*/*s*. With quantitative data, one can define connectance C_q in a similar way as LD_q/s, and C'_q as LD'_q/s.

Qualitative descriptors customarily used to categorize links are the proportions of links between top, intermediate and basal taxa, namely *%TI*, *%TB*, *%II*, and *%IB*. Above, we proposed two "positional" indices (Eqs. 9 and 10) to render the functional status of the taxa in a community, and suggested the possibility of more categories being defined from these indices than just basal, intermediate and top. Whatever the convention adopted (more categories and/or categories defined with different limits), one can compute a quantitative equivalent of the proportions of links between two categories of taxa, A (the prey) and B (the consumers), in the following way :

$$\%AB_q = \frac{\Phi_{AB}}{\Phi} \text{ , with} \tag{17}$$

$$\Phi_{AB} = \sum_{k=1}^{\alpha} \frac{b_{i_k \cdot}}{b_{\cdot\cdot}} \cdot \left(-\sum_{n=1}^{\beta} \frac{b_{i_k j_n}}{b_{i_k \cdot}} \cdot \log_2 \frac{b_{i_k j_n}}{b_{i_k \cdot}} \right) + \sum_{k=1}^{\beta} \frac{b_{\cdot j_k}}{b_{\cdot\cdot}} \cdot \left(-\sum_{n=1}^{\alpha} \frac{b_{i_n j_k}}{b_{\cdot j_k}} \cdot \log_2 \frac{b_{i_n j_k}}{b_{\cdot j_k}} \right). \tag{18}$$

Φ, the overall average amount of choice in the trophic pathways, is measured as in equation 16; Φ_{AB} is similar to Φ, but computed over the taxa belonging to categories A and B only (group A includes taxa $i_1, i_2, \ldots, i_\alpha$, and group B taxa $j_1, j_2, \ldots, j_\beta$), and with sums of rows $b_{i_k\cdot}$ and of columns $b_{\cdot j_k}$ measured over all taxa. The value of $\%AB_q$ is the contribution of the links between taxa of groups A and B to Φ; with the s taxa of a food web distributed in two groups A and B, we have $\Phi_{AB} + \Phi_{BA} + \Phi_{AA} + \Phi_{BB} = \Phi$. An unweighted version of the proportion of links between A and B ($\%AB'_q$) can be measured simply by replacing the weightings $b_{i_k\cdot}/b_{\cdot\cdot}$, $b_{\cdot j_k}/b_{\cdot\cdot}$, $b_{k\cdot}/b_{\cdot\cdot}$, and $b_{\cdot k}/b_{\cdot\cdot}$ in equations 16 and 18 by $1/s$.

Chain properties – The length (cl_c) of food chain c can be adjusted for the importance of each trophic link comprised in the chain in the following way :

$$cl'_{q,c} = 2^{-\sum_{l=1}^{n_l} \frac{b_{c,l}}{\sum b_{c,l}} \cdot \log_2 \frac{b_{c,l}}{\sum b_{c,l}}} \text{ ,} \tag{19}$$

with n_l the number of links forming chain c, and $b_{c,l}$ the biomass flow of the lth link of chain c. The corrected length $cl'_{q,c}$ reaches the original value cl_c only if all fluxes of the chain are equal in magnitude. Equation 19 gives the same importance to each maximal food chain, disregarding the total amount of biomass flowing through it. We suggest the following approach to take the magnitude of flows of a chain into account for the computation of the weighted quantitative chain length ($cl_{q,c}$); for each maximal food chain c, we compute the average biomass per effective link :

$$\bar{b}_c = \frac{\sum b_{c,l}}{cl'_{q,c}}.$$

The weighted quantitative chain length $cl_{q,c}$ is then :

$$cl_{q,c} = \left(\frac{\bar{b}_c \cdot n_f}{\sum \bar{b}_c} \right) \cdot cl'_{q,c} \ , \tag{20}$$

with n_f the number of maximal food chains. As a measure of the importance of a maximal food chain, we use the average biomass $\bar{b}_c$ per effective link, and not the total amount of flows $\Sigma b_{c,l}$, because long chains would tend to have large values simply as they are summed over more $b_{c,l}$ than short chains. The weighted and unweighted quantitative equivalents of the mean, median, standard deviation, and maximum of the lengths of food chains are computed for the $cl_{q,k}$ and $cl'_{q,k}$ values, respectively.

The formulation of a quantitative counterpart for the number of food chains is problematic because there is no unequivocal way of defining the importance of a chain. One could measure the reciprocal of the Shannon index for the $cl'_{q,k}$ or $cl_{q,k}$ values, which would equate to the equivalent number of maximal food chains assuming they all have a similar length; another possibility is to assign a "transfer efficiency" value e_c to each maximal food chain, e_c being measured as :

$$e_c = \prod_{l=1}^{n_l} b_{c,l} \ . \tag{21}$$

The equivalent number of maximal food chains is then the reciprocal of the Shannon index measured over the e_c values. Other definitions built in a similar way are conceivable, for example using $\Sigma b_{c,l}$. We see however no legitimacy for preferring one of these measures, and feel that the number of maximal food chains is by essence a qualitative property that has no adequate quantitative equivalent.

Omnivory properties – Among the many ways of defining an index of omnivory that considers the quantitative nature of trophic links, we chose first to define an individual index of omnivory o_k, applied to each taxon k, which is based on the distribution of trophic levels among the prey of k. The trophic level of taxon k is t_k, and n_t is the number of prey taxa located at trophic level t; the index reads :

$$o'_k = -1 + 2^{-\sum_{t=1}^{t_k} \frac{n_t}{\Sigma n_t} \cdot \log_2 \frac{n_t}{\Sigma n_t}} \ . \tag{22}$$

Note that o'_k does not take the importance of the trophic links into account, and can be applied to qualitative data. A weighted version o_k can take on the following form :

$$o_k = -1 + 2^{-\sum_{t=1}^{t_k} \frac{b_t}{\Sigma b_t} \cdot \log_2 \frac{b_t}{\Sigma b_t}} \ , \tag{23}$$

with b_t the total amount of biomass passing from trophic level t to taxon k. This index equals 0 if taxon k is basal or if it consumes prey belonging to the same trophic level; it equals 1 if taxon k

consumes prey located at two different levels in equal proportion, and has an upper bound of t_k-1. An adequate index of omnivory for the whole food web, O_q, is the average of the o_k values over all taxa; the unweighted version O'_q is the average of all o'_k values. Note that, unlike Goldwasser and Roughgarden's (1993) index of omnivory, we do not build our indices on the variability of chain lengths. In such a case, a consumer taxon 'inherits' the variability of its prey, which, for example, renders omnivorous a monophagous taxon eating an omnivore.

It may seem desirable to base the individual quantitative omnivory properties on a quantitative definition of trophic level. Possibilities may be found by weighting the links by their proportional biomass (Yodzis 1989), by computing the “trophic position” of the taxa (Levine 1980), or by the use of the cl_q values defined above. However, these will yield non-integer trophic levels, which in turn will raise a problem with the summation in equations 22 and 23. Since we see no satisfactory answer to that difficulty, we base our indices of omnivory on the adequate and customarily used qualitative definition (i.e., one plus the length of the longest chain from the focal taxon to a basal taxon).

Consumer-prey asymmetries – Generality G is the average number of prey taxa per consumer. A quantitative unweighted version G'_q can be defined simply as the average number of effective prey taxa, n_N, over all consumer taxa, or for the weighted version G_q as a weighted average :

$$G'_q = \frac{1}{n_T + n_I} \sum_{k=1}^{s} n_{N,k} \qquad G_q = \sum_{k=1}^{s} \frac{b_{\cdot k}}{b_{\cdot\cdot}} \cdot n_{N,k} \quad , \qquad (24\text{-}25)$$

with n_T and n_I the number of top and intermediate taxa, respectively. Quantitative versions of the vulnerability V follow accordingly as :

$$V'_q = \frac{1}{n_I + n_B} \sum_{k=1}^{s} n_{P,k} \qquad V_q = \sum_{k=1}^{s} \frac{b_{k\cdot}}{b_{\cdot\cdot}} \cdot n_{P,k} \quad , \qquad (26\text{-}27)$$

with n_B the number of basal taxa. Quantitative versions of the standard deviation of normalized generality, and of normalized vulnerability require a standardization of the equivalent numbers of prey n_N, and of consumers n_P, respectively (Martinez and Williams 2000). This is achieved in the following way :

$$g'_k = \frac{s}{\sum_{k=1}^{s} n_{N,k}} \cdot n_{N,k} \qquad g_k = \frac{s}{\sum_{k=1}^{s} b_{\cdot k} \cdot n_{N,k}} \cdot b_{\cdot k} \cdot n_{N,k} \quad , \qquad (28\text{-}29)$$

with g'_k the unweighted, and g_k the weighted standardized generality of taxon k. The standard deviations sd_{Gq} and sd_{Vq} are then computed with these standardized values. The unweighted and weighted standardized vulnerability for taxon k (v'_k and v_k) follow accordingly. Note that Levine (1980) has defined indices of trophic specialization, computed for each taxon, which are especially interesting if loops are present. They are based on the variance of weighted path lengths for a taxon, or on the variance of the trophic positions of the prey of a taxon.

An example application

The results of applying the various food web properties defined above to the Chesapeake Bay ecosystem (Appendix) are given in Table 1 for the taxon specific indices, and in Table 2 for the food web descriptors. The positional indices d'_k and d_k (Table 1) indicate to what extent a taxon is basal (value of 0) or top (value of 1). We observe an important difference between the unweighted (d'_k, where the same weight is given to each taxon) and the weighted indices (d_k, where the total amount of flows to and from a taxon are taken into account). This reflects the fact that inflows to a taxon are generally much larger than the outflows, which is consistent with trophodynamics (Lindeman 1942, Odum 1971). However, that is not a mandatory feature, especially in small and open systems where allochthonous inputs are important (Polis and Hurd 1996). These differences in the distribution of d values is reflected in the unequal percentages of top and intermediate taxa when computed using the d_k or d'_k values, i.e., $\%T'_q \neq \%T_q$, and $\%I'_q \neq \%I_q$ (Table 2). Using 0.99 as the lower limit for top taxa, we find that three taxa (19, blue crab; 21, alewife and blue herring; 27, spot) increase the proportion of top taxa from 0.36 for the unweighted to 0.45 for the weighted version. The taxon 14 (other polychaetes) witnesses the highest jump between unweighted and weighted index. Polychaetes prey on a single taxon (3, sediment bacteria) and are consumed by five fish species; however, the inflows outweigh the outflows to such an extent that d rises close to the 0.99 limit.

The qualitative ratio of prey to consumers (N:P) equals 0.75, meaning that there is an average of four consumer taxa for three prey taxa. This may be an intuitively strange result, which can however be explained for the present food web by the difference in taxonomic resolution between invertebrates on the one hand, and fishes on the other. While the former, which make up the bulk of the prey taxa, are often taxonomically highly aggregate, the later dominate in their role as consumers and are often resolved at the species level. Due to a slightly stronger disequitability in the distribution of the equivalent number of consumers, the unweighted quantitative index $N{:}P'_q$ yields 0.71. The weighted version $N{:}P_q$ is 0.32, which reveals a much higher disequitability in the distribution of the equivalent numbers of consumers once multiplied by the outflows, i.e., the distribution of $b_{.k} \cdot n_{N,k}$ is much more even than that of $b_{k.} \cdot n_{P,k}$, which increases the denominator of Eq. 12. A closer inspection of the original data set (Appendix) shows that this is mainly due to the sediment bacteria, which are, by their huge biomass and large number of consumers, the dominant prey taxon in the system.

The qualitative link density LD for the Chesapeake Bay ecosystem is 2.21, meaning that each taxon has on average 2.21 prey and 2.21 consumers. This value falls to 1.37 when computed as the average of the effective numbers of prey and consumers, LD'_q. It can be shown that LD'_q is always smaller or equal to LD, and this decrease reflects the degree of

Table 1. Taxon specific qualitative and quantitative descriptors for the Chesapeake Bay mesohaline ecosystem (see Appendix).

	qualitative		marginal sums		quantitative indices									
taxon	#	#	sum of inflows	sum of outflows	effective # pred.	prey	positional index		index of omnivory		standardized generality		standardized vulnerability	
k	prey	pred.	$b_{k.}$	$b_{.k}$	$n_{N,k}$	$n_{P,k}$	d'_k	d_k	o'_k	o_k	g'_k	g_k	v'_k	v_k
1	0	7	0	80051	0	3.19	0	0	0	0	0	0	2.62	5.47
2	0	8	0	2977	0	3.21	0	0	0	0	0	0	2.64	0.21
3	0	6	0	294955	0	3.63	0	0	0	0	0	0	2.99	22.96
4	0	1	0	18086	0	1	0	0	0	0	0	0	0.82	0.39
5	0	1	0	88721	0	1	0	0	0	0	0	0	0.82	1.90
6	1	1	88721	31638	1	1	0.5	0.74	0	0	0.65	3.90	0.82	0.68
7	3	5	64224	11742	2.13	2.42	0.47	0.83	0.89	1.00	1.39	6.00	2.00	0.61
8	3	7	46389	9855	1.81	2.48	0.42	0.77	0.89	0.56	1.19	3.69	2.04	0.52
9	3	1	10447	552	2.01	1	0.67	0.97	2	1.01	1.31	0.92	0.82	0.01
10	2	0	1711	0	1.88	0	1	1	1	0.88	1.23	0.14	0	0
11	3	1	4594	538	1.41	1	0.58	0.92	0.89	0.27	0.92	0.28	0.82	0.01
12	3	2	2488	224	1.41	1.18	0.54	0.93	0.89	0.26	0.92	0.15	0.97	0.01
13	3	0	4830	0	1.41	0	1	1	0.89	0.26	0.92	0.30	0	0
14	1	5	160831	609	1	3.41	0.23	0.99	0	0	0.65	7.06	2.80	0.04
15	1	6	25062	547	1	2.94	0.25	0.94	0	0	0.65	1.10	2.42	0.03
16	1	2	57335	4593	1	1.07	0.48	0.92	0	0	0.65	2.52	0.88	0.11
17	2	0	54048	0	1.89	0	1	1	0	0	1.24	4.49	0	0
18	1	6	14075	1027	1	1.31	0.43	0.91	0	0	0.65	0.62	1.08	0.03
19	7	2	8593	295	4.12	1.05	0.80	0.99	2.59	1.48	2.69	1.55	0.86	0.01
20	1	0	4.9	0	1	0	1	1	0	0	0.65	<0.01	0	0
21	1	1	26	0.2	1	1	0.5	0.99	0	0	0.65	<0.01	0.82	<0.01
22	3	6	1823	153	1.59	3.58	0.31	0.84	0.89	0.55	1.04	0.13	2.94	0.01
23	3	3	273	21	1.42	2.64	0.35	0.87	0.89	0.36	0.93	0.02	2.17	<0.01
24	1	0	5	0	1	0	1	1	0	0	0.65	<0.01	0	0
25	3	0	10	0	1.93	0	1	1	0	0	1.26	<0.01	0	0
26	4	0	96	0	2.95	0	1	1	0.75	0.36	1.93	0.01	0	0
27	5	1	483	10	2.66	1	0.72	0.99	0.65	0.14	1.74	0.06	0.82	<0.01
28	3	0	150	0	2.56	0	1	1	0.89	0.38	1.67	0.02	0	0
29	3	0	219	0	2.24	0	1	1	0	0	1.46	0.02	0	0
30	3	0	16	0	2.41	0	1	1	0.89	0.9	1.58	<0.01	0	0
31	1	1	91	4	1	1	0.5	0.96	0	0	0.65	<0.01	0.82	<0.01
32	4	0	26	0	3.11	0	1	1	1.83	0.82	2.03	<0.01	0	0
33	4	0	30	0	2.52	0	1	1	0	0	1.65	<0.01	0	0

Notes : Taxon numbers refer to those of the food web matrix in the Appendix. (In general, high numbers are near the top of the food web.) Quantitative indices come in two versions: unweighted (denoted by the "prime"), where the same weight is given to each taxon; and weighted, where the total amount of flows from and to the taxon are taken into account.

departure from a uniform distribution in flows from prey and to consumers. The weighted quantitative link density LD_q reaches a value of 2.1, which indicates that taxa having high total inflows $b_{.k}$ and/or outflows $b_{k.}$ also have high $n_{N,k}$ and/or $n_{P,k}$ values. Accordingly, the weighted and unweighted quantitative connectance follow a similar trend.

Table 2. Values of the qualitative and quantitative descriptors for the Chesapeake Bay mesohaline ecosystem (see Appendix).

Property :	qualitative descriptor		unweighted[1] quantitative descriptor		weighted quantitative descriptor	
Species properties :						
proportion of top taxa	$\%T$	0.364	$\%T'_{q[0.99,1]}$	0.364	$\%T_{q[0.99,1]}$	0.455
proportion of intermediate taxa	$\%I$	0.485	$\%I'_{q(0,0.99)}$	0.485	$\%I_{q(0,0.99)}$	0.394
proportion of basal taxa	$\%B$	0.152	$\%B'_{q[0]}$	0.152	$\%B_{q[0]}$	0.152
ratio of prey to consumers	$N{:}P$	0.75	$N{:}P'_q$	0.711	$N{:}P_q$	0.316
Link properties :						
link density	LD	2.212	LD'_q	1.372	LD_q	2.096
connectance	C	0.067	C'_q	0.042	C_q	0.064
proportion of links between :						
- top and intermediate	$\%TI$	0.397	$\%TI'_q$	0.451	$\%TI_q$	0.011
- top and basal	$\%TB$	0.055	$\%TB'_q$	0.055	$\%TB_q$	0.195
- intermediate and intermediate	$\%II$	0.288	$\%II'_q$	0.287	$\%II_q$	0.112
- intermediate and basal taxa	%IB	0.260	$\%IB'_q$	0.207	$\%IB_q$	0.682
Chain properties :						
average chain length	M_{cl}	3.157	$M'_{cl,q}$	1.605	$M_{cl,q}$	1.517
median chain length	MD_{cl}	3	$MD'_{cl,q}$	1.618	$MD_{cl,q}$	0.675
standard deviation of chain length	SD_{cl}	1.096	$SD'_{cl,q}$	0.488	$SD_{cl,q}$	1.910
maximum chain length	MAX_{cl}	6	$MAX'_{cl,q}$	2.970	$MAX_{cl,q}$	6.408
Omnivory properties :						
Degree of omnivory	$\%O$	0.455	O'_q	0.510	O_q	0.280
Consumer-prey asymmetries :						
Generality	G	2.607	G'_q	1.801	G_q	1.375
Vulnerability	V	3.476	V'_q	1.911	V_q	2.812
SD of standardized generality	sd_G	0.739	sd'_{Gq}	0.645	sd_{Gq}	1.882
SD of standardized vulnerability	sd_V	1.195	sd'_{Vq}	1.032	sd_{Vq}	4.066

Note: A maximal ffod chain is one linking a top and a basal taxon; this table only deals with maximal food chains.

[1] unweighted = the same weight is given to each taxon (or each maximal food chain for chain properties), irrespective of the total amount of flows from and to the taxon.

As for the proportion of top, intermediate, and basal taxa, the unweighted quantitative proportions of links $\%TI'_q$, $\%TB'_q$, $\%II'_q$, and $\%IB'_q$ are not markedly different from their qualitative counterparts (Table 2). This reflects similar distributions of link magnitude in the four groups, so that their contributions to Φ, the overall average amount of choice in the trophic pathways, remains essentially unaffected. Deviations from the qualitative proportions are particularly manifest in a higher value for $\%TI'_q$ and a lower value for $\%IB'_q$, which highlights a more equitable distribution of link magnitudes between top and intermediate taxa than between intermediate and basal taxa. The results change markedly with the weighted proportions $\%TI_q$, $\%TB_q$, $\%II_q$, and $\%IB_q$, which again reflect trophodynamics.

There is a total of 217 food chains in the Chesapeake Bay ecosystem, of which 134 are maximal ones, in the Chesapeake Bay ecosystem. Note that there is no loop in the food web graph, except for a cannibalistic one (taxon 19, Fig. 1). The unweighted quantitative properties describing the maximal food chains always produce lower values than their qualitative counterparts (only maximal food chains are treated in Table 2). This is an expected feature since the "effective" chain length attains the qualitative one only if the flows comprised in the chain are equal in magnitude. The weighted quantitative average chain length $M_{cl,q}$ is smaller than the unweighted $M'_{cl,q}$, indicating that, on average, long chains are less important in term of average biomass than short chains.

In the Chesapeake Bay ecosystem, 45% of the taxa are omnivorous. Our unweighted index of omnivory O'_q comes close to this figure, with a value of 0.51. Inspection of the taxon specific indices of omnivory o'_k (Table 1) shows that most omnivorous taxa consume prey in unequal proportions from two trophic levels, in which case o'_k is smaller than 1. Three taxa consume on more than two trophic levels, of which the blue crab (taxon 19) has the widest regime. The value of most taxon specific indices o_k is lower than their unweighted counterpart : the disequitability is higher once the biomass coming from the various trophic levels is taken into account, since omnivorous taxa eat preferentially from one trophic level, and consequently the value of the weighted quantitative omnivory index O_q falls to 0.28. Microzooplankton (taxon 7) forms an exception, consuming prey in very equal proportions from two trophic levels.

The qualitative generality G for the Chesapeake data set shows that each consumer taxon feeds on average on 2.61 prey taxa. Once computed over the effective number of prey, this index decreases to 1.8, and further drops down to 1.38 when weighted by the outflows. When considering the vulnerability V, we find that each prey taxon has on average 3.48 consumers, and that this value decreases to 1.91 with the unweighted quantitative index V'_q. It is noteworthy that prey taxa have more consumers than consumer taxa have prey, but that this inequality is inversed once one considers the effective numbers of consumers and prey. It is further interesting to note that, in contrast to a comparison of the respective quantitative measures of generality (G'_q and G_q) the weighted vulnerability (V_q) is much larger than the unweighted one (V'_q). This indicates that important prey taxa in term of outflows are also those with the highest number of consumer taxa, and that the contrary is true for consumer taxa. The variability in number of prey and of consumers is measured by the standard deviation of generality (sd_G) and of vulnerability (sd_V), respectively. Note also that the weighted quantitative sd_{Gq} and sd_{Vq}, are much higher than their respective qualitative and unweighted quantitative versions. This indicates a strong variability once total inflows and outflows are taken into account. The standardized generality and vulnerability (Table 1) show which taxa are responsible for this increase in inequitability : the polychaetes (taxon 14), the microzooplankton (taxon 7), and the meiofauna (taxon 17) on the side of the consumers; the sediment bacteria (taxon 3), and to a lesser extent the phytoplankton (taxon 1) on the side of the prey. Again, the higher sd_{vq}

compared to sd_{Gq} is consistent with the difference between quantitative vulnerability and generality.

Discussion

The purpose of formulating quantitative properties is to gain ecological information from a weighted food web. The qualitative approach collapses the quantitative data of the Chesapeake Bay ecosystem (Appendix) into its bare connective structure, which is pictured in Fig. 1. From such a graph, one would for example assume that taxon 21 (alewife and herring) is a typical “intermediate” taxon, with one prey and one consumer; our positional index *d* (Table 1) indicates however that it is functionally very close to a top taxon, being preyed upon only marginally by taxon 33 (striped bass). Taxon 9 (ctenophores) is seen as an important omnivorous species, eating prey at three different trophic levels; this is indeed captured by our unweighted omnivory index (*o’*); but once the magnitude of inflows are taken into account, the value of the index (*o*) drops, reflecting the fact that only 1% of the inflows to ctenophores come from trophic level 1. The weighted indices of standardized generality (*g*) and vulnerability (*v*) may seem to yield puzzling results. For example, taxon 14 (other polychaetes) has a *g*-value of 7.06 and preys upon a single taxon, while taxon 32 (summer flounder) has 4 prey and a *g*-value close to zero. This apparent inconsistency is explained by the huge differences in magnitude of inflows between low- and high trophic level taxa, which is intentionally taken into account by the weighted index. The usual concepts of generality and vulnerability are suitably expressed by the unweighted indices *g’* and *v’*, respectively. Over all, our taxon specific indices appear to correctly capture the quantitative information of trophic interactions. Synthetic properties of food webs shed light on more hidden characteristics of food webs. Those built up from the individual descriptors (species and omnivory properties, predator-prey asymmetries) are expected to carry with them the biological realism seen in the taxon-specific indices. We believe that the others global descriptors (link and chain properties) suitably incorporate the quantitative information. For example, the fact that the unweighted link density (LD'_q) yields the same result as its qualitative counterpart (*LD*) when applied to qualitative food webs supports this view.

For each qualitative measure, we propose a so-called unweighted version, where each taxon (or food chain) is given the same value, and a weighted version, where total inflows and outflows are taken into account. We believe that there is no primacy of using weighted quantitative, unweighted quantitative or qualitative properties, but that it is their combined use that provides the best insight into the studied system, as demonstrated in the Result section. However, these three categories of descriptors do not behave alike with regard to varying levels of sampling effort. Our preliminary results of sensitivity tests show that a stronger sampling effort is required for most qualitative properties to attain their original values than for the unweighted quantitative versions, and that weighted quantitative measures are those reaching an asymptote the fastest (Banašek-Richter et al. 2004). Note that it has already been shown how qualitative properties vary with sampling effort (Goldwasser and Roughgarden 1997, Bersier et al. 1999, Martinez et al. 1999). In sum, quantitative properties are not only useful as bearer of ecological information, they also represent a much more robust description of weighted matrices. Such quantitative data have been advocated by many (e.g., May 1983, Kenny and Loehle 1991, Cohen et al. 1993), and are now becoming available (e.g., Winemiller 1990, Ulanowicz and Wolff 1991, Goldwasser and Roughgarden 1993, Memmotet al. 1994, de Ruiter et al. 1995, Tavares-Cromar and Williams 1996, Omacini et al. 2001).

We devised the computation of our descriptors on information-based indices. There are probably infinite possibilities for using quantitative information to compute food web properties. A simple and natural approach is to calculate the qualitative properties at various levels of link importance (Winemiller 1990). We chose information theoretical indices because they allow finding the number of elements that would give a similar value of the same index given these elements occur in equal proportion (what we call the "reciprocal" of *H* above). Hence the original units (e.g., number of flows) are recovered, and it is then easier to construct a property that conforms with its original qualitative essence. However, while some conversions follow naturally (e.g., the quantitative link density, Eqs. 15 and 16), we found some properties to be more resistant to any evident formulation in quantitative terms, the epitome being the weighted quantitative number of maximal food chains for which we found no satisfactory counterpart.

Instead of using Shannon's formula, other diversity measures, such as the Simpson index (Simpson 1949), or indices based on Rényi's generalized entropy formula (Hill 1973, Legendre and Legendre 1998), are conceivable. For each of these, it is possible to compute their corresponding “diversity number” (our reciprocal of *H*). They may be even less sensitive to varying levels of sampling effort as they give less weight to small proportions. Note however that Brillouin’s formula (Pielou 1966a) is not applicable because of its inconsistency in respect to the units of b_{ij}. We tested the Simpson index in lieu of the Shannon index for the quantitative link density property (Eqs. 15 and 16). Indeed, we found that it performed slightly better than the Shannon index, the original value being reached slightly earlier. However, a disadvantage is a higher variance of the estimate, with a CV about 10% larger than with Shannon’s index. Thus, the use of the Shannon index appears to be a good compromise between accuracy and precision.

The use (and misuse) of diversity indices and especially of the Shannon index has raised much discussion in ecological literature (e.g., Pielou 1966b, Hurlbert 1971, Margalef 1995, Gotelli and Graves 1996). Nowadays, the use of the Shannon index as a measure of diversity per se is less popular among ecologists, and evenness measures are often preferred (e.g., Smith and Wilson 1996, Hofer and Bersier 2001). Indices based on information theory are however pertinent as phenomenological measures of growth and development for large systems (e.g., Ulanowicz 1986; Hirata 1995). The rationale for their suitability can be summarized as follows: as developing systems are changing, the “probabilities of microscopic events internal to maturing systems change accordingly. The study of what gives rise to a change in probability assignment defines the realm of information theory" (Ulanowicz 1986:81). The indices developed by these authors are derived in mathematically strict form from information theory; the overall average amount of choice in the trophic pathways Φ and the effective connectance *m* (Ulanowicz and Wolff 1991) are excellent examples (Eqs. 13 and 14). In our case, the utilization of the Shannon index follows from more simple grounds, and is justified operationally as an adequate method for taking the quantitative nature of trophic links into account.

Qualitative properties have been analyzed as dependent variables against a measure of food web size, the number of taxa *s*, using various analytical techniques (e.g., Briand and Cohen 1984, Sugihara et al. 1989, Bengtsson 1994, Bersier and Sugihara 1997). There is much contention about the regularities found from such studies (e.g., Havens 1993, Martinez 1993), and we think that much of the disagreement has its roots in the sensitivity of qualitative properties to sampling effort (Bersier et al. 1999). We hope that the descriptors we propose will help settle these controversies. However, their interpretation is more difficult, since their value is a function of two components : the number of flows, and the shape of the relative frequency distribution of the magnitude of these flows. Thus, the same value of an index can be obtained from many flows if few flows dominate the frequency distribution, or from few flows with a more even distribution. Such indeterminacy can be resolved by comparing the values obtained with the corresponding qualitative property, or simply by examination of the distributions of link importance for each taxon.

A difficulty with the use of quantitative properties lies in the choice of a currency for the trophic interactions. Different approaches have been used: measures based on the quantity of biomass transferred (e.g., flow of carbon : Baird and Ulanowicz 1989; feeding rate : de Ruiter et al. 1995; volume: Winemiller 1990; index of relative importance: Tavares-Cromar and Williams 1996) are adequate for a 'static' representation of web structure, while measures based on interaction strength (e.g., Paine 1992, Wootton 1994, Raffaelli and Hall 1996, Laska and Wootton 1998) and on the frequency of trophic interactions (Goldwasser and Roughgarden 1993) would better describe the 'dynamical' aspect of web structure. As mentioned above, the units must be comparable row- and columnwise. This criterion is not fulfilled by the index of relative importance (Tavares-Cromar and Williams 1996), which gives the same weight to all consumers. It is also important to be aware that measures of interaction strength and of flow of biomass may yield quite different values for the same trophic interaction (Polis 1994). Thus, when comparative studies are undertaken, it is essential to respect the consistency in the units quantifying trophic interactions. With these constraints kept in mind, we believe that the tools proposed here will be useful to extract meaningful information from objects as complex as weighted food webs, and will help develop a deeper insight into the structure of quantitative food webs.

Acknowledgments

We are grateful to R. Baltensperger, J.R. Bence, J. Chattopadhyay, D. Deb, J.P. Gabriel, C. Mermod, R.S. Sarkar, R. Ulanowicz, and an anonymous reviewer for their help and comments on the manuscript. This work was supported by Swiss NSF grant 31-52566.97, the Novartis Foundation, and partly the NCCR Plant Survival.

Literature cited

Austin, M. P. 1999. A silent clash of paradigms : some inconsistencies in community ecology. Oikos **86**:170-178.

Baird, D., and R. E. Ulanowicz. 1989. The seasonal dynamics of the Chesapeake bay ecosystem. Ecological Monographs **59**:329-364.

Bengtsson, J. 1994. Confounding variables and independent observations in comparative analyses of food webs. Ecology **75**:1282-1288.

Bersier, L. F., and G. Sugihara. 1997. Scaling regions for food web properties. Proceedings of the National Academy of Sciences of the United States of America **94**:1247-1251.

Bersier, L. F., P. Dixon, and G. Sugihara. 1999. Scale-invariant or scale-dependent behavior of the link density property in food webs : A matter of sampling effort? American Naturalist **153**:676-682.

Briand, F., and J. E. Cohen. 1984. Community food webs have scale-invariant structure. Nature (London) **307**:264-267.

Carney, H. J., K. E. Havens, and L. F. Bersier. 1997. Nonlinear scale dependence and spatiotemporal variability in planktonic food webs. Oikos **79**:230-240.

Closs, G., G. A. Watterson, and P. J. Donnelly. 1995. Constant predator-prey ratios : an arithmetical artifact? Ecology **74**:238-243.

Cohen, J. E. 1977. Ratio of prey to predators in community food webs. Nature (London) **270**:165-167.

———. 1978. Food Webs and Niche Space. Princeton University Press, Princeton, New Jersey.

Cohen, J. E., and C. M. Newman. 1985. A stochastic theory of community food webs I. Models and aggregated data. Proceedings of the Royal Society of London B Biological Sciences **224**:449-461.

Cohen, J. E. 1989. Food webs and community structure. Pages 181-202 in Roughgarden, J., R. M. May, and S. A. Levin, editors. Perspectives in ecological theory. Princeton University Press, Princeton, NJ.

Cohen, J. E., R. A. Beaver, S. H. Cousins, D. L. DeAngelis, L. Goldwasser, K. L. Heong, R. Holt, A. J. Kohn, J. H. Lawton, N. Martinez , R. Omalley, L. M. Page, B. C. Patten, S. L. Pimm, G. A. Polis, M. Rejmanek, T. W. Schoener, K. Schoenly, W. G. Sprules, J. M. Teal, R. E. Ulanowicz, P. H. Warren, H. M. Wilbur, and P. Yodzis. 1993. Improving Food Webs. Ecology **74**:252-258.

de Ruiter, P. C., A. M. Neutel, and J. C. Moore. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. Science (Washington DC) **269**:1257-1260.

Deb, D. 1995. Scale-dependence of food web structures : Tropical ponds a paradigm. Oikos **72**:245-262.

Goldwasser, L., and J. Roughgarden. 1993. Construction and Analysis of A Large Caribbean Food Web. Ecology **74**:1216-1233.

———. 1997. Sampling effects and the estimation of food-web properties. Ecology **78**:41-54.

Gotelli, N. J., and G. R. Graves. 1996. Null Models in Ecology. Smithsonian Institution Press, Washington DC.

Hall, S. J., and D. Raffaelli. 1991. Food-web patterns : lessons from a species-rich web. Journal of Animal Ecology **60**:823-842.

Havens, K. E. 1992. Scale and Structure in Natural Food Webs. Science (Washington DC) **257**:1107-1109.

———. 1993. Effect of scale on food web structure - Response. Science (Washington DC) **260**:243-243.

Hirata, H. 1995. Information theory and ecological networks. Pages 623-642 *in* Patten, B. C., S. E. Jorgensen, and S. I. Auerbach, editors. Complex Ecology. The Part-Whole Relation in Ecosystems. Prentice Hall PTR, Englewood Cliffs, New Jersey.

Hill, M. O. 1973. Diversity and evenness : a unifying notation and its consequences. Ecology **54**:427-432.

Hofer, U., and L.F. Bersier. 2001. Herpetofaunal diversity and abundance on tropical upland forests of Cameroon and Panama. Biotropica, in press.

Hurlbert, S. H. 1971. The nonconcept of species diversity : a critique and alternative parameters. Ecology **52**:577-586.

Kenny, D., and C. Loehle. 1991. Are Food Webs Randomly Connected? Ecology **72**:1794-1799.

Laska, M. S., and J. T. Wootton. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. Ecology **79**:461-476.

Lawton, J. H. 1989. Food webs. Pages 43-78 *in* Cherrett, J. M., editor. Ecological Concepts. Blackwell Scientific, Oxford.

Legendre, P., and L. Legendre. 1998. Numerical Ecology. Elsevier, Amsterdam.

Levine, S. 1980. Several measures of trophic structure applicable to complex food webs. Journal of Theoretical Biology **83**:195-207.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology **23**:399-418.

Margalef, R. 1995. Information theory and complex ecology. Pages 40-50 *in* Patten, B. C., S. E. Jorgensen, and S. I. Auerbach, editors. Complex Ecology. The Part-Whole Relation in Ecosystems. Prentice Hall PTR, Englewood Cliffs, New Jersey.

Martinez, N. D. 1991. Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. Ecological Monographs **61**:367-392.

———. 1992. Constant connectance in community food webs. American Naturalist **139**:1208-1218.

———. 1993. Effects of scale on food web structure. Science (Washington DC) **260**:242-243.

Martinez, N. D., and J. H. Lawton. 1995. Scale and food-web structure : from local to global. Oikos **73**:148-154.

Martinez, N. D., B. A. Hawkins, H. A. Dawah, and B. P. Feifarek. 1999. Effects of sampling effort on characterization of food-web structure. Ecology **80**:1044-1055.

May, R. M. 1974. Stability and Complexity of model ecosystems. Princeton University Press, Princeton, NJ.

———. 1983. The structure of food webs. Nature **301**:566-568.

Memmott, J., H. C. J. Godfray, and I. D. Gauld. 1994. The structure of a tropical host-parasitoid community. Journal of Animal Ecology **63**:521-540.

Odum, E. 1971. Fundamentals of Ecology. Saunders Co., Philadelphia, USA.

Omacini, M., E. J. Chaneton, C. M. Ghersa, and C. B. Müller. 2001. Symbiotic fungal endophytes control insect host–parasite interaction webs. Nature (London) **409**:78-81.

Paine, R. T. 1988. Food web : road maps of interactions or grist for theoretical development? Ecology **69**:1648-1654.

———. 1992. Food-web analysis through field measurement of per capita interaction strength. Nature (London) **355**:73-75.

Pielou, E. C. 1966a. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology **13**:131-144.

———. 1966b. Shannon's formula as a measure of specific diversity : its use and misuse. American Naturalist **100**:463-465.

Pimm, S. L. 1982. Food webs. Chapman and Hall, London.

———. 1984. The complexity and stability of ecosystems. Nature (London) **307**:321-326.

Pimm, S. L., J. H. Lawton, and J. E. Cohen. 1991. Food web patterns and their consequences. Nature (London) **350**:669-674.

Polis, G. A. 1991. Complex trophic interactions in deserts : an empirical critique of food-web theory. American Naturalist **138**:123-155.

———. 1994. Food-web, trophic cascades and community structure. Australian Journal of Ecology **19**:121-136.

Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs : Allochthonous input from the ocean supports high secondary produtivity on small islands and coastal land communities. American Naturalist **147**:396-423.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist **147**:813-846.

Raffaelli, D. G., and S. J. Hall. 1996. Assessing the relative importance of trophic links in food webs. Pages 185-191 *in* Polis, G. A., and K. O. Winemiller, editors. Food Webs : Integration of Patterns and Dynamics. Chapman & Hall, New York.

Shannon, C. E. 1948. A mathematical theory of communications. Bell System Technical Journal **27**:379-423.

Schoener, T. W. 1989. Food webs from the small to the large. Ecology **70**:1559-1589.

Simpson, E. H. 1949. Measurement of diversity. Nature **163**:688-688.

Smith, B., and J. B. Wilson. 1996. A consumers guide to evenness indices. Oikos **76**:70-82.

Solow, A. R., and A. R. Beet. 1998. On lumping species in food webs. Ecology **79**:2013-2018.

Sprules, W. G., and J. E. Bowerman. 1988. Omnivory and food chain length in zooplankton food webs. Ecology **69**:418-426.

Sugihara, G. 1982. Niche hierarchy : structure assembly and organization in natural communities. Ph.D. diss. University of Princeton, Princeton, NJ.

———. 1984. Graph theory, homology and food webs. Pages 83-101 *in* Levin, S. A., editor. Population Biology. Proceedings of Symposia in Applied Mathematics, Vol. 30. American Mathematical Society, Providence, Rhode Island.

Sugihara, G., K. Schoenly, and A. Trombla. 1989. Scale invariance in food web properties. Science (Washington DC) **245**:48-52.

Tavares-Cromar, A. F., and D. D. Williams. 1996. The importance of temporal resolution in food web analysis : Evidence for a detritus-based stream. Ecological Monographs **66**:91-113.

Ulanowicz, R. E. 1986. Growth and Development : Ecosystems Phenomenology. Springer Verlag, New York.

Ulanowicz, R. E., and W. F. Wolff. 1991. Ecosystem flow networks : loaded dice? Mathematical Biosciences **103**:45-68.

Ulanowicz, R. E. 1997. Ecology, the Ascendent Perspective. Columbia University Press, New York, NY.

Warren, P. H. 1989. Spatial and temporal variation in the structure of a freshwater food web. Oikos **55**:299-311.

———. 1994. Making connections in food webs. Trends in Ecology & Evolution **9**:136-141.

Williams, R. J., and N. D. Martinez. 2000. Simple rules yield complex food webs. Nature (London) **404**:180-183.

Winemiller, K. O. 1990. Spatial and temporal variation in tropical fish trophic networks. Ecological Monographs **60**:331-367.

Wootton, J. T. 1994. Predicting direct and indirect effects : an integrated approach using experiments and path analysis. Ecology **75**:151-165.

Yodzis, P. 1989. Introduction to Theoretical Ecology. Harper & Row, New York.

Abstract.

A food web customarily describes the qualitative feeding relationships in a community. Descriptors have been used to extract ecologically meaningful information from such data, e.g., the proportion of top species (the proportion of taxa without consumers) or vulnerability (the average number of consumers per taxon). Analyses of collections of food webs based on these properties have revealed regularities that fostered the formulation of models of food web structure. However, it has been shown that most of these qualitative descriptors are highly sensitive to varying levels of sampling effort used to document a food web. The principal problem is that webs described extensively include trophic links of highly uneven magnitude, with typically few strong/important links and a wealth of weak ones; with qualitative descriptors, the same weight is given to all trophic interactions. To overcome this problem, food webs should be described and analyzed quantitatively. Consequently, we propose here a suite of food web descriptors, which are built on information theory indices and take the magnitude of the trophic interactions into account. We define descriptors having a similar meaning as the classical qualitative indices. Two versions of each quantitative descriptor are proposed, one giving the same weight to each taxon, and one weighing each taxon by the total amount of its incoming and outgoing biomass flows. We use a published quantitative food web to exemplify the computation of the new descriptors, and discuss their potential and limitations.

Appendix. Example of a quantitative food web, representing the annual carbon flows among the 33 major taxa of the Chesapeake mesohaline ecosystem (data from Baird and Ulanowicz 1989). Rows are consumed taxa, and columns consumer taxa. Flows are in $mg \cdot m^{-2} \cdot yr^{-1}$.

	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
1	0	31715	37149	0	0	4199	2275	4415	0	0	0	0	0	0	0	0	277	20.8	0	0	0	0	0	0	0	0	0	0
2	0	870.9	1685.4	131.5	0	105.2	56.9	110.6	0	0	0	0	0	0	0	0	12.3	4.2	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	160831	25062	57335	35962	14075	1690	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	18086	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	88721	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	31638	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	7555	3437	0	290	156	304	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	6878	1159	0	0	0	0	0	0	0	0	0	4.9	25.7	1534	248.2	5.2	0	0	0	0	0	0	0	0	0
9	0	0	0	0	552	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	538	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	215	0	0	0	0	0	0	9	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7.2	59	314	76	152.8	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	352	0	0	0	0	0	2.1	14	97	59	22.6	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0	0	4538	0	0	0	0	0	0	0	55	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	967	0	0	0	0	0	0.3	14	2	0	43.1	0	0	0.9	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	293	0	0	0	0	0	0	0	0	0	0	0	0	0	2.4
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14.5	14.6	0	2.7	91.4	12.3	17.2
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.6	0	8	10.6
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10.2	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4.3	0

List of taxa. 1 : phytoplankton; 2 : bacteria attached to suspended particles; 3 : sediment bacteria; 4 : benthic algae; 5 : free bacteria in water column; 6 : heterotrophic microflagellates; 7 : microzooplankton; 8 : zooplankton; 9 : ctenophores; 10 : sea nettles *Chrysaora quinquecirrha*; 11 : other suspension feeders; 12 : *Mya*; 13 : oysters, *Crassostrea virginica*; 14 : other polychaetes; 15 : *Nereis*; 16 : *Macoma* spp.; 17 : meiofauna; 18 : crustacean deposit feeders; 19 : blue crabs *Callinectes sapidus*; 20 : fish larvae; 21 : alewife *Alosa pseudoharengus* and herring (Clupeidae Fam.); 22 : bay anchovy *Anchoa mitchilli*; 23 : menhaden *Brevoortia tyrannus*; 24 : shad *Alosa sapidissima*; 25 : atlantic croaker *Micropogonius undulatus*; 26 : hog choker *Trinectes maculatus*; 27 : spot *Leiostomus xanthurus*; 28 : white perch *Morone americana*; 29 : catfish *Arius felis*; 30 : blue fish *Pomatomus saltatrix*; 31 : weak fish *Cynoscion aregalis*; 32 : summer flounder *Paralichthys dentatus*; 33 : striped bass *Morone saxatilis*. Note that only living compartments are included in this version of the food web; ignored compartments are : exogenous inputs, dissolved organic carbon, suspended particulate organic carbon, sediment organic carbon, exploitation, exports and respiration. Columns and rows with zero marginal sums are excluded for economy.

III SAMPLING EFFECTS AND THE ROBUSTNESS OF QUANTITATIVE AND QUALITATIVE FOOD-WEB DESCRIPTORS[1]

1. **Introduction**

One key aspect of food-web ecology centers on the question of how food webs can be described in a way that allows feasible comparisons between webs compiled from different communities, and at the same time serves to uncover general patterns inherent to all of them (Cohen et al. 1993). Up to now, food-web properties drawn up from binary (qualitative) food web matrices were employed to serve this purpose. These descriptors and their behaviour when analyzed over a number of webs with differing species richness fostered the postulation of generalities such as scale-invariance (e.g., Pimm 1982; Briand and Cohen 1984; Cohen and Briand 1984; Cohen 1989; Lawton 1989; Sugihara et al. 1989; Cohen et al. 1990; Pimm et al. 1991; Bersier and Sugihara 1997) and constant connectance (Havens 1992; Martinez, 1992, 1993, 1994; Williams and Martinez 2000). The former theory, prematurely termed "scaling laws" (Cohen and Newman 1985), assumes that certain food-web properties, e.g., the proportion of top species (*%T*, who experience no predation by others in the specific community), or link density (LD, the ratio of realized links *L* to the total number of species comprising the web *s*), remain constant regardless of species richness (scale). If however, in accordance with the second hypothesis, connectance (*C*), defined as the ratio of realized links (*L*) to possible links (S^2), is declared as constant with scale, scale-invariance for the link density property has invariably to be rejected. At the heart of these controversies lies the question of how reliable or exhaustive the data sets on which such hypothesis are based can be and in how far the collections which are considered for among-web comparisons are uniformly aggregated (May 1983; Paine 1988; Lawton 1989; Sugihara et al., 1989, 1997; Winemiller 1990; Hall and Raffaelli, 1991, 1993; Pimm et al. 1991; Schoenly and Cohen 1991; Winemiller et al. 2001). For link-density Bersier et al. (1999) have proposed that much of the controversy about patterns in food webs could be understood when considering that the level of sampling effort employed in the construction of a web varies considerably between different studies.

A mere qualitative approach to food-web ecology, as is the one that brought forth the afore mentioned theories, will however always result in a poor description of reality (May 1983; Pimm and Kitching 1988; Lawton 1989; Pimm et al. 1991). Considering a food web qualitatively implies that the same weight is given to all trophic interactions (links) irrespective of their

---

[1] Chapter published: Banašek-Richter C., Cattin M.-F. & Bersier L.-F. 2004. *Journal of Theoretical Biology* **226**: 23-32.

magnitude. By inadequately considering the complexity of the data material at hand, which often times exceeds qualitative information alone, the qualitative approach to food-web data distorts our perception of food-web structure (Kenny and Loehle 1991; Closs and Lake 1994; Benke and Wallace 1997; Bersier et al. 1999). Furthermore, qualitative properties have been criticized due to their sensitivity to sampling effort with high levels of sampling effort being necessary in order to reach original values (Goldwasser and Roughgarden 1997; Bersier et al. 1999; Martinez et al. 1999). In the light of these developments, there has been a call for descriptors based on quantitative data measurements to overcome the apparent shortcomings of the qualitative perspective (Paine 1988; Kenny and Loehle 1991; Ulanowicz and Wolff 1991; Bersier et al. 1999). This led us to derive quantitative counterparts for the most widely used qualitative food-web properties (Bersier et al. 2002).

Undoubtedly all compiled webs can only be the result of a lesser or greater effort exerted towards sampling (Goldwasser and Roughgarden 1997). Thus the assessment of trophic interactions within a web can only be an approximation of the true state as a function of sampling effort. Goldwasser and Roughgarden (1997) have addressed the incompleteness of data collections that inevitably results from limits in detectability in an attempt to assess in how far this will affect food-web properties. They found a vast majority of commonly employed food-web properties to be sensitive to incomplete data compilations and reason that the true properties of a given community may diverge considerably. To circumvent these predicaments we need to correct biases that are attributable to variable observational effort (Martinez et al. 1999), compile new data sets exerting exceedingly greater observational effort (Paine 1988; Pimm and Kitching 1988; Lawton 1989; Winemiller 1990; Martinez 1991; Polis 1991; Goldwasser and Roughgarden 1997), and attempt to define new properties that are less sensitive to these imperfections. We opt to concentrate on the latter of these three possibilities and make use of Goldwasser and Roughgarden's approach (1997) to test the performance of our newly defined quantitative descriptors on ten well-defined web compilations.

We consider the effect of sampling effort on the qualitative and quantitative properties by examining the behaviour of these descriptors in respect to varying levels of sampling intensity. Descriptors that are employed to compare webs of differing or unknown levels of observational effort ideally should show little sensitivity to sampling effort. By evaluating the performance of quantitative versus qualitative descriptors we try to gain insight into their potential quality as descriptors of among-web comparisons. In quantitative food webs, one can envision that the distribution of link magnitudes is affected by rather convoluted influences (e.g., ecological, environmental, and methodical constraints). We thus expect considerable variance in the link distribution between webs. Consequently, we further examine if the performance of the descriptors is a function of the shape of the frequency distribution of link magnitude.

2. Methods

2.1. Food-web descriptors

Onset for our analysis will be an s-by-s quantitative food-web matrix $\mathbf{b} = [b_{ij}]$ with s equating to the total number of taxa in the web. Within this matrix columns delineate consumers, rows stand for species of prey, and $b_{ij} > 0$ if species j feeds on i. The value assumed by b_{ij} represents the magnitude of the trophic interaction between i and j. Inspired by the work of Ulanowicz and Wolff (1991) the quantitative descriptors we will be dealing with are mathematically based on information theory, namely the diversity index of Shannon and Wiener. We chose information theoretical indices because they allow finding the number of elements that would give a similar value of the same index given these elements occur in equal proportion (for a Shannon index H measured in $\log_2$, this number of elements is 2^H). Hence the original units (e.g., number of flows) are recovered, and it is then easier to construct a property that conforms with its original qualitative essence. Indices based on information theory have been used as phenomenological measures of growth and development for large systems (e.g., Ulanowicz 1986). The rationale for their suitability can be summarized as follows: as developing systems are changing, the “probabilities of microscopic events internal to maturing systems change accordingly. The study of what gives rise to a change in probability assignment defines the realm of information theory” (Ulanowicz 1986:81). In our case, the utilization of the Shannon index follows from more simple grounds, and is justified operationally as an adequate method for taking the quantitative nature of trophic links into account.

The properties considered here can be divided into 3 groups: 1) species properties: proportion of top (species having no predator; $\%T$), intermediate (species having prey and predators; $\%I$), basal species (species with no prey; $\%B$), and the ratio of prey to predators (N:P); 2) link properties: link density (LD), directed connectance (C), proportion of links between top and intermediate (%T-I), top and basal (%T-B), intermediate (%I-I), and intermediate and basal (%I-B) links; 3) predator-prey asymmetries: generality (G, the mean number of prey per predator), vulnerability (V, the mean number of predators per prey), standard deviation in generality (sd$G$), standard deviation in vulnerability (sd$V$). For each of these 14 properties, the customary qualitative version, as well as the unweighted quantitative and the weighted quantitative versions are analyzed. While the unweighted version gives the same weight to each species irrespective of the magnitudes of in- and outflows, the weighted one takes these biomass flows for each species into account. We will denote the quantitative indices with a subscripted "q", followed by an apostrophe for the unweighted version (e.g., $\%T_q$, $\%T_q'$). The reader may refer to Bersier et al. (2002) for exact definitions and derivations of these quantitative descriptors.

2.2. Dataset

We chose to examine these newly described quantitative measures of food-web properties on a number of species-rich, well defined systems, whose construction was preceded by the investment of a large amount of observational effort, and for which quantitative information about link magnitude is provided. Among the tested webs are two ecosystems that can be described as truly aquatic: Chesapeake Bay (Baird and Ulanowicz 1989) and Florida Bay (Ulanowicz, <http://cbl.umces.edu/~atlss>), one that comes from a terrestrial habitat: St. Martin (Goldwasser and Roughgarden 1993), while all others delineate an interface between the two milieus: Cypress, Everglades Graminoids, Mangrove estuary (Ulanowicz, <http://cbl.umces.edu/~atlss>). For each of these last three communities and the Florida Bay ecosystem we have access to two web compilations: one for the wet, one for the dry season respectively. With one exception, the currency of the trophic interactions for all webs is biomass flow in gram per unit area and time. Link importance on St. Martin is measured as acts or frequencies of predation per hectare and day. For the sake of simplicity and unless specified otherwise, we will henceforth confine ourselves to the expression "flows of biomass" when referring to the unit of measurement for trophic interactions. Web compartments for which the inflows are not ascribed to acts of predation were disregarded (e.g., respiration).

2.3. Simulation of sampling effort

The idea of sampling effort will be of central importance in the course of our further undertakings. In a theoretical approach, increasing the number of trophic interactions that are sampled from a given food-web matrix can serve as a simulation of empirical data collection. In the field, the number of trophic interactions discovered will increase with the extent of effort exerted. Effort in this case is a function of the number of sampling repetitions, the amount of time spent collecting data, the number of people engaged in the collection, etc. While various factors will influence the detectability of a link (Goldwasser and Roughgarden 1997) we presume that those trophic interactions which are large in their quantitative dimension, will be the ones that are most likely to be discovered first. Consequently, we simulated sampling by sequentially drawing links in the food-web matrix, with the probability of choosing a link proportional to its magnitude. Several theoretical considerations preceded our sampling simulations however. Since enormous discrepancies in link magnitudes are common for most of the analyzed data sets, we opted to ensure that the likelihood of sampling a predator is equal for all consumer species. Instead of using the original quantitative matrix **b** to examine the effect of varying levels of sampling effort, we thus employed a modified version of **b**, the "predator (food-web) matrix" **p**. Within **p,** total inflows equal 1 for each consumer. This is accomplished by simply calculating $p_{ij} = b_{ij} / b_{\cdot j}$.

Species richness for the webs analyzed ranges from 33 to 121 taxa for the original data sets and the total number of links (*L*) varies from 73 to 1799. To ensure comparable probabilities of link detection we opted to test for eight levels of sampling effort that are multiples of the respective web's original number of links: 0.5**L*, *L*, 2**L*, …, 64**L*. The level of sampling effort represents the number of chosen links from the predator matrix, which can be thought of as the number of trophic interactions observed. The probability of detecting a link is set in proportion to its p_{ij}-value. Upon having sampled a specific link, the newly being built matrix is extended by both the link's corresponding predator and its prey species. Each "hit" for a link increases its magnitude by one unit. Sampling from the predator (food-web) matrix **p** we attain a sampled predator matrix (**p'** = $[p'_{ij}]$). The resulting number of hits per link for a given predator is multiplied by the respective predator's inflow sum ($p'_{ij} * b_{\cdot j}$). This reincorporates the original distribution of biomass inflows between predators that is needed in order to correctly compute the quantitative descriptors. One hundred sampling replicates are undertaken per sampling intensity for each food web.

This sampling procedure – although different in its practical implementation – can from a logical point of view be regarded as equivalent to Goldwasser and Roughgarden's (1997) "sampling in the prey direction". It simulates a sampling procedure that concentrates on the diet of a focal species. Goldwasser and Roughgarden (1997) chose additionally to simulate sampling in the "predator direction", concentrating on the focal species' consumption by others, and in both directions simultaneously. According to their results, sampling in both directions ensures a faster approach to the original property values as compared with sampling in one of the two directions only. Our restriction to the prey direction is for reasons of parsimony, and because we feel that looking at feeding interactions from the predators' perspective more realistically mirrors the actual situation in the field, where upon the discovery of a species, its diet is more readily accessible than its role as prey (Schoener 1989). We calculated the 14 food-web properties in their three versions on the basis of the matrices obtained from the above described sampling procedures.

2.4. Analyses

The accuracy of a descriptor is visualized by plotting the simulated values against the degree of sampling effort. To ensure a compact representation, we first computed the average $\overline{z'}$ of the 100 sampling replicates per web for each property. We compared this average with the reference value z obtained from the original food web by calculating the percentage of agreement $\overline{z'}/z$. Second, we calculated the overall accuracy of a property as the median of each percentage of agreement over the ten webs analyzed. This value was plotted against the degree of sampling effort (see Fig. 1). As a measure of a descriptor's precision we furthermore computed the coefficient of variation (CV); for each sampling intensity it determines the degree of relative scatter of data between replicates with respect to the mean. The average over the CV-results for all ten webs summarizes the within-web precision. We complemented this information by providing a global measure of among-web precision, which was measured as the average of the quartile ranges over the eight sampling intensities for the ten webs (i.e., an average over 80 values).

In order to be able to give practical advice for food-web documentation, we estimated the level of sampling effort necessary to attain a given accuracy. This was done by performing a nonlinear regression on the data of Fig. 1. A power law of the form $y = 1 + ax^b$ (y = overall accuracy in percent of the original value; x = level of sampling effort) adequately describes our results, with only 2 coefficients of variation smaller than 0.97 among the 42 fits. For the three versions of all 14 properties, the corresponding parameters for a and b were estimated by nonlinear regression before computing the level of sampling effort required for 95 % accuracy.

Discrepancies in performance between the different webs for specific properties can be attributed to a number of factors. One possibility is that the shape of the distribution of link magnitude affects the properties' performance, with highly uneven distributions likely to yield more robust estimates, as strong links will be sampled first. Consequently, we compare the equitability of link magnitude per web with the quality of prediction of the analyzed web properties. Equitability is measured for the **p** matrices by means of Shannon's evenness index (Legendre and Legendre 1998). Quality of prediction is understood as the average deviation from the property's original values over all eight sampling intensities; deviation being the absolute difference between simulated and original value divided by the original value ($\left|\overline{z'} - z\right| / z$). The quality of prediction is calculated for each of the ten data sets for all three versions of the properties under examination. Since there are groups of properties that per definition are mutually dependent on each other ($\%B + \%I + \%T = 1$, $C = LD/s$, $\%T\text{-}B + \%T\text{-}I + \%I\text{-}I + \%I\text{-}B = 1$) we disregarded one property from each of these groups (*%B, C, %T-B*) for this analysis.

3. Results

The results of our sensitivity tests are presented in Fig. 1 and Table 1. The behaviour of each property with increasing sampling effort with respect to the values acquired for the original data sets are depicted for the qualitative and both quantitative versions. Thus for Fig. 1 the horizontal at f(x) = 1 represents the "original value". The degree to which the curves for the 3 different versions of web properties converge towards this horizontal are a measure of their performance or how well they are able to predict the original values with increasing sampling effort. As expected, we observe an increasingly better match to the original value with increasing sampling intensity for all properties. For a majority of the properties, the performance at low levels of sampling effort differs considerably between the three versions. This discrepancy decreases with increasing sampling effort. The information drawn from Fig. 1 can be summarized as follows: for all properties either one or both quantitative versions do as well as or better than the qualitative version when considering their performance in respect to the original values. Only in 2 of 14 instances does the qualitative version outperform one of the quantitative versions, never does it outperform both. The quartile ranges for every property

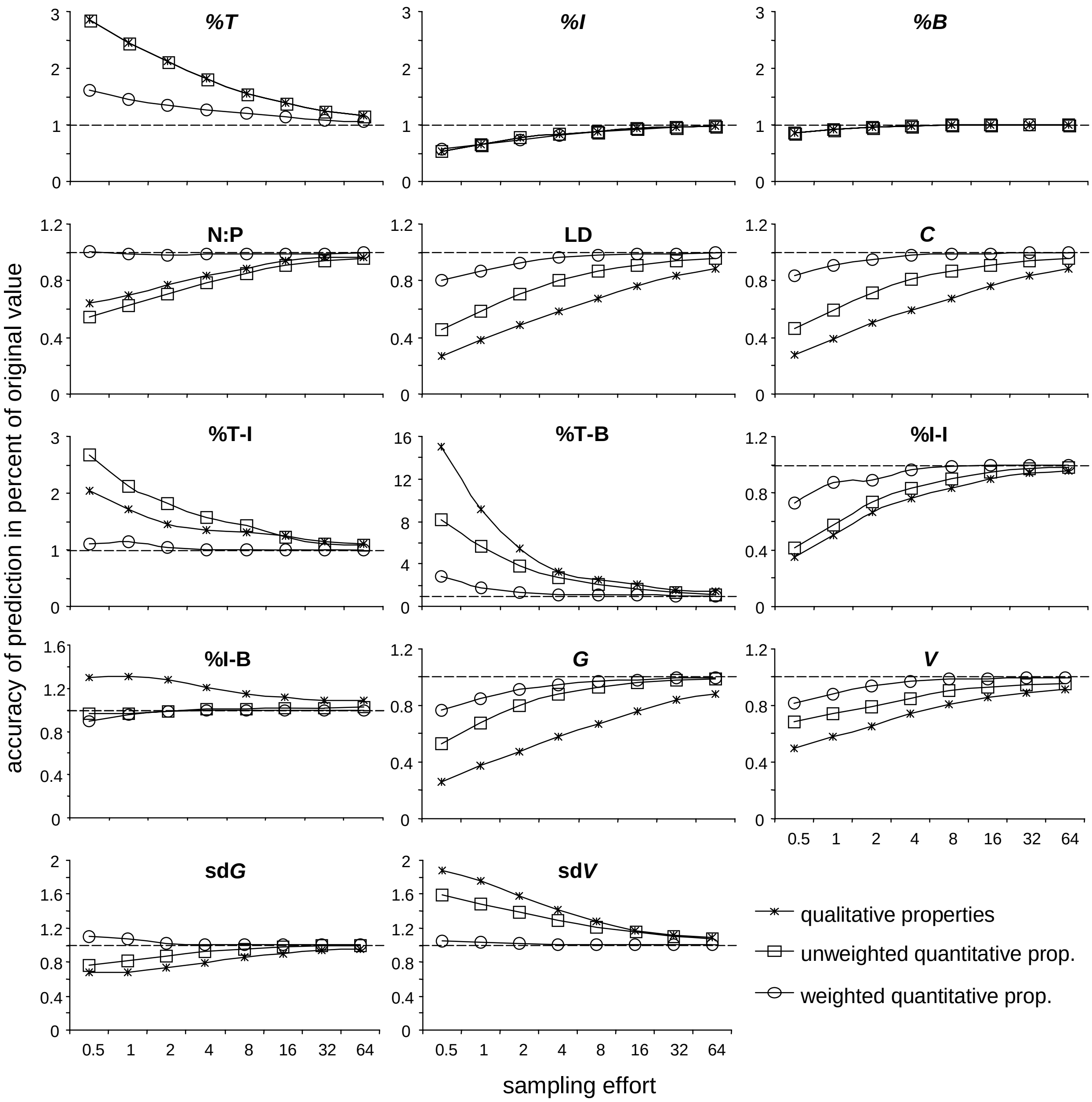


Fig. 1. Accuracy of the qualitative and quantitative properties with increasing sampling effort. Accuracy is measured in percent of the original values (broken line). Given are the median values of accuracy for the ten examined food webs; accuracy within a food web is measured as the mean percentage deviation of 100 simulations for each intensity of sampling. Sampling effort is given as a multiple of the total number of trophic links in each food web. Information about the dispersion of the accuracy curves for the ten food webs are given in Table 1.

presented in Table 1 specify the degree of dispersion between the results for the ten individual webs. Among-web spreading of values is inferior or equal to that of the respective qualitative version for all weighted quantitative properties. With the exception of the proportion of links between top and intermediate species (%T-I) this also applies to the unweighted quantitative representations. Note that the %T-I and especially the %T-B properties show an unusually high level of divergence from the original values as delineated in Fig. 1. This is simply attributable to

Table 1. Mean quartile ranges for the food-web properties over the ten examined food webs and the eight levels of sampling effort; the mean quartile range is a measure of among-web dispersion for the accuracy curves presented in Fig. 1.

Property	qualitative	quantitative unweighted	quantitative weighted
proportion of top species *%T*	0.558	0.558	0.327
proportion of intermediate species *%I*	0.114	0.114	0.091
proportion of basal species *%B*	0.065	0.065	0.065
prey to predators ratio N:P	0.082	0.075	0.026
link density LD	0.074	0.043	0.028
connectance	0.079	0.065	0.034
proportion of links between :			
- top and intermediate %T-I	0.429	0.572	0.399
- top and basal %T-B	4.411	2.345	0.772
- intermediate and intermediate %I-I	0.178	0.177	0.095
- intermediate and basal species %I-B	0.331	0.111	0.042
generality *G*	0.067	0.020	0.035
vulnerability *V*	0.087	0.078	0.027
standard deviation in *G*, sd*G*	0.126	0.028	0.043
standard deviation in *V*, sd*V*	0.241	0.197	0.021

very small original values for the respective properties, which can bring about large proportional divergences even when absolute differences are small.

In accordance with these findings, a higher level of sampling intensity is needed for the qualitative as opposed to the quantitative versions to reach an accuracy of 95%. While 10 of the 14 weighted quantitative properties attain an accuracy of 95% after merely having sampled 4**L* times, this value rises to approximately 260**L* for the quantitative unweighted and to 1700**L* for the qualitative properties. Assuming a conservative connectance of 0.2, for a food web of 100 taxa this would imply the necessity to independently observe 8’000 trophic interactions for most quantitative weighted properties to reach 95 % accuracy. Under the same conditions, this value increases to approximately 500’000 for the unweighted quantitative version and to more than 3’000’000 for the qualitative properties. Although these values are extremely crude estimates, they highlight the enormous discrepancy in sensitivity of the three property versions.

As expected, we found most *CV*-functions to decline with increasing sampling intensity, indicating that the variance for within-web replicates is negatively correlated to the degree of effort exerted toward sampling. The mean *CV*-value over all ten food webs for each property is presented in Fig. 2. Most *CV*-functions decline smoothly with increasing sampling effort; only

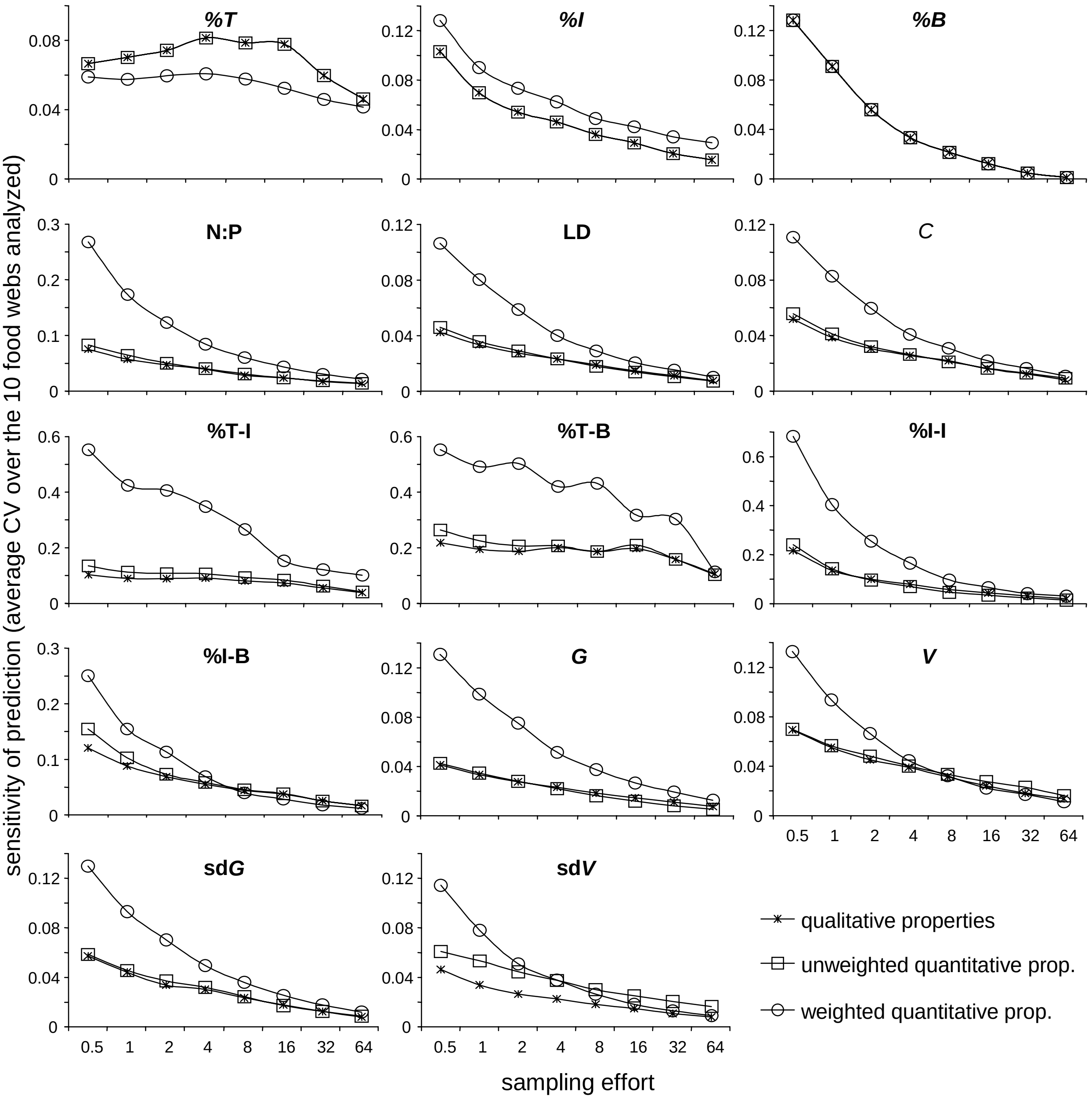


Fig. 2. Within-web precision of the qualitative and quantitative properties with increasing sampling effort. Precision is measured as the average coefficient of variation for the ten examined food webs at each sampling intensity. Sampling effort is given as a multiple of the total number of trophic links in each food web.

%T, %T-I, and %T-B show a more erratic behaviour. This feature can again be attributed to the very small means of these properties. For the individual webs analyzed, the *CV* functions of the qualitative and unweighted quantitative properties assume a very similar course throughout the full range of sampling effort examined. The scatter of data about the mean at an early stage of sampling tends however to be exceedingly greater for the weighted quantitative version of a given property as compared to the two other versions. A two-fold discrepancy at sampling intensities of 0.5**L* is a prevalent feature.

The relationship between the overall quality of prediction for the properties and the shape of the frequency distribution of link magnitude are given in Table 2. The former was measured

Table 2. Relationship between evenness of distributions of link magnitude and overall quality of prediction of the food-web properties.

	qualitative		unweighted quantitative		weighted quantitative	
property	ρ	P	ρ	P	ρ	P
proportion of top species *%T*	-0.406	0.244	-0.406	0.244	-0.139	0.701
proportion of intermediate species *%I*	-0.467	0.174	-0.467	0.174	-0.539	0.108
prey to predators ratio N:P	-0.467	0.174	**-0.806**	**0.005**	0.285	0.425
link density LD	**-0.903**	**<0.001**	**-0.903**	**<0.001**	-0.382	0.276
proportion of links between :						
top and intermediate %T-I	-0.321	0.365	-0.358	0.310	**0.733**	**0.016**
intermediate and intermediate %I-I	-0.442	0.200	-0.394	0.260	-0.345	0.328
intermediate and basal species %I-B	0.164	0.200	0.297	0.405	0.261	0.467
generality *G*	**-0.855**	**0.002**	0.212	0.556	-0.321	0.365
vulnerability *V*	-0.055	0.881	-0.164	0.651	-0.467	0.174
standard deviation in *G*, sd*G*	**-0.879**	**0.001**	-0.345	0.328	0.018	0.960
standard deviation in *V*, sd*V*	**-0.891**	**0.001**	**-0.976**	**<0.001**	-0.115	0.751
# of negative / positive correlations	10 / 1		9 / 2		7 / 4	
binomial probability (two-tailed)	0.012		0.065		0.549	

Relationship is measured by Spearman's correlation coefficient ρ. Three properties dependent on others are disregarded (*%B*, *C*, %T-B). Significant results are in bold face type. The cumulative binomial probability that the observed numbers of negative and positive correlations is similar is given for each type of descriptors.

as the average of the percentage of absolute deviation over the eight sampling intensities, the latter as the evenness of the distribution. We expected that a more even distribution would yield less accurate estimations. Indeed, we found most Spearman's correlation coefficients to be negative: of the 11 properties considered 10, 9, and 7 had negative coefficients for the qualitative, the unweighted quantitative, and the weighted quantitative version respectively. Among these, four correlations were significant for the qualitative, three for the unweighted quantitative, and only one for the weighted quantitative properties (the latter being attained for a positive correlation). In accordance with the number of positive versus negative correlations for the three types of properties (Table 2), we deduce that quantitative weighted properties are more robust against differences in the shape of the distribution of link magnitude than quantitative unweighted ones, which are in turn more robust than qualitative properties.

4. Discussion

Our theoretical analysis of the performance of food-web properties in respect to varying levels of observational effort lead us to conclude that the so defined quantitative properties are more robust against sampling effort than their qualitative counterparts. We come to this conclusion under the assumption that the most important feeding interactions in the context of a quantitative approach are the ones most likely to be discovered first. For the quantitative approach a large part of the information inherent to a food web is therefore taken into consideration at an early stage of sampling, thus achieving a better representation of the web relative to the qualitative approach.

The consequences of calculating food-web properties from incomplete data sets have been of interest before. Based on their analysis of a highly sampled grassland web Martinez et al. (1999) found the proportion of top *%T*, intermediate *%I*, and basal species *%B*, as well as link density LD to strongly depend on the extent of observational effort. Only connectance *C* proved to be robust against variable levels of sampling effort. Goldwasser and Roughgarden (1997) found conventional (qualitative) web properties to vary extensively in dependence of the level of sampling intensity for the data from St. Martin Island. Original values were only reached after a vast magnitude of endeavor toward sampling for most properties including connectance. In light of the extensive sensitivity of most qualitative food-web properties to the incompleteness of data assemblages, Goldwasser and Roughgarden thus question the role of these properties as guides to ecological function. Bersier et al. (1999) further showed that the scaling behaviour of link density LD is affected by sampling effort: intrinsically scale-dependent collections of food webs appear scale-invariant when sampling is simulated at low intensities. All these results highlight the difficulties inherent to the use of qualitative descriptors as a means to uncover basic regularities in food webs (Winemiller et al. 2001).

We are convinced that the problems revealed by these authors can be resolved by applying a method of quantitatively defining food-web properties. The properties analyzed in this paper were delineated for this purpose (Bersier et al. 2002). They proved to be more accurate than their qualitative counterparts in the sense that they are less biased. More accuracy seems to be accomplished at the cost of less precision, since there is generally more variability between individual sampling replicates (as depicted by measuring the coefficient of variation) for the weighted quantitative properties. Because qualitative and unweighted quantitative descriptors behave quite similarly in regard to their CV-curves (Fig. 2), a feasible explanation for the larger scatter of the weighted quantitative measurements lies in the magnitudes of total in- and outflows. These are only accounted for by the weighted quantitative versions and may be highly variable. In contrast to the results for the within-web evaluation, precision on the level of a between-web comparison (demonstrated by way of the mean quartile ranges), is however higher for the quantitative property versions. Moreover, weighted quantitative descriptors appear to be less sensitive to variable levels of evenness in the distribution of link magnitude. In sum, the small loss in precision exhibited by the weighted quantitative properties is offset by their higher accuracy and robustness; in respect to the degree of precision, accuracy, and robustness unweighted quantitative descriptors take on an intermediate position (between weighted and qualitative descriptors), while qualitative descriptors proved to be the least robust measurements of food-web structure.

The importance of a link is regarded as a function of its magnitude, which is the amount of biomass flow from the prey species constituting the link to the links' associated predator. In the case of the data collection from St. Martin Island, importance is a function of the frequency of predation. When contemplating feeding interactions holistically, these definitions can of course each only account for one aspect in a suite of attributes that may be employed to measure the ecological relevance of a trophic interaction (Paine 1980; Lawton 1989; Cohen et al. 1993; Raffaelli and Hall 1996; Laska and Wootton 1998). The impact a certain feeding interaction has on the species engaged may stand in no direct or intuitive (clear-cut) relation to the amount of biomass flow or predation frequency involved (Polis 1994; Benke and Wallace 1997). For example, parasites may exert a highly detrimental effect, even though this is not reflected in the amount of biomass they consume (Lawton 1989; Huxham et al. 1995), a generalist may drive one of the species it preys upon to extinction even if the associated biomass flow only accounts for a small portion of the total diet intake (e.g., Bondavalli and Ulanowicz 1999; Courchamp et al. 2000), a predator may peril in lack of specific nutrients it only takes up in mere traces with a certain kind of prey (e.g., Gaedke et al. 2002). Depending on the size of the predator and prey species involved, a high frequency of predation may furthermore not be equivalent to a large flux of biomass. Importance may be a parameter that cannot be described entirely objectively in so far as that its definition depends on the investigators' idiosyncratic perspective of the specific biological system based on his or her own research intentions (Paine 1980, 1992; Winemiller 1990; Martinez 1991; Closs and Lake 1994; Goldwasser and Roughgarden 1997; Laska and Wootton 1998; Martinez et al. 1999). There is thus no unequivocal unit to measure link importance but we comply with Benke and Wallace (1997) who assert that the "measurement of energy flows in food webs is a quantification of the strength of actual linkages, regardless of what may or may not be controlling those flows". In any case, the use of quantitative descriptors appears sensible to extract ecological information from these systems.

The quantitative analysis of food-web structure as propagated here, is limited to web data that was compiled empirically. When information obtained from literature is used to deduce web interactions, the quantitative perspective is inevitably disregarded (though see Neutel et al. 2002; <http://www.ecopath.org>). The corresponding data sets, among them several recently recorded and highly detailed assemblages (e.g. those of Martinez 1991; Havens 1992; Deb 1995), can therefore not be referred to for a quantitative evaluation. Presently available web assemblages that appear appropriate for quantitative analysis (e.g., Winemiller 1990; Tavares-Cromar and Williams 1996; de Ruiter et al. 1995) may be prerequisite to certain modifications to meet our need for units of measurement that allow a comparison of data row- and columnwise; the "index of relative importance" (*IRI*) employed by Tavares-Cromar and Williams (1996) to quantify link importance is an example for a measurement requiring such modifications. For these compilations it will undoubtedly be worthwhile to examine the behaviour of quantitative food-web properties in respect to between-web regularities and characteristics.

The newly defined quantitative properties are certainly not as straightforward in their calculation as the traditionally applied qualitative counterparts. This disadvantage is negligible given the possibility of adequately incorporating the information inherent to quantitative food-web compilations. Due to the lower sensitivity to sampling effort, they appear more reliable for between-web comparisons (which up to now were often constricted due to varying or unknown levels of sampling intensity). Consequently, we are confident that these new tools will help foster the formulation of food-web regularities that are more robust to criticism (than e.g. the "food-web laws") and thus contribute to a better understanding of food-web structure.

Acknowledgments

We are grateful to R. Baltensperger, J.P. Gabriel, C. Mermod, R. Ulanowicz, and an anonymous reviewer for their help and comments. We are indebted to all people involved in food web compilation. This work was supported by Swiss NSF grant 31-52566.97, the Novartis Foundation, and partly the NCCR Plant Survival.

References

Baird, D., Ulanowicz, R.E., 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. Ecological Monographs 59:329-364.

Benke, A.C., Wallace, J.B., 1997. Trophic basis of production among riverine caddisflies: Implications for food web analysis. Ecology 78:1132-1145.

Bersier, L.F., Sugihara, G., 1997. Scaling regions for food web properties. Proceedings of the National Academy of Sciences of the United States of America 94:1247-1251.

Bersier, L.F., Dixon, P., Sugihara, G., 1999. Scale-invariant or scale-dependent behaviour of the link density property in food webs: A matter of sampling effort? American Naturalist 153:676-682.

Bersier, L.F., Banašek-Richter, C., Cattin, M.F., 2002. Quantitative descriptors of food-web matrices. Ecology 83:2394-2407.

Bondavalli, C., Ulanowicz, R.E., 1999. Unexpected effects of predators upon their prey: The case of the American Alligator. Ecosystems 2:49-63.

Briand, F., Cohen, J.E., 1984. Community food webs have scale-invariant structure. Nature 307:264-267.

Closs, G.P., Lake, P.S., 1994. Spatial and temporal variation in the structure of an intermittent-stream food web. Ecological Monographs 64:1-21.

Cohen, J.E., 1978. Food webs and niche space. Princeton University Press, Princeton, New Jersey.

Cohen, J.E., 1989. Food webs and community structure, in: Roughgarden, J., May, R.M., Levin, S.A. (Eds.), Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey, pp. 181-202.

Cohen, J.E., Briand, F., 1984. Trophic links of community food webs. Proceedings of the National Academy of Sciences of the United States of America 81:4105-4109.

Cohen, J.E., Newman, C.M., 1985. A stochastic theory of community food webs I. Models and aggregated data. Proceedings of the Royal Society of London B Biological Sciences 224:449-461.

Cohen, J.E., Briand, F., Newman, C.M., 1990. Community food webs: data and theory. Springer-Verlag, Berlin, Germany.

Cohen, J.E., Beaver, R.A., Cousins, S.H., DeAngelis, D.L., Goldwasser, L., Heong, K.L., Holt, R., Kohn, A.J., Lawton, J.H., Martinez, N., Omalley, R., Page, L.M., Patten, B.C., Pimm, S.L., Polis, G.A., Rejmanek, M., Schoener, T.W., Schoenly, K., Sprules, W.G., Teal, J.M., Ulanowicz, R.E., Warren, P.H., Wilbur, H.M., Yodzis, P., 1993. Improving food webs. Ecology 74:252-258.

de Ruiter, P.C., Neutel, A.M., Moore, J.C., 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. Science (Washington DC) 269:1257-1260.

Deb, D., 1995. Scale-dependence of food web structures: Tropical ponds a paradigm. Oikos 72:245-262.

Gaedke, U., Hochstadter, S., Straile, D., 2002. Interplay between energy limitation and nutritional deficiency: Empirical data and food web models. Ecological Monographs 72:251-270.

Goldwasser, L., Roughgarden, J., 1993. Construction and analysis of a large Caribbean food web. Ecology 74:1216-1233.

Goldwasser, L., Roughgarden, J., 1997. Sampling effects and the estimation of food-web properties. Ecology 78:41-54.

Hall, S.J., Raffaelli, D.G., 1991. Food-web patterns: lessons from a species-rich web. Journal of Animal Ecology 60:823-842.

Hall, S.J., Raffaelli, D.G., 1993. Food webs: theory and reality. Advances in Ecological Research 24:187-239.

Havens, K.E. 1992. Scale and structure in natural food webs. Science (Washington DC) 257:1107-1109.

Huxham, M., Raffaelli, D., Pike, A., 1995. Parasites and food web patterns. Journal of Animal Ecology 64:168-176.

Kenny, D., Loehle, C., 1991. Are food webs randomly connected? Ecology 72:1794-1799.

Laska, M.S., Wootton, J.T., 1998. Theoretical concepts and empirical approaches to measuring interaction strength. Ecology 79:461-476.

Lawton, J.H., 1989. Food webs, in: Cherrett, J.M. (Ed.), Ecological concepts. Blackwell Scientific, Oxford, pp. 43-78.

Legendre, P., Legendre, L., 1998. Numerical ecology. Elsevier, Amsterdam.

Martinez, N.D., 1991. Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. Ecological Monographs 61:367-392.

Martinez, N.D., 1992. Constant connectance in community food webs. American Naturalist 139:1208-1218.

Martinez, N.D., 1993. Effects of scale on food web structure. Science (Washington DC) 260:242-243.

Martinez, N.D., 1994. Scale-dependent constraints on food-web structure. American Naturalist 144:935-953.

Martinez, N.D., Hawkins, B.A., Dawah, H.A., Feifarek. B.P., 1999. Effects of sampling effort on characterization of food-web structure. Ecology 80:1044-1055.

May, R.M., 1983. The structure of food webs. Nature 301:566-568.

Neutel A.M., Heesterbeek, J.A.P., de Ruiter, P.C., 2002. Stability in real food webs: Weak links in long loops. Science (Washington DC) 296:1120-1123.

Paine, R.T., 1988. Food web: Road maps of interactions or grist for theoretical development? Ecology 69:1648-1654.

Paine, R.T., 1992. Food-web analysis through field measurement of per capita interaction strength. Nature (London) 355:73-75.

Paine, R.T., 2002. Trophic control of production in a rocky intertidal community. Science (Washington DC) 296:736-739.

Pimm, S.L., 1982. Food webs. Chapman and Hall, London.

Pimm, S.L., 1984. The complexity and stability of ecosystems. Nature (London) 307:321-326.

Pimm, S.L., Kitching R.L., 1988. Food web patterns: Trivial flaws or the basis of an active research program? Ecology 69:1669-1672.

Pimm, S.L., Lawton, J.H., Cohen. J.E., 1991. Food web patterns and their consequences. Nature (London) 350:669-674.

Polis, G.A., 1991. Complex trophic interactions in deserts: An empirical critique of food-web theory. American Naturalist 138:123-155.

Polis, G.A., 1994. Food-web, trophic cascades and community structure. Australian Journal of Ecology 19:121-136.

Raffaelli, D.G., Hall, S.J., 1996. Assessing the relative importance of trophic links in food webs. in: Polis, G.A., Winemiller, K.O. (Eds.), Food webs: Integration of patterns and dynamics. Chapman and Hall, New York, pp. 185-191.

Schoener, T.W., 1989. Food webs from the small to the large. Ecology 70:1559-1589.

Schoenly, K., Cohen, J.E., 1991. Temporal variation in food web structure: 16 empirical cases. Ecological Monographs 61: 267-298.

Sugihara, G., Schoenly, K., Trombla, A., 1989. Scale invariance in food web properties. Science (Washington DC) 245:48-52.

Sugihara G., Bersier, L.F., Schoenly, K., 1997. Effects of taxonomic and trophic aggregation on food web properties. Oecologia (Berlin) 112:272-284.

Tavares-Cromar, A.F., Williams, D.D., 1996. The importance of temporal resolution in food web analysis: Evidence for a detritus-based stream. Ecological Monographs 66:91-113.

Ulanowicz, R.E., 1986. Growth and development: Ecosystems phenomenology. Springer Verlag, New York.

Ulanowicz, R.E., Wolff, W.F., 1991. Ecosystem flow networks: Loaded dice? Mathematical Biosciences 103:45-68.

Williams, R.J., Martinez, N.D., 2000. Simple rules yield complex food webs. Nature (London) 404:180-183.

Winemiller, K.O., 1990. Spatial and temporal variation in tropical fish trophic networks. Ecological Monographs 60:331-367.

Winemiller, K.O., Pianka, E.R., Vitt, L.J., Joern, A., 2001. Food web laws or niche theory? Six independent empirical tests. American Naturalist 158:193-199.

Abstract.

Food-web descriptors serve as a means for among-web comparisons that are necessary for the discovery of regularities in respect to food-web structure. Qualitative descriptors were however found to be highly sensitive to varying levels of sampling effort. To circumvent these shortcomings, quantitative counterparts were proposed which take the magnitude of trophic interaction between species into consideration. For 14 properties we examined the performance with increasing sampling effort of a qualitative, an unweighted quantitative (giving the same weight to each taxon), and a weighted quantitative version (weighing each taxon by the amount of incoming and outgoing flows). The evaluation of ten extensively documented quantitative webs formed the basis for this analysis. The quantitative versions were found to be much more robust against variable sampling effort. This increase in accuracy is accomplished at the cost of a slight decrease in precision as compared to the qualitative properties. Conversely, the quantitative descriptors also proved less sensitive to differences in evenness in the distribution of link magnitude. By more adequately incorporating the information inherent to quantitative food-web compilations, quantitative descriptors are able to better represent the web, and are thus more suitable for the elucidation of general trends in food-web structure.

IV COMPLEXITY IN QUANTITATIVE FOOD WEBS[1]

Food webs depict the paths of biomass flow in communities[1]. They are highly complex and variable, but nevertheless possess regularities. First compilations revealed that food webs have scale-invariant structure[2;3]; however, recent, more highly resolved datasets did not uphold these scaling laws[4-6]. This search for regularities rested on qualitative food webs, thus disregarding the partly huge disparity in magnitude of biomass involved in trophic links between species[7;8]. To include this aspect we devised quantitative descriptors[9], and present the first analysis based on seven collections of quantitative food webs. Concentrating on link density, a fundamental descriptor of complexity, we found the conventional qualitative version to increase with the number of species, while quantitative counterparts remain largely scale-invariant within each collection. However, when viewed over the whole range of food-web sizes from all collections, quantitative link density is scale-dependent. This result has strong implications for the stability-complexity debate, indicating that complex systems must possess a special structure to remain stable.

The paradigm of complexity begetting stability in natural systems was challenged by May[10] on the basis of mathematical models[11]. Since this pioneering work, the link density property (LD, the total number of trophic links L divided by the number of species S in a food web) has played a central role for questions of complexity and stability[12]. Randomly assembled systems governed by generalized Lotka-Volterra equations will remain stable if the product of average interaction strength and the square root of LD remains smaller than one[10]. For early collections of food webs, LD was found to be scale-invariant, i.e., it remained more or less constant in food webs spanning a wide range in species richness[3;13;14]. This invariance was perceived as a fundamental result, since it represents a basic constraint on food webs that should prevent species rich communities to fall into the unstable region of parameters' space[7;13]. Following legitimate critique of the quality of these early datasets[15], a reappraisal of this assertion came from the analyses of more explicit, more highly resolved food webs that comprise a greater number of species and proved link density to increase with scale[4-6]. This debate however relied on traditionally designed, qualitative food webs, in which all links are treated as equal, and for which LD has been found to be highly sensitive to sampling effort[16;17]. Intrinsically scale-dependent systems have in fact been shown to appear scale-invariant when

---

[1] Chapter in preparation for publication.

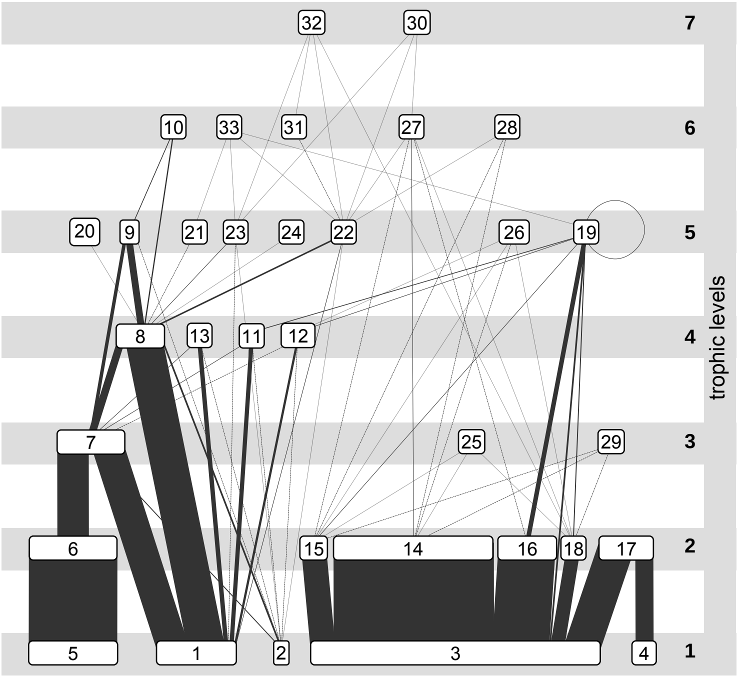


Fig. 1. Quantitative representation of the food web from the Chesapeake Bay mesohaline ecosystem (see Ref. 9 for a species list). Feeding interactions (links) are represented by lines connecting the two species involved. The width of each line is proportional to the magnitude of the corresponding link (in mgC m^{-2} y^{-1}). Traditional food-web analyses disregard quantitative information and treat all trophic interactions as equal in magnitude.

sampled with low intensity[18]. In highly resolved qualitative food webs, which include trophic links with huge differences in magnitude (see Fig. 1), the number of "weak" links is strongly affected by variation in sampling effort. This problem called for a quantitative approach of food webs[7;8], and descriptors taking the quantitative information on link magnitude into account have been devised since[9].

These quantitative descriptors are based on the reciprocal of Shannon's index of entropy. For each traditional qualitative property we postulated two versions: an unweighted version giving the same weight to each species, and a weighted version, which accounts for the amount of each species' total in- and outflow[9;19]. In the following, we are interested in assessing and elucidating the behaviour of these new quantitative versions of link density with respect to scale.

Quantitative datasets are scarce given the difficulty of quantifying or even detecting trophic interactions empirically. We were able to acquire seven compilations of food webs suited for a quantitative analysis[20]. These include: **a**) seven belowground webs from native and agricultural soils in Georgia and Colorado (USA), The Netherlands, and Sweden, which are detritus-based[21;22]; **b**) eight seasonal food webs from the Everglades of south Florida (USA)[23]; **c**) eight invertebrate dominated food webs sampled during two seasons in wet meadows in Switzerland[24]; **d**) ten seasonal food webs of Little Rock Lake, Wisconsin (USA)[25]; **e**) the five largest aquatic food webs from the collection of Ulanowicz and Wolff[26]; **f**) seven time-specific, detritus-based food webs from the macroinvertebrate riffle community of Duffin Creek, Ontario (Canada)[27]; **g**) the 13 largest time-specific, parasitoid webs compiled by Schönrogge and Crawley[28] from across Britain. For our analyses, we chose only webs with $S \geq 12$ to avoid bias due to small web size[29]. The datasets can be divided into two groups according to their scope: while collections **a** to **e** were designed to give a complete picture of the respective (feeding) communities, collections **f** and **g** represent only a fraction of a food web concentrating on a particular functional group. Furthermore, collections **a**, **c** and **g** encompass terrestrial systems, while **d**, **e** and **f** are aquatic, and **b** stems from the aquatic-terrestrial interface. In a first step, we analyse the collections independently since mixing datasets drawn up using different methodologies could affect the outcome of our analysis[30]. In a second step however, we also proceed to an analysis over all community webs since quantitative descriptors have been proven to be robust against sampling variation[31].

The results are given in Fig. 2 and Table 1. As found for other highly resolved food-webs collections[4-6], qualitative link density (LD) is scale dependent. This dependence is however weak in collection **e** and in both subsystems **f** and **g**, to a point that the slope is not significantly different from 0. With one exception (**d**), the slope for qualitative link density is larger than for either of the quantitative versions. Quantitative unweighted link density (LDq') considers link magnitude and gives the same weight to each species. It is nearly scale-invariant for both subsystems **f** and **g**, both collections of aquatic community webs **d** and **e**, and terrestrial system **c**, but scale-dependent for the terrestrial systems **a** and collection **b**. Taking total in- and outflows into account, the quantitative weighted link density (LDq) is statistically scale-invariant for all complete communities with the notable exception of the Little Rock Lake seasonal webs (**d**). For subsystems **f** and **g**, it is slightly negative, but not significantly different from zero.

Scale-dependence for qualitative link density LD stems from the fact that species are generally adapted to feed on resources that fall within a more or less restricted range of features in reference to size, morphology, behaviour, or habitat use; with increasing species richness, the number of resources that fall within this range are likely to increase and consequently be exploited[32]. This increase allows predators to feed on more prey, and thus explains the scale-dependence of qualitative link density. The same reasoning applies to species in their role as prey, since they suffer from more potential predators in rich environments. We ascribe the more moderate increase in qualitative link density with scale observed for subsystems (i.e., **f** and **g**) to the exclusion of trophic levels outside these systems. Consequently, many of the potential links that could have been realised with increasing species richness are also excluded.

The difference between qualitative (LD) and unweighted quantitative link density (LDq') is an expression of the degree to which in- and outflows for each species in the webs depart from a uniform distribution. Since weighted qualitative link density (LDq) further weighs the species

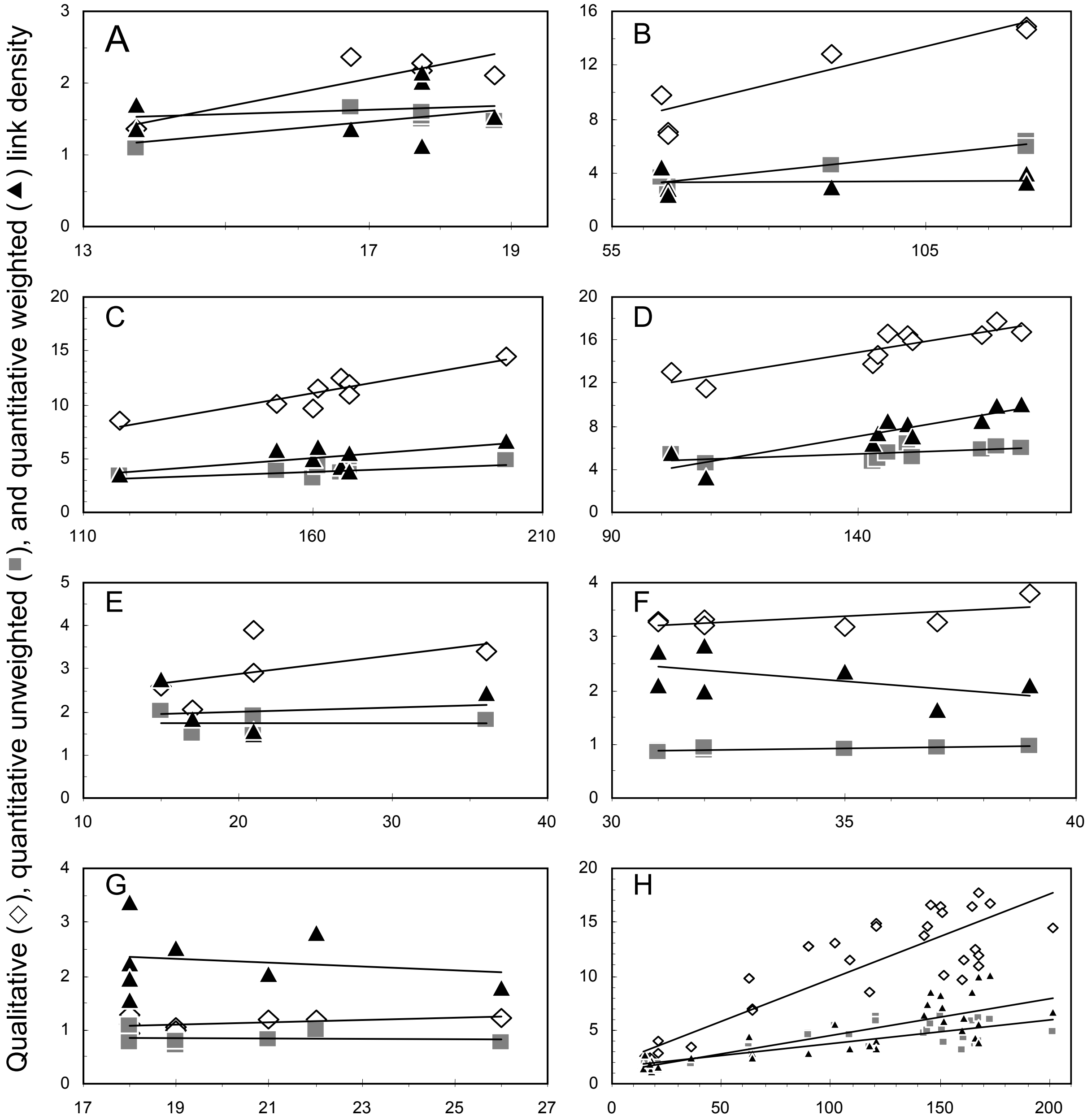


Fig. 2. Data and least-squares regressions (solid lines) of qualitative (diamonds), unweighted quantitative (squares), and weighted quantitative (triangles) link density for (**A** to **G**) seven collections of food webs (collections **a** to **g**, see text), and (**H**) for all community webs (collections **a** to **e**).

by their total in- and outflows, the difference between LDq' and LDq is attributable to the variation between species with respect to the partitioning of total biomass flowing in the system (the total system throughput of Ulanowicz[33]). The value of LDq is thus constrained by trophodynamics[34]: species with many predators and prey (who stand at a high trophic level) typically have low biomass and consequently little in- and outflow, while those with few predators and prey (who take on a low trophic position) generally have high biomass (Fig. 3).

For community webs **c**, **d**, and **e**, as well as for subsystems **f** and **g,** we find LDq' to be approximately independent of scale. At the same time, the scale-dependence of LD implies that

Table 1. Results of linear regression analyses for the three versions of link density over species number in the food webs of each collection (see Fig. 2).

Food-web	qualitative (LD)			quantitative unweighted (LDq')					
collection	slope	R^2	*P*	slope	R^2	*P*	slope	R^2	*P*
a	0.192	0.803	0.006	0.090		0.018	0.031	0.029	0.715
b	0.114	0.827	0.002	0.049	0.919	<0.001	0.001	0.002	0.917
c	0.074	0.823	0.002	0.016	0.447	0.070	0.032	0.414	0.085
d	0.075	0.788	0.001	0.015	0.353	0.070	0.079	0.814	<0.001
e	0.045	0.268	0.371	0.001	<0.001	0.974	0.011	0.024	0.804
f	0.042	0.414	0.119	0.010	0.633	0.032	-0.066	0.251	0.252
g	0.018	0.218	0.174	-0.003	0.004	0.866	-0.033	0.025	0.662
a-e	0.078	0.795	<0.001	0.022	0.667	<0.001	0.034	0.688	<0.001

species eat and are eaten by more species with increasing scale. In sum, these results indicate that the partitioning of biomass, within each species inflows and outflows, must become more inequitable with increasing species richness, thus compensating for the increase of LD. In terrestrial system **a** and collection **b**, on the other hand, this compensation is not as complete, giving rise to moderately scale-dependent LDq'. Two non-exclusive explanations could account for this difference: firstly, species in systems **a** and **b** may be more prone to adapt to new food sources, and are thus able to use new prey species more equitably; secondly, higher heterogeneity in some terrestrial habitats may limit the accessibility to potential prey, thus preventing rare species to fall within consumers' diets.

Weighted quantitative link density LDq appears scale invariant for all datasets except **d**. Fig. 3 elucidates that species of low trophic levels generally prevail in contributing to LDq. In a species-rich environment, indiscriminate consumers of the lowest trophic levels have the opportunity to eat a large number of prey, as well as accounting for a large portion of total in- and outflows. Thus, for a system which comprises a large number of such consumers, we expect LDq to behave in a scale-dependent manner. Such a trophic constellation is a common

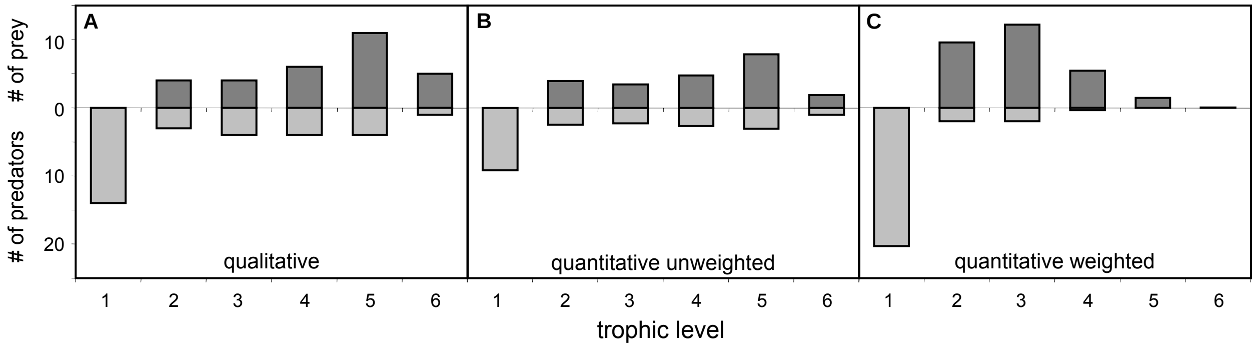


Fig. 3. Total number of prey species (dark grey) and of predators species (light grey) in six trophic levels for a food web of collection **e**. In (**A**), values are species counts; in (**B**) they correspond to "effective" numbers of prey and predators[9], and in (**C**) to effective numbers weighted by inflows and outflows to each species. Averaging these numbers of prey and predators over the number of species will yield LD, LDq', and LDq, respectively.

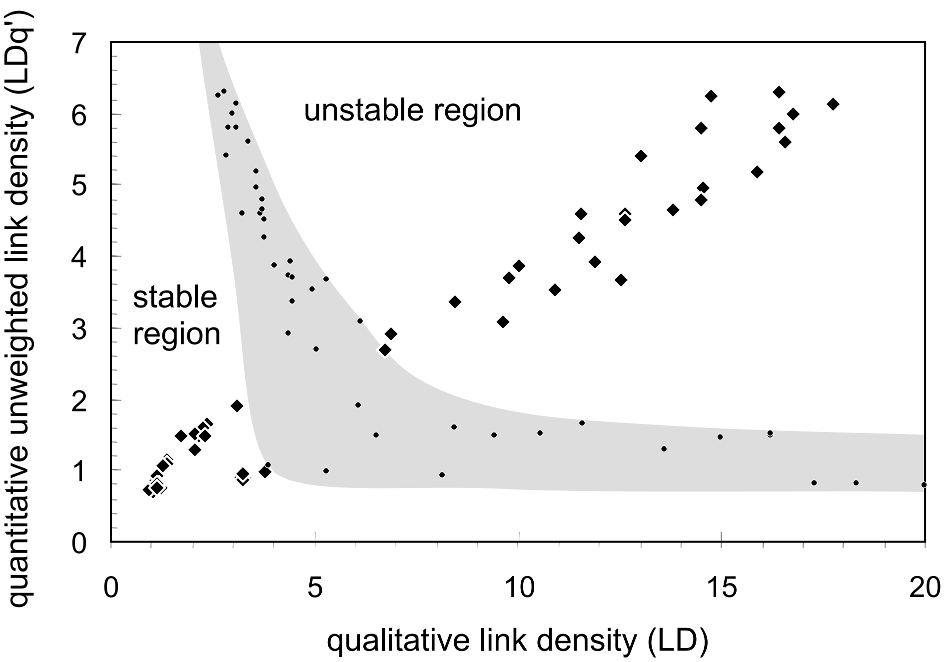


Fig. 4. Relationship between qualitative and quantitative unweighted link density for the food webs of collections **a** to **g**. From this information, an estimate of the average interaction strength can be computed, and the dynamical stability of the food web can be deduced following the May and Wigener stability criterion. Diamonds represent observed food webs; small dots, which designate the boundary between the stable and the unstable domain, correspond to hypothetical food webs with LDs calculated on the basis of LDq' values. The shaded region separates food webs predicted to be stable from those predicted to be unstable according to the May and Wigener criterion.

feature of many aquatic systems, while herbivores in terrestrial systems are known to be more specialized[35]. In accordance with the aforesaid, we find scale-dependence for the Little Rock Lake food webs (**d**), but not for dataset **e**. This discrepancy presumably stems from the fact that in the latter aquatic systems, most plankton species are aggregated into a small number of functional groups.

In sum, scale-dependence is clearly observed for the qualitative link density, while both measures of quantitative link density are close to scale-invariance within each collection of food webs. Invariance is however superseded by moderate scale-dependence when viewing both quantitative properties over the whole range of species richness of the five collections containing community food webs (Fig. 2H). This is unlikely an artefact due to merging studies performed with different methodologies and sampling effort[18;30], as we have shown that the quantitative descriptors are quite robust to such source of variability[31]. Two possibilities remain: First, scale-invariance within food-web collections may reflect insufficient statistical power; second, such systems may be internally scale-invariant, while the dependence seen over all food webs proceeds in a stepwise fashion. Whatever the explanation, scale-dependence of quantitative link density has profound implications for our understanding of the dynamical behaviour of these systems.

To elucidate the relationship between link density and stability, we follow Ulanowicz[36] by assuming that the unweighted quantitative link density LDq' is an expression of both qualitative (or topological) link density LD and average interaction strength *a*. It is thus possible to express *a* in terms of both LD and LDq'[37], enabling to find the region dividing the unstable and stable domains in the LD–LDq' plane on the basis of May and Wigener's stability criterion[10]. Plotting all food webs on this plane results in a predominance of webs that fall within the "unstable" domain (Fig. 4). As a consequence, real ecosystems must possess some special features that keep them from collapsing. Clearly, three strong assumptions of May's models can be challenged to explain this pattern. Firstly, generalized Lotka-Volterra equations do not correctly capture the dynamic of species interactions, and other equations are more stabilizing[38]. Secondly, the theoretical distribution of interaction strengths (Gaussian) does not reflect the one observed in real systems, where very few strong interactions and a wealth of very weak ones are prevalent[39]. This feature again affects the stability properties[40]. Finally, real food webs are not randomly connected; instead the architecture of interactions may be structured in a way that stabilizes the system[41-43]. Our results on the relationship between species richness and link density not only give insights into basic structural constraints pertaining to food webs, but also provide the boundaries within which to explore the three aforementioned non-exclusive explanations of the relationship between complexity and stability.

---

1. S. L. Pimm, J. H. Lawton, J. E. Cohen, *Nature* 350, 669-674 (1991).
2. J. E. Cohen, F. Briand, C. N. Newman, Community Food Webs: Data and Theory (Springer-Verlag, Berlin, 1990).
3. G. Sugihara, K. Schoenly, A. Trombla, *Science* 245, 48-52 (1989).
4. K. O. Winemiller, *Ecol.Monogr.* 60, 331-367 (1990).
5. K. E. Havens, *Science* 257, 1107-1109 (1992).
6. D. Deb, *Oikos* 72, 245-262 (1995).
7. R. M. May, *Nature* 301, 566-568 (1983).
8. D. Kenny and C. Loehle, *Ecology* 72, 1794-1799 (1991).
9. L. F. Bersier, C. Banašek-Richter, M. F. Cattin, *Ecology* 83, 2394-2407 (2002).
10. R. M. May, Stability and Complexity of model ecosystems. (Princeton University Press, Princeton NJ, ed. 2, 1974).
11. K. S. McCann, *Nature* 405, 228-233 (2000).
12. P. H. Warren, *Trends Ecol.& Evol.* 9, 136-141 (1994).
13. M. Rejmánek and P. Stary, *Nature* 280, 311-313 (1979).
14. J. E. Cohen and F. Briand, *Proc.Natl.Acad.Sci.USA* 81, 4105-4109 (1984).
15. R. T. Paine, *Ecology* 69, 1648-1654 (1988).
16. L. Goldwasser and J. Roughgarden, *Ecology (Washington D C)* 78, 41-54 (1997).
17. N. D. Martinez, B. A. Hawkins, H. A. Dawah, B. P. Feifarek, *Ecology* 80, 1044-1055 (1999).
18. L. F. Bersier, P. Dixon, G. Sugihara, *Am.Nat.* 153, 676-682 (1999).
19. Given an *S*-by-*S* quantitative food web matrix $\mathbf{b} = [b_{ij}]$, with b_{ij} the amount of biomass (or other measures of importance for trophic interactions) passing from taxon *i* to taxon *j* per unit surface

area and time, one can express the quantitative unweighted link density as

$$LD'_q = \frac{1}{2S}\left(\sum_{i=1}^{s} n_{P,i} + \sum_{j=1}^{s} n_{N,j}\right), \tag{1}$$

and the quantitative weighted link density as

$$LD_q = \frac{1}{2}\left(\sum_{i=1}^{s} \frac{b_{i\cdot}}{b_{\cdot\cdot}} \cdot n_{P,i} + \sum_{j=1}^{s} \frac{b_{\cdot j}}{b_{\cdot\cdot}} \cdot n_{N,j}\right), \tag{2}$$

with $n_{P,i}$ the effective number of predators

$$n_{P,i} = \exp\left(-\sum_{j=1}^{s} \frac{b_{ij}}{b_{i\cdot}} \cdot \ln\frac{b_{ij}}{b_{i\cdot}}\right), \tag{3}$$

and $n_{N,j}$ the effective number of prey

$$n_{P,i} = \exp\left(-\sum_{i=1}^{s} \frac{b_{ij}}{b_{\cdot j}} \cdot \ln\frac{b_{ij}}{b_{\cdot j}}\right). \tag{4}$$

20. With the exception of datasets **c** and **f**, all authors report the amount of biomass flow per unit area and time between species as a measure of linkage magnitude. Tavares-Cromar and Williams (**f**) employ the IRI-value instead, which constrains the column sums to be constant for all consumers. Their data was subject to modifications to accord to our need for units of measurement that are comparable row and column wise: body mass m_j and abundance a_j of each consumer was estimated; for a consumer *j*, each inflow b_{ij} was multiplied by a constant such that $\Sigma_i\ b_{ij}=a_j \cdot m_j^{3/4}$. For collections **c**, binary information on feeding links as well as species abundance and body mass were available. Magnitude of trophic links was deduced as follows: for consumer *j*, the column sum is equal to *j's* abundance times its body mass raised to the power of ¾ ($\Sigma_i\ b_{ij}=a_j \cdot m_j^{3/4}$); each b_{ij} is then set in proportion to the biomass of prey *i* with respect to the biomass of all prey of consumer *j*.
21. P. C. de Ruiter, A. M. Neutel, J. C. Moore, *Science* 269, 1257-1260 (1995).
22. P. C. de Ruiter, A. M. Neutel, J. C. Moore, *Applied Soil Ecology* 10, 217-228 (1998).
23. Ulanowicz, com. pers.
24. M. F. Cattin, Food web ecology: models and application to conservation (PhD thesis, University of Neuchâtel, Switzerland, 2004).
25. Y. Merz, Food web properties: a re-examination of Little Rock Lake food web through seasonal resolution (Diploma thesis, University of Neuchâtel, Neuchâtel, Switzerland, 2003).
26. R. E. Ulanowicz and W. F. Wolff, *Math.Biosci.* 103, 45-68 (1991).
27. A. F. Tavares-Cromar and D. D. Williams, *Ecol.Monogr.* 66, 91-113 (1996).
28. K. Schonrogge and M. J. Crawley, *J.Anim.Ecol.* 69, 841-868 (2000).
29. L. F. Bersier and G. Sugihara, *Proc.Natl.Acad.Sci.USA* 94, 1247-1251 (1997).
30. K. O. Winemiller, E. R. Pianka, L. J. Vitt, A. Joern, *Am.Nat.* 158, 193-199 (2001).
31. C. Banašek-Richter, M. F. Cattin, L. F. Bersier, *J.Theor.Biol.* 226, 23-32 (2004).
32. P. H. Warren, *Am.Nat.* 136, 689-700 (1990).
33. R. E. Ulanowicz, Growth and Development: Ecosystems Phenomenology (Springer Verlag, New York, 1986).
34. R. L. Lindeman, *Ecology* 23, 399-418 (1942).
35. K. E. Havens, *Oikos* 78, 75-80 (1997).
36. R. E. Ulanowicz, *BioSystems* 64, 13-22 (2002).
37. Following ref. 36, we define the average interaction strength *a* for a given food web as the constant value that, when multiplying each b_{ij} in equation (1) or rather (3) and (4), yields $LD_q'=LD$. When all b_{ij} are equal, $a=1$; the more inequitable the distribution of b_{ij} , the smaller *a* ($0<a\leq1$).
38. M. Kondoh, *Science* 299, 1388-1391 (2003).
39. R. T. Paine, *Nature* 355, 73-75 (1992).
40. K. McCann, A. Hastings, G. R. Huxel, *Nature* 395, 794-798 (1998).
41. D. L. DeAngelis, *Ecology* 56, 238-243 (1975).
42. G. Sugihara, Niche hierarchy: Structure, Organization and Assembly In Natural Communities (PhD thesis. Princeton University, 1982).
43. J. M. Dambacher, H. W. LI, P. A. Rossignol, *Ecol.Modell.* 161, 79-93 (2003).

V THE STRUCTURE OF QUANTITATIVE FOOD WEBS[1]

Introduction

Food web ecology aims to describe and explain the biological processes that drive feeding interactions between species. A prerequisite in the context of this objective is to have descriptors at hand that enable a sensible comparison of food webs compiled for systems that encompass different taxa or originate from different environments. Similarities or differences can thus be discerned and consequently explained. A host of such properties has been proposed in the past (e.g. Yodzis 1989, Hall and Raffaelli 1993), including descriptors that are rather straightforward (e.g. link density, which is the number of links divided by the total number of species, L/S) as well as more elaborate ones, e.g. intervality (Cohen 1978), or the lumpability of food webs (Solow and Beet 1998). If with the help of these descriptors it is possible to discern food web regularities proving valid over a large range of systems, we would proceed one step forward in understanding the mechanisms responsible for the patterns we observe in nature. With few exceptions, e.g. Ulanowicz's (1986) ascendancy, these descriptors are based on binary information on trophic interactions: an interaction is reported as being present or absent. Details on the strength of the interactions are not considered.

Research in this field dates back to the work of Hutchinson (1959) who suggested that food chains, which depict the path within a food web matrix from any taxon to a basal taxon, tend to be short. A number of authors furthermore maintained that the ratio of the number of predators to the number of prey in a web should be constant at approximately 3:4 (e.g. Evans and Murdoch 1968, Arnold 1972, Cameron 1972, Cohen 1977, 1978). Most often, regularities were sought that relate descriptive features to the species richness (or scale) of the web. Rejmánek and Stary for example, found connectance to decrease hyperbolically with increasing species richness for 31 plant-aphid-parasitoid communities (1979). This implies that link density is independent of scale (i.e. stays constant over webs that span a wide range in species richness), a result confirmed by Cohen and Briand (1984) for 62 community food webs. Consequently the "link-species scaling law" was deduced (Cohen and Newman 1985), alongside the "species scaling law" and the "link scaling law", which are also based on the findings of Cohen and Briand (1984) and Briand and Cohen (1984). These "laws" anticipate the proportion of top species (%T, species having no predators), the proportion of intermediate species (%I, species having prey and predators) and the proportion of basal species (%B,

---

[1] Chapter in preparation for publication.

species without prey), as well as the proportion of links between top and intermediate (%T-I), top and basal (%T-B), intermediate (%I-I), and intermediate and basal (%I-B) links to be scale-invariant.

In the aftermath, while some authors consented to the notion of scale-invariant properties (Sugihara et al. 1989, Havens 1992), the results of an increasing number of investigations based in part on more extensive data material rejected this idea (Schoener 1989, Warren 1989, 1990, Winemiller 1989, 1990, Deb 1995, Winemiller et al. 2001). They suggested instead that most descriptors do vary with scale, while directed connectance (the ratio of realised to maximally possible links, L/S^2) is a constant (Martinez 1992, 1993, 1994). However, the idea of constant connectance in turn was also challenged on the basis of disagreeing results (e.g. Winemiller et al. 2001).

This topic of debate was extended by results drawn from the investigation of the effects of variable sampling intensity (Goldwasser and Roughgarden 1997, Bersier et al. 1999, Martinez et al. 1999). It became apparent that conventionally employed food web descriptors are not independent of the amount of effort expended in the process of sampling. These findings infer that the basis of conventional descriptors, namely qualitative information on food web interactions, can only poorly depict complex biocoenoses (Kenny and Loehle 1991). In an attempt to provide a more thorough approach to web comparisons and descriptions, new properties were designed that take quantitative information on feedings interactions between species into account (Bersier et al. 2002). We found these descriptors to be more robust against varying levels of sampling effort than their qualitative counterparts (Banašek-Richter et al. 2004). Consequently, these new tools have the potential to uncover regularities that are more immune to criticism and that contribute to a better understanding of food-web structure.

Here we present the first analysis of quantitative descriptors over five collections of community food webs. The dataset comprises food webs from a wide variety of aquatic and terrestrial environments, spanning 13 to 202 species. Various models were used to regress the properties against scale over all collections. We additionally checked if the properties consistently decreased or increased with scale between collections. Quantitative properties have the desirable characteristic of being more robust to sampling effort, but this may be at the cost of being less sensitive in detecting differences between systems. This possibility is evaluated in a comparison between aquatic and terrestrial systems. We show that quantitative descriptors provide new insights to the structure and organization of the studied systems, and that they aptly discern differences between habitats.

Material and Methods

Datasets

The data analyzed stems from five collections of food webs that span a wide range in species richness from varying habitats. Each collection is assigned a number from **1** to **5**, which for practicality is henceforth used to refer to each dataset. They comprise:

1) Seven belowground, detritus-based webs from native and agricultural soils in Colorado and Georgia (USA), The Netherlands, and Sweden (de Ruiter et al. 1995, 1998). For each of the latter three sites, two webs are available that differ with respect to the farming practice applied to the sampled area (14 ≤ S ≤ 19).

2) Eight seasonal food webs from four sites in the Everglades of southern Florida (USA) (Ulanowicz, <http://cbl.umces.edu/~ãtlss>). For each site (cypress wetlands, Florida Bay, mangroves, marshes/sloughs) one web was assembled during the dry, one during the wet season (66 ≤ S ≤ 124).

3) Eight seasonal food webs from wet meadows on the southern shore of Lake Neuchâtel, Switzerland (Cattin 2004). Four webs were collected during early summer, four during late summer/early fall. For each season, two webs come from a *Schoenus nigricans* dominated vegetation zone, two from a *Cladium mariscus* dominated vegetation zone, and each pair consists of one web from an area with triennial mowing treatment, and one web from a control area left unmown (118 ≤ S ≤ 202).

4) Ten seasonal food webs of Little Rock Lake, Wisconsin (USA) (Martinez 1991, Bersier et al. 1999, Merz 2003). Within the lake, two basins were separated to carry out an acidification experiment. Five seasonal webs were assembled for each basin (102 ≤ S ≤ 173).

5) The five largest aquatic food webs from the collection of Ulanowicz and Wolff (1991). These include two tidal marsh gut webs from Crystal River, Florida (USA) (Homer and Kemp unpl., Ulanowicz 1986), one web from Ythan Estuary in Aberdeenshire (Scotland) (Baird and Milne 1981), one seasonal web from the Chesapeake Bay mesohaline ecosystem (Baird and Ulanowicz 1989), and one web from the Baltic Sea ecosystem. Note that the species in this collection are highly aggregated (13 ≤ S ≤ 36).

A quantitative matrix that denotes trophic interactions in terms of biomass flow in units weight per unit area and time was derived for each of these 38 webs. While we had this information at hand for our own collection **3**, it could be taken directly from the published data for collection **2** and **4**, and was kindly provided to us by the respective authors for collections **1** and **5**. Note that for collections **3** and **4**, the quantitative importance of links was deduced from the binary food-web matrices and information on abundance and body mass of all species. It was assumed that, for each consumer, the total amount of food ingested per unit space and time was proportional to its abundance times its body mass raised to the power of $^3/_4$;

additionally, each prey of a given species is consumed in proportion to its biomass (i.e. its body mass times its abundance) with respect to the biomass of all prey of the consumer of interest.

Food-web properties

On the basis of the quantitative food web matrixes, a set of 14 descriptors was calculated in a qualitative, a quantitative unweighted, and a quantitative weighted version. The properties analyzed are: the proportion of top, intermediate, and basal species (%T, %I, and %B), the ratio of prey to predators (N:P), link density (LD), directed connectance (*C*), the proportion of links between top and intermediate (%TI), top and basal (%TB), intermediate (%II), and intermediate and basal (%IB), generality (*G*, the average number of prey eaten per predator), vulnerability (*V*, the average number of predators per prey), standard deviation in generality (sd*G*), and standard deviation in vulnerability (sd*V*). The quantitative counterparts for each of these properties are calculated in accordance with Bersier et al. (2002) to whom the reader may refer for an exact account of definitions and derivations. Shannon and Wiener's diversity index (Shannon 1948) forms the basis for the derivation of quantitative properties, which thus account for the variability in the amount of biomass flow to and from all species in the system. Unweighted and weighted quantitative properties differ insofar as the former give the same weight to each species, while the latter take the inequality between species with respect to the amount of biomass they transfer into consideration by weighing each species by its contribution to total biomass flux. In the following, the quantitative indices will be represented with a subscripted "q", followed by an apostrophe for the unweighted version (e.g., $\%T_q$, $\%T_q'$).

Analyses

In a first step we analyze the scaling behaviour of the above listed 42 food web properties over the webs of all collections. All properties are regressed against web size (S) employing a suite of five classical models to find the best fit for each dataset. These models are a linear, a power, an exponential, a logarithmic, and an inverse regression. Because all models have two parameters, the best fit is evaluated by the adjusted coefficient of determination (R^2). Additionally, we attempt to uncover those properties that are "consistent" in the sense that, in an among-web comparison, a similar trend in terms of the linear regression slopes is discernable.

In the next step, we search for differences between collections from aquatic as opposed to terrestrial environments that are manifest independent of the influence scale has on the examined properties (Bengtsson 1994). A non-parametric Mann-Whitney U-test is therefore performed on the residuals of the regressions. The terrestrial category comprises collections **1** and **3**, the aquatic category collections **4** and **5**. Collection **2** is at the interface of aquatic and terrestrial systems and is thus excluded from the analysis. Since multiple tests are performed on the same dataset, we correct all P-values according to Holm (1979).

Results

Overall, the trend lines for the qualitative and unweighted quantitative version are very similar for most properties considered (Fig. 1 - 3). Correspondingly, in 12 of 14 cases, the best fit model for the quantitative unweighted property is the same as for its qualitative counterpart. Note however that the ordinate does not always span the same range and despite identical models for LD and LDq', G and Gq', as well as for V and Vq' there is a large discrepancy in absolute values within these three pairs. The weighted quantitative properties are most often best described by an exponential function. They show only few similarities with the corresponding qualitative and unweighted quantitative counterparts, to the extent that regression parameters have opposite signs for five properties (e.g. negative for N:Pq, positive for N:P and N:Pq'). With the exception of sdVq', all qualitative and quantitative unweighted properties have regression slopes that are significantly different from 0 at the 0.05 level (most even at 0.01). Nevertheless, the quantitative weighted versions of %I, %TB, %TI, %IB, and sdG appear independent of scale, and coincidently all have very low R^2-values (< 0.14).

Linear regression analyses within each collection renders three properties that behave similarly throughout all five datasets: Link density (LD), generality (G) and vulnerability (V) consistently increase with scale for all three versions of each property (with the exception of collection **5** for the quantitative weighted versions). Most other properties show discrete trends, but without bearing significant results in opposite directions. This is not surprising for moderately scale-dependent properties, and given the small span in species richness of some datasets. However, all versions of the proportion of basal species (%B), the qualitative and quantitative unweighted version of %I, as well as the proportion of links between intermediate and basal species (%IB), yield significant trends in opposite directions, reflecting basic differences between collection **4** versus **1** and **2**.

When comparing aquatic and terrestrial food webs, 18 of the 42 properties considered make out a significant pair wise difference between habitats at the 0.05 level (Table 1). This is the case for 7 qualitative, 6 unweighted quantitative, and 5 weighted quantitative properties. For the qualitative version, terrestrial environments mark a higher proportion of intermediate species (%I) and greater standard deviation in generality (sdG) than aquatic systems. These in turn had a higher proportion of basal species (%B) and of intermediate to basal links (%IB), as well as higher link density (LD), generality (G), and vulnerability (V). The same results are observed for the respective unweighted quantitative versions with the exception of sdGq' for which we find no significant difference (identical results for %I and %Iq' as well as %B, %Bq', and %Bq are self-evident, given identical results for the calculation of these properties in Fig. 1). The results for

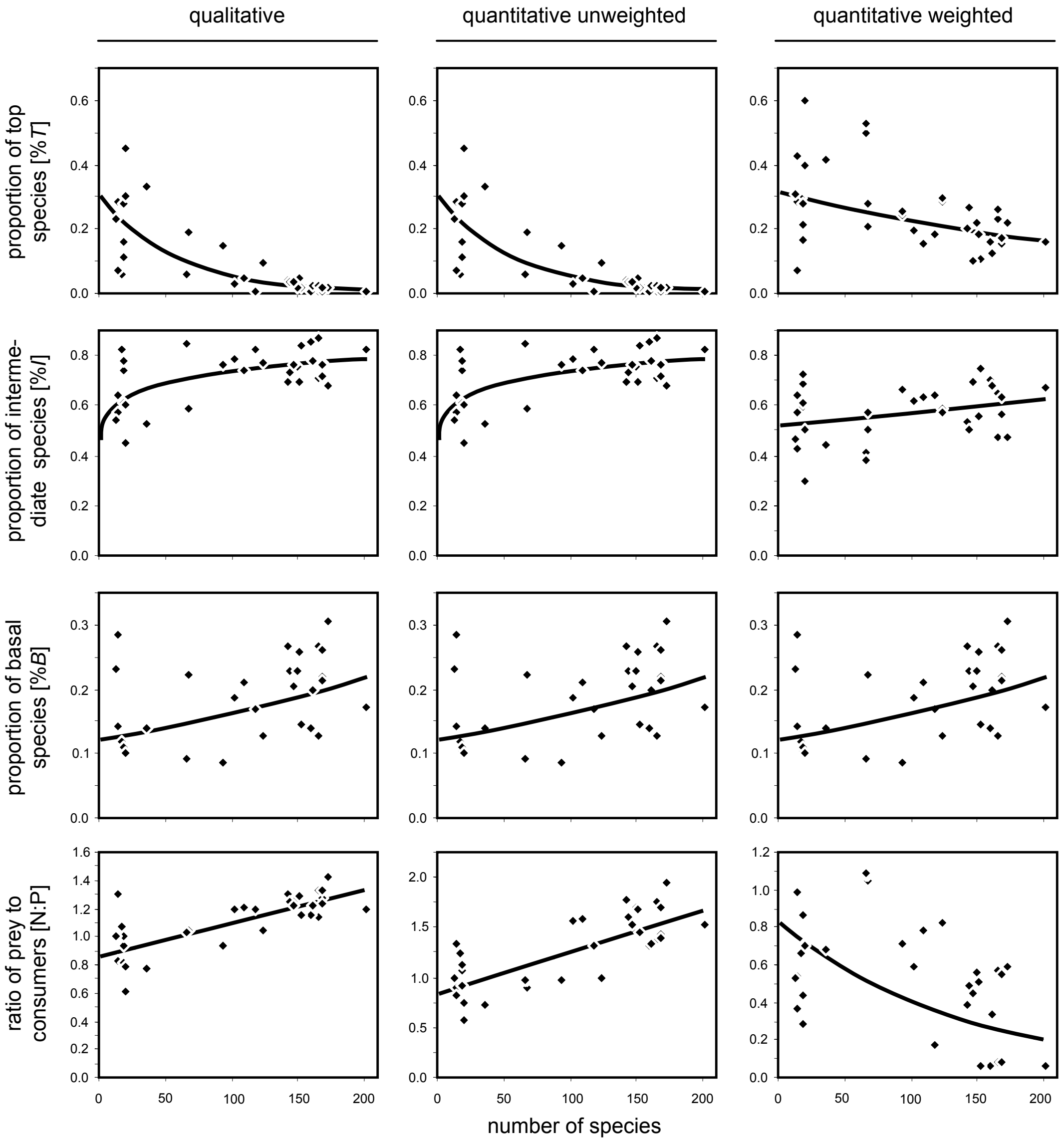


Fig. 1 Regression analyses of qualitative and quantitative food web properties for five food web collections. Depicted is the best 2-parameter model for each property. Best fit model, results from regression analysis, and Holm-corrected P-values are as follows: [%T]: exp, $R^2 = 0.70$, $P < 0.001$; [%Tq']: exp, $R^2=0.70$, $P<0.001$; [%Tq]: exp, $R^2=0.19$, $P=0.027$; [%I]: power, $R^2=0.37$, $P<0.001$; [%Iq']: power, $R^2=0.35$, $P=0.002$; [%Iq]: exp, $R^2=0.07$, $P=0.19$; [%B]: exp, $R^2=0.21$, $P=0.021$; [%Bq']: exp, $R^2=0.21$, $P=0.021$; [%Bq]: exp, $R^2=0.21$, $P=0.021$; [N:P]: linear, $R^2=0.58$, $P<0.001$; [N:Pq']: linear, $R^2=0.56$, $P<0.001$; [N:Pq]: exp, $R^2=0.23$, $P=0.014$.

the quantitative weighted versions of generality (Gq), link density (LDq), and the proportion of basal species (%Bq) correspond to those of the other two versions. Aquatic habitats are furthermore distinguished by significantly higher values of N:Pq and less sdVq than terrestrial systems.

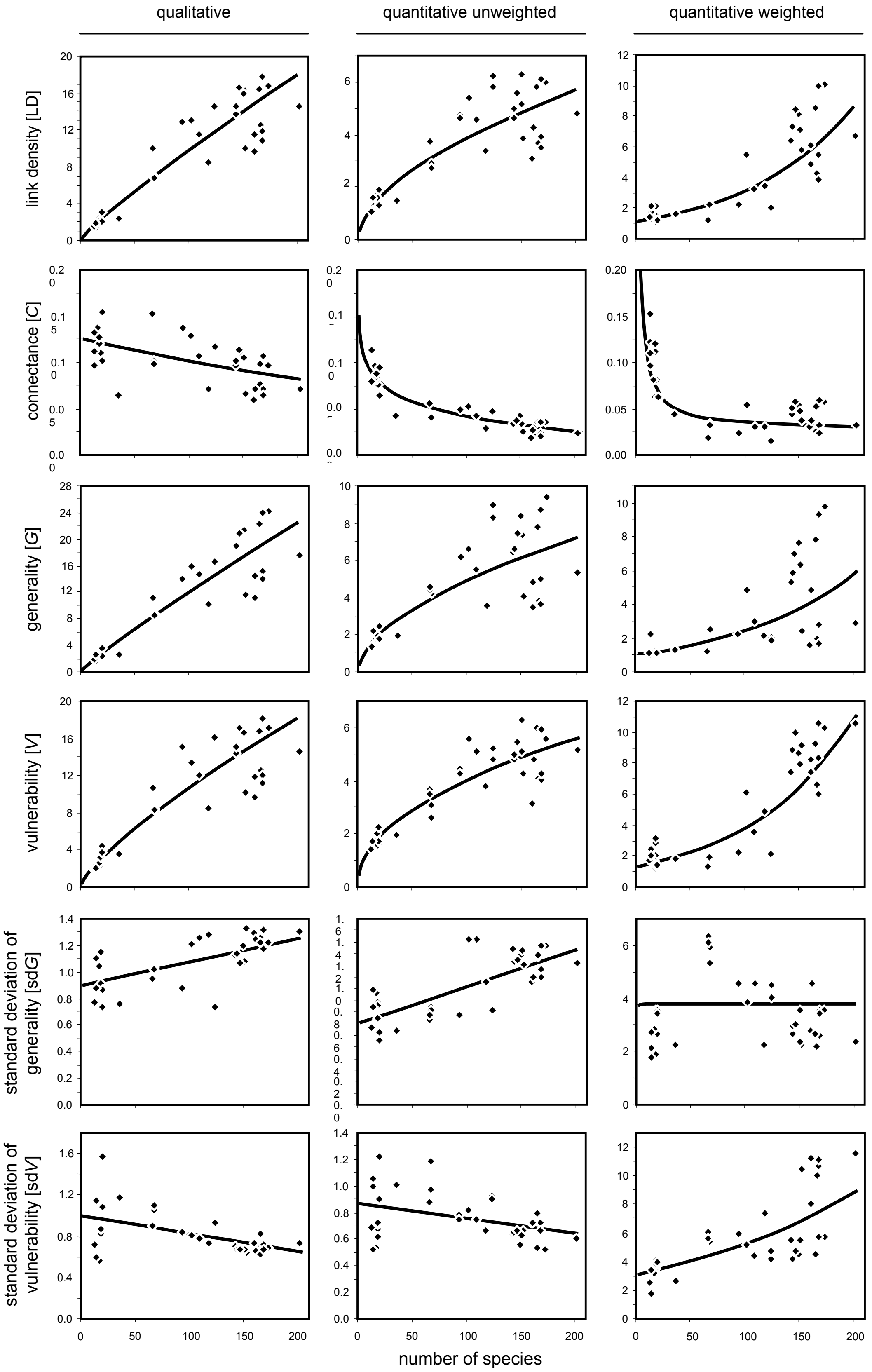


Fig. 2 Regression analyses of qualitative and quantitative food web properties for five food web collections. Depicted is the best 2-parameter model for each property. Best fit model, results from regression analysis, and Holm-corrected P-values are as follows: [LD]: power, R^2=0.93, P<0.001; [LDq']: power, R^2=0.85, P<0.001; [LDq]: exp, R^2=0.75, P<0.001; [C]: exp, R^2=0.25, P=0.01; [Cq']: log, R^2=0.84, P<0.001; [Cq]: inverse, R^2=0.70, P<0.001; [G]: power, R^2=0.93, P<0.001; [Gq']: power, R^2=0.77, P<0.001; [Gq]: exp, R^2=0.55, P<0.001; [V]: power, R^2=0.91, P<0.001; [Vq']: power, R^2=0.89, P<0.001; [Vq]: exp, R^2=0.73, P<0.001; [sdG]: linear, R^2=0.34, P=0.002; [sdGq']: linear, R^2=0.57, P<0.001; [sdGq]: inverse, R^2=0.12, P=0.092; [sdV]: linear, R^2=0.26, P=0.008; [sdVq']: linear, R^2=0.14, P=0.079; [sdVq]: exp, R^2=0.55, P<0.001.

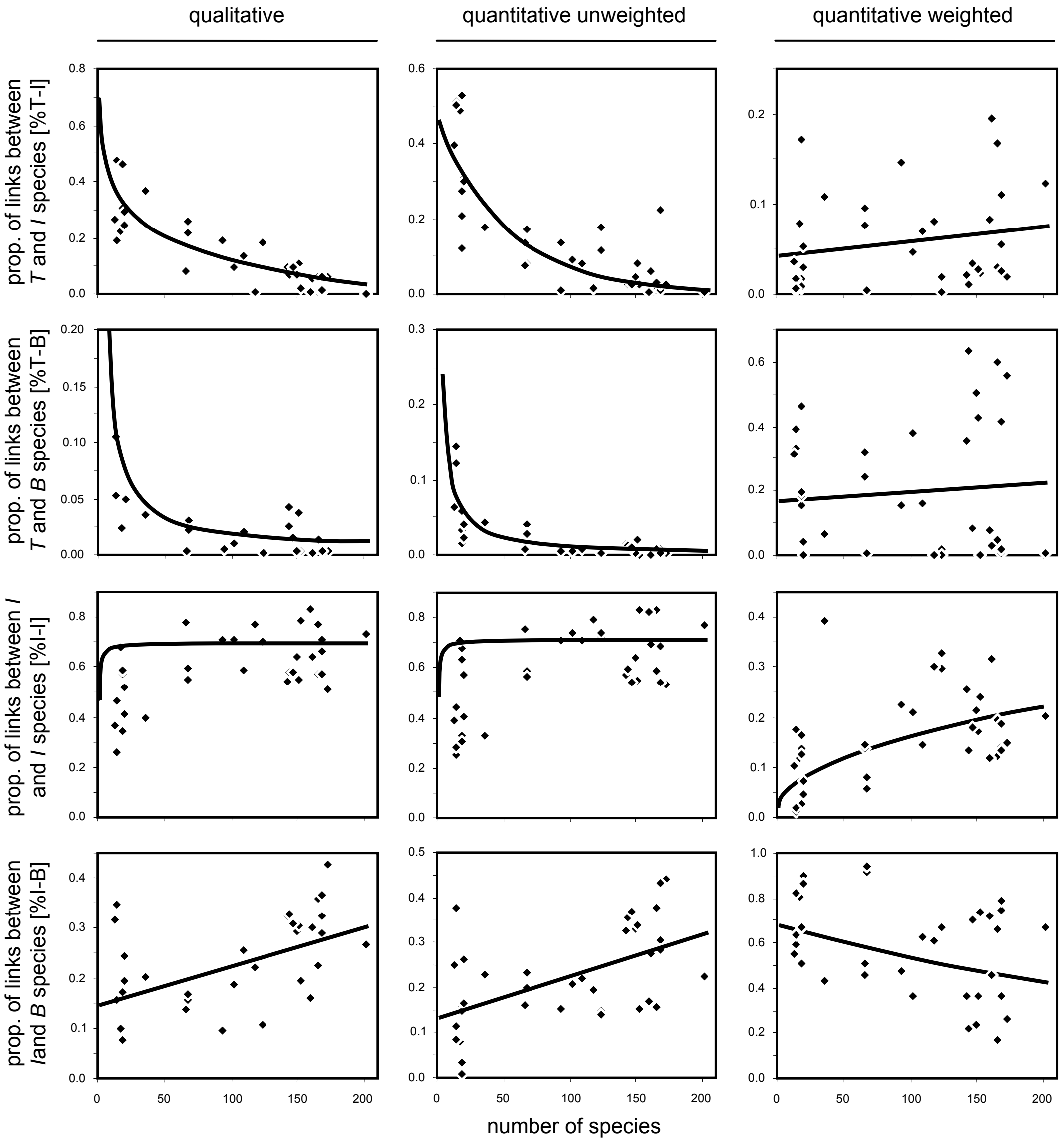


Fig. 3 Regression analyses of qualitative and quantitative food web properties for five food web collections. Depicted is the best 2-parameter model for each property. Best fit model, results from regression analysis, and Holm-corrected P-values are as follows: [%TI]: log, R^2=0.71, P<0.001; [%TIq']: exp, R^2=0.77, P<0.001; [%TIq]: linear, R^2=0.01, P=0.50; [%TB]: inverse, R^2=0.39, P<0.001; [%TBq']: inverse, R^2=0.40, P<0.001; [%TBq]: linear, R^2=0, P=0.59; [%II]: inverse, R^2=0.49, P<0.001; [%IIq']: inverse, R^2=0.43, P<0.001; [%IIq]: power, R^2=0.31; P=0.002; [%IB]: linear, R^2=0.25, P=0.011; [%IBq']: linear, R^2=0.28, P=0.006; [%IBq]: exp, R^2=0.106, P=0.105.

Discussion

Scaling behaviour

In light of the discussion about food web regularities outlined above, an important result of our analyses is the observation that properties are not scale invariant, meaning that food web structure changes with scale. Scale invariance is currently ascribed to connectance (Martinez 1992), a generalization that our data collections also contradict.

Qualitative and quantitative unweighted properties render very similar results with respect to their scaling behaviour (Fig. 1 - 3). This trend was expected, since quantitative unweighted

Table 1 Analyses of habitat differences for qualitative and quantitative properties. Results of a Mann-Whitney U-test performed on the residuals of the regressions illustrated in Fig.1-3. P-values in bold denote significant habitat differences, shaded figures indicate the habitat with the greater value.

	qualitative			quantitative unweighted			quantitative weighted		
property	terrestrial	aquatic	P-value	terrestrial	aquatic	P-value	terrestrial	aquatic	P-value
%T	-0.014	0.023	1	-0.014	0.023	1	-0.023	0.024	1
%I	0.050	-0.047	**0.026**	0.050	-0.047	**0.025**	0.072	-0.040	0.103
%B	-0.015	0.052	**0.012**	-0.015	0.052	**0.012**	-0.015	0.052	**0.011**
N:P	-0.022	0.051	0.859	-0.020	0.146	0.588	-0.196	0.165	**0.003**
LD	-2.019	1.060	**0.003**	-0.654	0.451	**0.008**	-0.410	1.595	**0.050**
C	-0.013	0.007	0.055	-0.004	0.002	0.681	0.008	0.016	1
G	-2.731	2.202	**0.003**	-1.199	0.947	**0.004**	-0.944	2.085	**0.001**
V	-2.275	1.053	**0.002**	-0.453	0.455	**0.006**	0.362	1.339	0.974
sdG	0.114	-0.031	**0.013**	0.016	0.082	1	-1.115	-0.768	1
sdV	-0.036	-0.011	0.885	-0.038	-0.035	1	1.624	-1.246	**0.001**
%TI	-0.006	-0.012	1	0.019	-0.004	1	0.019	-0.022	0.688
%TB	-0.027	-0.014	0.684	-0.011	-0.010	1	-0.066	0.107	0.266
%II	-0.092	-0.159	0.996	-0.084	-0.163	0.935	0.006	0.023	1
%IB	-0.025	0.072	**0.003**	-0.060	0.084	**0.001**	0.099	-0.056	0.320

descriptors give the same weight to each species as do qualitative descriptors. Basically, the former provide similar information on scaling behaviour as qualitative descriptors do, but have the desirable feature of being more robust to sampling effects (Banašek-Richter et al. 2004). Below we will show that a comparison between qualitative and quantitative descriptors sheds light on otherwise hidden features of food web structure.

The proportion of top species decreases with scale for all three property versions which is in agreement with the results of other authors (Martinez 1994, Carney et al. 1997, Martinez and Lawton 1997). This trend is least pronounced for the quantitative weighted version (%Tq), simply due to the convention we adopted to distinguish top and intermediate species (Bersier et al. 2002). In a qualitative sense, species with very few or a sole predator, which are especially numerous in species rich systems are considered intermediate. We define them as top species for the quantitative weighted version. Concurrently, the proportion of intermediate species increases in all three versions as expected (Deb 1995, Carney et al. 1997, Havens 1997, Martinez and Lawton 1997), even though this trend is not significant for %Iq. Contradictory to results from earlier studies (Winemiller 1990, Martinez 1994, Deb 1995, Havens 1997, Martinez and Lawton 1997) and therefore unexpected, is the increase in basal species with species richness for all versions. This result is attributable to the high number of phytoplankton species in the Little Rock Lake webs (collection **4**). When this data is excluded from the evaluation, %B shows scale-invariant behaviour (results from best fit linear regression are: $R_{adj}^2 = 0$, F = 0.97, P = 0.33, a = 0.0002, b = 0.135), which suggests that (with the exception of phytoplankton rich systems) food webs generally comprise approximately 14% basal species.

The trends observed for the proportions of top and basal species cause the prey-predator ratio to increase markedly for the qualitative and the unweighted quantitative version from approximately 1 for small webs to 1.2 and 1.5 respectively at the far end of the range considered (S = 202). This contradicts Schoener's predictions that the ratio of prey to predators should decrease with S (Schoener 1989). A comparison between our prey-predator ratio N:P and the predator-prey ratio PP (PP = 1/N:P) used in other studies proves to be informative: in concert with earlier results (Sugihara et al. 1989, Cohen et al. 1990), Deb (1995) observed constant predator-prey ratios in two tropical freshwater ponds with mean values near 1. For two compilations of food webs comprising 60 invertebrate-dominated and 50 pelagic webs respectively, Havens (1997) also reported scale invariant behaviour and average PP values of 2.2 and 0.6 respectively. Transferring this approach to our data renders PP values that decrease with scale with means of 1.0 for terrestrial and 1.3 for aquatic systems. The discrepancies between our results and those of other studies with respect to scaling behaviour are not solely attributable to high %B values for collection **4** (disregarding **4** from the analysis in Fig. 1 renders $N{:}P = 0.0019S + 0.866$, $p < 0.01$, linear regression). Thus, the systems we analyzed are distinguished by the feature of an approximately equivalent number of predator and prey species in small webs, and a shift towards more prey species per predator in large systems. This means that in species-rich environments, predators feed on a broader range of resources. The exponential decrease of N:Pq is at first sight surprising since the results for %Bq match those of the other two versions and %Tq decreases with scale as do %T and %Tq' (even though less steeply). The result for N:Pq can however be explained as follows: in species-rich systems, there is an asymmetry in the distribution of in- and outflows. The latter become more inequitable due to a few dominant prey species, while inflows to consumers are more evenly distributed.

A power function best describes the analyzed webs' behaviour with respect to LD, which takes on values greater 15 for $S \approx 150$. As commented above for N:P in a species-rich environment, consumers feed on a wider range of prey than in an environment with a more limited diversity of resources. Apparently however, this process is not associated with only a few prey (or predators) being predominantly preyed on (or that predominate the amount consumed), since LDq' also increases with S. Instead, the diet of consumers (and the preys' predator list) must be more diverse not only with respect to species number but also with respect to the partitioning of biomass consumed (or allocated) per species in large ecosystems. This is understandable given that the difference between qualitative and quantitative unweighted descriptors is an expression of the inequalities in distributions of in- and outflows. The scaling behaviour of LDq' is also best described by a power function which levels off more strongly in large webs than LD does (the same applies to G and Gq' or V and Vq', see below). Thus, the distributions of in- and outflows are less equitable in large systems. When considering LDq, our results furthermore indicate that species with a highly diverse diet (or with highly diverse predators) in large systems also outweigh the others with respect to the amount of inflow (or outflow). We deduce this from the observation that LDq, which takes in- and outflows per species into account, takes on an exponential course with scale. The three versions of connectance are obtained by dividing the respective version of link density by S. Thus, the results for connectance are in concert with the discussion lead above. Noteworthy is that the analyzed data does not support the prediction of "constant connectance" (Martinez 1992) since C decreases with species richness.

Generality (or "generalization") and vulnerability are defined to reflect how link density is partitioned between consumers and prey respectively. First introduced by Schoener (1989), G was predicted to be scale-invariant, implying that there is a limit to the number of different prey species a predator can consume. V on the other hand should increase with S due to a predicted increase in the number of predators with S, and a fixed number of predators a prey species should be able to defend against. Since both properties increase in all three versions, our analyses only confirm the latter hypothesis, albeit for different reasons. As already asserted on the basis of the N:P results, the predators in the webs analyzed here seem to be more generalist when more species are present. Generality exceeding vulnerability for the qualitative and the quantitative unweighted version implies that the inflows to a species are generally more diverse than the outflows. However, %Vq roughly equals or exceeds %Gq in large webs. This asymmetry can be explained by the nature of plant-herbivore interactions: plants are often consumed in great amounts by numerous herbivores. In terms of food web properties this translates into species with high qualitative vulnerability (plants) also having large total outflows (the same relation is valid for phyto- and zooplankton in aquatic systems).

Standard deviation in generality increases while standard deviation in vulnerability decreases for the qualitative and the unweighted quantitative version. This means on the one hand that the variability in numbers of prey increases in species-rich systems. On the other hand, variability in numbers of predators decreases with scale. The quantitative weighted versions of sdG and sdV are numerically much larger, which entails total in- and outflows to be highly heterogeneous. Furthermore, sdGq is invariant across the species range considered. In concert with the increase in sdG and sdGq' this means that total inflows are more equitable in large systems. The contrary is true for the outflows, since sdVq increases while the other two versions decrease. Apparently there is much heterogeneity between prey species with respect to the magnitude of outflows in large systems.

In food web literature, link proportions have been reported to be scale-invariant (Cohen et al. 1990, Havens 1992) or instead, %II is observed to increase, while %TB decreases and %TI and %IB are constant with scale (Martinez 1994, Deb 1995). Our analyses provide quite a different picture. Due to the steep decrease in percentage of top species with scale, %TI and %TIq' drop to below 10% for large systems, while %TB and %TBq' are diminished to less than 5%. The proportion of intermediate links (%II, %IIq') on the other hand, strongly increases for small webs, then levels off to invariant behaviour for S>50. Since %TI + %TB +%II + %IB = 1, the concurrent decrease in %TB and %TI along with the constancy of %II call for an increase in %IB with S (the same applies to the quantitative unweighted version). In our analysis the linear increase of %IB and %IBq' again owes to the data from Little Rock Lake. When these webs are excluded the properties behave invariant of scale. Due to highly variable results for %TIq, %TBq, and %IBq between webs we are not able to ascertain a behaviour significantly different from scale-invariance for these properties. In large systems, top-intermediate and top-basal links play a much bigger role once species are weighed by their respective in- and outflows. Nevertheless, most biomass in the systems is exchanged between intermediate and basal species with values of roughly 50% for %IBq even in large systems. I.e. depending on the milieu, plant-herbivore and phytoplankton-zooplankton interactions dominate the systems.

Aquatic vs. terrestrial systems

Schoener (1989) suggests that "genuine differences between kinds of food webs may exist", which would necessitate a distinction between systems from different habitats when food web hypotheses are tested. Extending this line of thought, Bengtsson pointed out that an ecologically meaningful comparison of food web descriptors between webs requires the dependence of food web variables on species richness to be accounted for (Bengtsson 1994, see also Goldwasser and Roughgarden 1993, Martinez 1994). Otherwise, differences in species richness may either be the actual factor that determines the acquired results or they may mask real differences between systems. Essentially, discerning differences between habitats brings us closer to explaining their true nature. In the analysis of Table 1 we distinguish between aquatic and terrestrial systems. The former are generally characterized by a modest degree of compartmentalization, combined with a large number of generalist feeders at low trophic levels, which account for much of the biomass in- and outflow in the system (Warren 1990, Winemiller 1990, Bengtsson 1994). Terrestrial ecosystems on the other hand, are usually more highly compartmented with more specialist species (e.g. Rejmánek and Stary 1979).

The aquatic and terrestrial webs we analyzed differ with respect to the proportion of intermediate and basal species. For all three property versions, aquatic systems have a significantly higher proportion of basal species, but significantly fewer intermediates which again goes back to the data of Little Rock Lake. The observation of generalist dominated aquatic systems versus more specialized consumers in terrestrial systems is supported by higher N:P values for aquatic ecosystems, which however, are only significant once in- and outflows are taken into account (N:Pq). From a mathematical perspective, a higher quantitative weighted prey-predator ratio for aquatic systems implies that either the numerator of the corresponding equation is higher (due to more equitable outflows) and/or that the denominator has lower values (due to less equitable outflows) as compared with terrestrial systems. Since we also observe higher %Bq-values for aquatic webs, it is the more equitable outflows that determine the results for N:Pq. Based on conventional (qualitative) definitions of C and LD, aquatic webs were found to be highly connected with a large number of links per species (Warren 1990, Bengtsson 1994). This was ascribed to the predominance of indiscriminate herbivores, which brings about that linkage is more size- than species-dependent, so that particle feeders (e.g. planktivores, zooplankton) can consume a potentially limitless number of prey species. Due to high resource specificity the number of feeding interactions per species in terrestrial environments are more limited so that C and LD are typically small (Warren 1990). Our results validate these observations with respect to link density, but not to connectance even though the habitat difference for qualitative directed connectance C is only marginally non-significant. Thus, connectance appears less apt at discerning structural variation. In accordance with the results for link density, generality and vulnerability yield similar patterns: both are greater in aquatic systems. We found no habitat differences regarding properties that describe the proportions of links, with the exception of %IB and %IBq. The proportion of intermediate-basal links is higher in aquatic food webs, which is in accordance with the predominance of indiscriminate herbivores in these systems.

Our analyses of quantitative food webs confirm food webs to be highly variable and complex and affirm scale-dependent behaviour with respect to most of the analyzed properties. Quantitative descriptors are designed to capture the structure of biomass in- and outflow within a community. Here we show how they can shed light on features that are not detectable qualitatively. In order to confirm, refute, or complement the results we obtained, new quantitative datasets and quantitative analyses of their web properties are necessary. Only when the structures that govern food webs are aptly described, can we go one decisive step further to attempt to explain the processes behind the observed structures (Cattin et al. 2004)

REFERENCES

Arnold, S.J., 1972. Species densities of predators and their prey. American Naturalist 106: 220-236.

Baird, D., Milne, H., 1981. Energy flow in the Ythan estuary, Aberdeenshire, Scotland. Estuarine, Coastal and Shelf Science 13: 455-472.

Baird, D., Ulanowicz, R.E., 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. Ecological Monographs 59:329-364.

Banašek-Richter, C., Cattin, M.F., Bersier, L.F., 2004. Sampling effects and the robustness of quantitative and qualitative food-web descriptors. Journal of Theoretical Biology 226: 23-32.

Bengtsson, J., 1994. Confounding variables and independent observations in comparative analyses of food webs. Ecology **75**:1282-1288.

Bersier, L.F., Dixon, P., Sugihara, G., 1999. Scale-invariant or scale-dependent behaviour of the link density property in food webs: A matter of sampling effort? American Naturalist 153:676-682.

Bersier, L.F., Banašek-Richter, C., Cattin, M.F., 2002. Quantitative descriptors of food-web matrices. Ecology 83:2394-2407.

Briand, F., Cohen, J.E., 1984. Community food webs have scale-invariant structure. Nature 307:264-267.

Cameron, G.N., 1972. Analysis of insect trophic diversity in two salt marsh communities. Ecology 53: 58-73.

Carney, H.J., Havens, K.E., Bersier. L.F., 1997. Nonlinear scale dependence and spatiotemporal variability in planktonic food webs. Oikos **79**:230-240.

Cattin, M.F., 2004. Food web ecology: models and application to conservation. PhD thesis, University of Neuchâtel, Switzerland.

Cattin, M.F., Bersier, L.F., Banasek-Richter, C., Baltensperger, R., Gabriel, J.P., 2004. Phylogenetic constraints and adaptation explain food-web structure. Nature 427: 835-839.

Cohen, J. E., 1977. Ratio of prey to predators in community food webs. Nature (London) **270**:165-167.

——— 1978. Food webs and niche space. Princeton University Press, Princeton, New Jersey.

Cohen, J.E., Briand, F., 1984. Trophic links of community food webs. Proceedings of the National Academy of Sciences of the United States of America 81:4105-4109.

Cohen, J.E., Newman, C.M., 1985. A stochastic theory of community food webs I. Models and aggregated data. Proceedings of the Royal Society of London B Biological Sciences 224:449-461.

Cohen, J.E., Briand, F., Newman, C.N., 1990. Community Food Webs: Data and Theory. Springer Verlag, Berlin.

Deb, D., 1995. Scale-dependence of food web structures: Tropical ponds a paradigm. Oikos 72:245-262.

de Ruiter, P.C., Neutel, A.M., Moore, J.C., 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. Science (Washington DC) 269:1257-1260.

——— 1998. Biodiversity in soil ecosystems: the role of energy flow and community stability. Applied Soil Ecology 10: 217-228.

Evans, F.C., Murdoch, W.W., 1968. Taxonomic composition, trophic structure, and seasonal occurrence in a grassland insect community. Journal of Animal Ecology, 37: 259-273.

Goldwasser, L., Roughgarden, J., 1993. Construction and analysis of a large Caribbean food web. Ecology 74: 1216-1233.

——— 1997. Sampling effects and the estimation of food-web properties. Ecology 78: 41-54.

Hall, S.J., Raffaelli, D.G., 1993. Food webs: theory and reality. Advances in Ecological Research 24: 187-239.

Havens, K.E., 1992. Scale and structure in natural food webs. Science (Washington DC) 257: 1107-1109.

——— 1997. Unique structural properties of pelagic food webs. Oikos 78: 75-80.

Holm, S., 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistic 6:65-70.

Homer, M., Kemp, W.M., 1975. Trophic exchanges in the ecosystem of a tidal marsh gut, Crystal River, Florida, unpl. manuscript, CEES Report.

Hutchinson. G.E., 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93: 145-159.

Kenny, D., Loehle, C., 1991. Are Food Webs Randomly Connected? Ecology 72: 1794-1799.

Martinez, N.D., 1992. Constant connectance in community food webs. American Naturalist 139:1208-1218.

——— 1993. Effects of scale on food web structure. Science (Washington DC) 260:242-243.

——— 1994. Scale-dependent constraints on food-web structure. American Naturalist 144:935-953.

Martinez, N.D., Lawton, J.H., 1995. Scale and food-web structure – from local to global. Oikos 73: 148-154.

Martinez, N.D., Hawkins, B.A., Dawah, H.A., Feifarek. B.P., 1999. Effects of sampling effort on characterization of food-web structure. Ecology 80:1044-1055.

Merz, Y., 2003. Food web properties: a re-examination of Little Rock Lake food web through seasonal resolution. Diploma thesis, University of Neuchâtel, Switzerland.

Rejmánek, M., Stary, P., 1979. Connectance in real biotic communities and critical values for stability of model ecosystems. Nature 280: 311-313.

Schoener, T.W., 1989. Food webs from the small to the large. Ecology 70:1559-1589.

Shannon, C.E., 1948. A mathematical theory of communications. Bell System Technical Journal **27**:379-423.

Solow, A.R., Beet, A.R., 1998. On lumping species in food webs. Ecology 79: 2013-2018.

Sugihara, G., Schoenly, K., Trombla, A., 1989. Scale invariance in food web properties. Science (Washington DC) 245:48-52.

Ulanowicz, R.E., 1986. Growth and development: Ecosystems phenomenology. Springer Verlag, New York.

Ulanowicz, R.E., Wolff, W.F., 1991. Ecosystem flow networks: Loaded dice? Mathematical Biosciences 103:45-68.

Warren, P.H., 1989. Spatial and temporal variation in the structure of a freshwater food web. Oikos 55: 299-311.

——— 1990. Variation in food-web structure: The determinants of connectance. American Naturalist 136, 689-700.

Winemiller, K.O., 1989. Must connectance decrease with species richness? American Naturalist 134: 960-968.

——— 1990. Spatial and temporal variation in tropical fish trophic networks. Ecological Monographs 60:331-367.

Winemiller, K.O., Pianka, E.R., Vitt, L.J., Joern, A., 2001. Food web laws or niche theory? Six independent empirical tests. American Naturalist 158:193-199.

Yodzis, P., 1989. Introduction to Theoretical Ecology. Harper and Row, New York.

Abstract.

The recognition of regularities in natural food webs is a decisive step toward an understanding of ecosystem structure and functioning. Early studies found scale-invariance in food web structure that gave rise to a large body of theory, which in turn eventually led to its rejection on the grounds of more recent analyses. The latter relied on highly resolved, but qualitative food webs that leave differences between biomass flows as large as six orders of magnitude unaccounted for. Without a quantitative approach, the question of how food webs are structured thus remains largely unsolved. Here we analyze the scaling behaviour of food web properties for five collections of highly resolved quantitative food webs spanning 13 to 202 species. For most properties considered, we ascertain that food web structure is not invariant of scale and that scale-dependence is nonlinear. For example, species-rich webs have less top, and more intermediate and basal species, as well as higher link density. We find the distribution of in- and outflow to be more asymmetric in species-rich food webs due to few prominent prey species but more evenly distributed inflows to consumers. Moreover, species with a highly diverse diet (or with highly diverse predators) in large systems also outweigh the others with respect to the amount of inflow (or outflow). By removing the effect of web size we are able to discern differences between aquatic and terrestrial systems and find both qualitative and quantitative property versions to aptly perceive such differences. Terrestrial systems are distinguished by a greater proportion of intermediate species, while more generality and vulnerability, higher link density, as well as a greater proportion of basal species and basal-intermediate links are features of the aquatic communities. Overall, quantitative properties uncover patterns in food webs with respect to the flux of biomass between links that are useful in complementing the results drawn from the analysis of qualitative descriptors. We expect this approach to foster the introduction of new concepts on the organization of quantitative food webs.

VI FOOD-WEB STRUCTURE: FROM SCALE INVARIANCE TO SCALE DEPENDENCE, AND BACK AGAIN?[1]

Introduction

Food webs are complex and variable objects, and a general understanding of their structure and functioning must thus rely on a careful examination of their regularities. The search for scale-invariant features is of special interest in this respect (Briand and Cohen 1984), since scale-invariance may represent basic structural constraints valuable for the discovery of underlying processes. An illuminating example of such a scale-invariant property drawn from astronomy and physics is Kepler's third law of planetary motion, which relates the revolution time t of a planet to its average distance from the sun d: t^2/d^3 is a constant value; the finding of this invariant property was a decisive step in the discovery of the underlying process, the law of universal gravitation. Most natural ecosystems are orders of magnitude more complicated and more variable than planetary motion. Their elements – species or sets of species – are themselves complex objects: they are composed of heterogeneous individuals, each involved in a wealth of interactions between themselves and their biotic and abiotic environment, and each able to adapt and to evolve. Many details have to be discarded to tackle the study of such intricate systems. Hence, food web ecologists concentrate on just one type of interaction depicting a vital aspect of ecosystems: trophic interactions describe the flows of biomass between species.

The burst of interest in the study of trophic interactions within communities stems from the stability-complexity debate; the finding that local stability in random systems is not a mathematical consequence of complexity (Gardner and Ashby 1970; May 1974, but see Cohen and Newman 1984) bolstered the study of natural systems. In this framework, complexity was expressed as the product of the number of species in the community (S) and connectance (C), calculated as the quotient of the number of effective interactions (L) and the number of possible interactions (S^2). The so defined measure of complexity equals link density ($LD = L/S$). Studies of initial compilations of food webs resulted in the intriguing generalization that LD is scale invariant, i.e., that this property remains constant across webs of varying size (Rejmánek and Stary 1979; Yodzis 1980; Cohen and Briand 1984; Sugihara et al. 1989). This finding is in agreement with May's stability criterion (May 1983) and was perceived as a fundamental structural constraint of food webs. However, together with criticism of the data used to assess the scaling behaviour of the link density property (e.g., Paine 1988; Polis 1991), a scale-dependent power law was soon proposed to provide a more accurate fit of link density to

---

[1] Book chapter in review: Banašek-Richter C., Bersier L.-F. and Cattin M.-F. In *Food web 2003*. de Ruiter, P., Wolters, V. and Moore, J.C. (eds).

variable food web collections (Schoener 1989; Cohen et al. 1990; Pimm et al. 1991). Indeed, subsequently compiled collections of food webs did not uphold scale invariance for this property (Warren 1989, 1990; Winemiller 1990; Havens 1992; Deb 1995).

Link density's scaling behaviour is illustrated in Fig. 1 for six food web compilations on which this debate is based. Collections **a** and **b** were compiled from early literature data and appear scale-invariant. More recently assembled collections on the other hand (**c** – **f**), are clearly scale-dependent. One hypothesis to explain this discrepancy is that link density's scaling behaviour is system dependent: all collections showing strong scale-dependence come from aquatic environments (Winemiller 1990; Havens 1992; Deb 1995; Little Rock Lake), while the other two combine webs from various habitats (Sugihara et al. 1989; Cohen et al. 1990). In the same vein, after factoring out the effect of web size, Bengtsson (1994) found a similar difference between aquatic and terrestrial webs in a data set extended from collection **a** (Schoenly et al. 1991). Havens (1997) proposed biological features to explain the scaling behaviour of link density in pelagic communities, namely 1) the predominance of filter-feeding predators and 2) the very high diversity of small autotrophic prey species. Most terrestrial systems however, may also be much more complex than those reported in data sets **a** and **b** (e.g., Polis and Hurd 1996; Reagan and Waide 1996). We studied terrestrial food webs in wet meadows, which exhibit scale-dependence for the link density property (see below). Thus, intrinsic differences between systems are likely, but they cannot explain the opposing results of Fig. 1 unanimously.

Another hypothesis relates these discrepancies to differences in sampling procedures and variable effort exerted toward the description of the data. Concerned specifically with the problem of sampling effort, Goldwasser and Roughgarden (1997) analyzed 21 web properties for a large, highly resolved food web (Goldwasser and Roughgarden 1993). These authors employed different procedures to mimic increasing sampling effort, and found most properties, link density included, to be sensitive to sampling effort with high levels of sampling necessary to reach the properties' original values . A similar conclusion was reached by Martinez et al. (1999) who analyzed sampling effects in a highly resolved food web consisting of grasses and stem-borer insects. However, both former studies did not tackle the effect of sampling effort on the scaling behaviour of *LD* in collections of food webs. Using two models and three data sets, Bersier et al. (1999) showed that low sampling effort tends to produce the appearance of scale invariance in intrinsically scale dependent systems. This is a simple explanation reconciling the studies in Fig. 1, since early collections of food webs taken from the literature (Cohen and Briand 1984; Sugihara et al. 1989; Cohen et al. 1990) were most often not intended to reflect the full complexity of the trophic interactions.

These sampling effects highlight the following problem inherent to the qualitative approach. The distribution of link importance in highly resolved food webs is likely to be strongly uneven (see e.g., Goldwasser and Roughgarden 1993). By giving the same weight to all links, binary food webs distorts the true picture of their structure (Kenny and Loehle 1991). Thus, quantitative data, which allows a more sensible approach to food web structure is needed (May

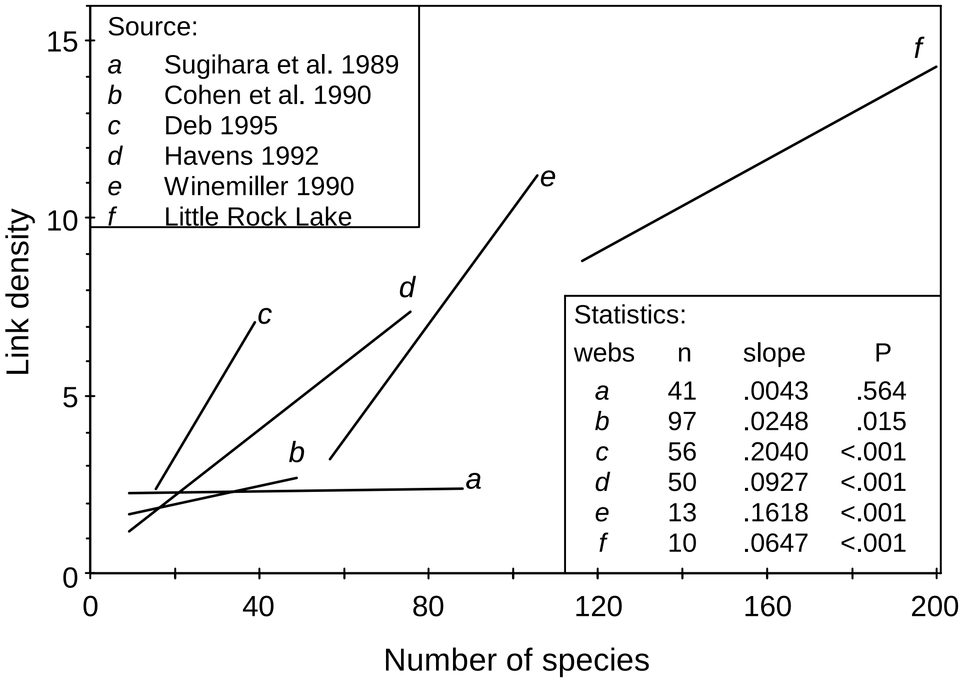


Fig. 1. Relationship between the link density property and web size for six collections of food webs. Lines are the results of linear regressions over the individual data points, which are omitted from the representation. Early collections of food webs drawn from literature studies not intended to represent the whole complexity of the systems (**a**, **b**) appear (approximately) scale invariant. More recent collections of webs characterized by high sampling effort (**c**, **d**, **e**, **f**) show strong scale dependence. Number of webs in each collection (n), estimates of the slope from linear regression, and *P*-values from a *t*-test are given in the inset. For collections **a** and **b**, webs with 10 species or less were omitted following Bersier and Sugihara (1997).

1983; Kenny and Loehle 1991; Pimm et al. 1991; Cohen et al. 1993; Bersier et al. 1999). Consequently, we must think of alternative ways of defining food web properties that take the disequitability in the distribution of link importance into account.

Quantitative link density

The process of formulating a quantitative counterpart for traditionally defined qualitative properties will be demonstrated in detail on the example of the link density property. The qualitative version, *LD*, is defined as the number of links (*L*) per species in the web ($LD = L/S$). For the quantitative version we base our calculations on information theory, namely the diversity index of Shannon (1948), *H*. For a system comprising *x* events, maximum diversity is attained when all events occur in equal proportion ($H_{max} = \log x$), while minimum diversity is a function of the number of cases that each event consists of. In our context, an event refers to a species and a case to a flux of biomass to or from a species (Ulanowicz and Wolff 1991). The application of Shannon's equation to a quantitative food web matrix is visualized step-by-step in Fig. 2: 1) In a food web matrix, species in their function as predators are conventionally listed column-wise (*j*), while the same species are arranged row-wise (*i*) in their function as prey. A matrix element b_{ij} thus expresses the amount of biomass passing from species i to species j (j eats i) per unit time and space. The total biomass output of species k to all its predators in the web consequently equals the sum of row k ($b_{k.}$). 2) The outflows from species k to each predator in the food web can be visualized, and 3) applying the Shannon index results in the diversity of species k's biomass outflows (H_{Pk}). 4) For our purposes, the "reciprocal" of H_{Pk} is more interesting; it is understood as the number of predators feeding on species k in equal proportion that would generate the same diversity as H_{Pk}, and is termed the "effective number of predators" (n_{Pk}). The reciprocal of H has the desirable feature of recovering the original units, namely the number of species, but is now a real number. 5) For the given example, n_{Pk} takes on a value of 3.7, rendering a distribution with 3.7 predators that display an equal intensity of consumption in respect to k. Thus, the diversity generated by this distribution is equivalent to that of species k's biomass output. The same approach is followed with regard to species k's biomass inflows in steps 6) to 9), yielding the effective number of prey (n_{Nk}).

A quantitative version of link density can be formulated on the basis of the above defined indices n_{Pk} and n_{Nk}. For easier comprehension it is important to note that qualitative link density LD can be calculated either as the average number of prey computed over all species (the total number of prey divided by S), or as the average number of predators (the total number of predators divided by S). In analogy, one could formulate a quantitative link density either by averaging over all n_{Pi} values, or by averaging over all n_{Nj} values. Since it seems implausible to only consider either biomass in- or outflows, we average over both means to obtain a quantitative version of the link density LD'_q:

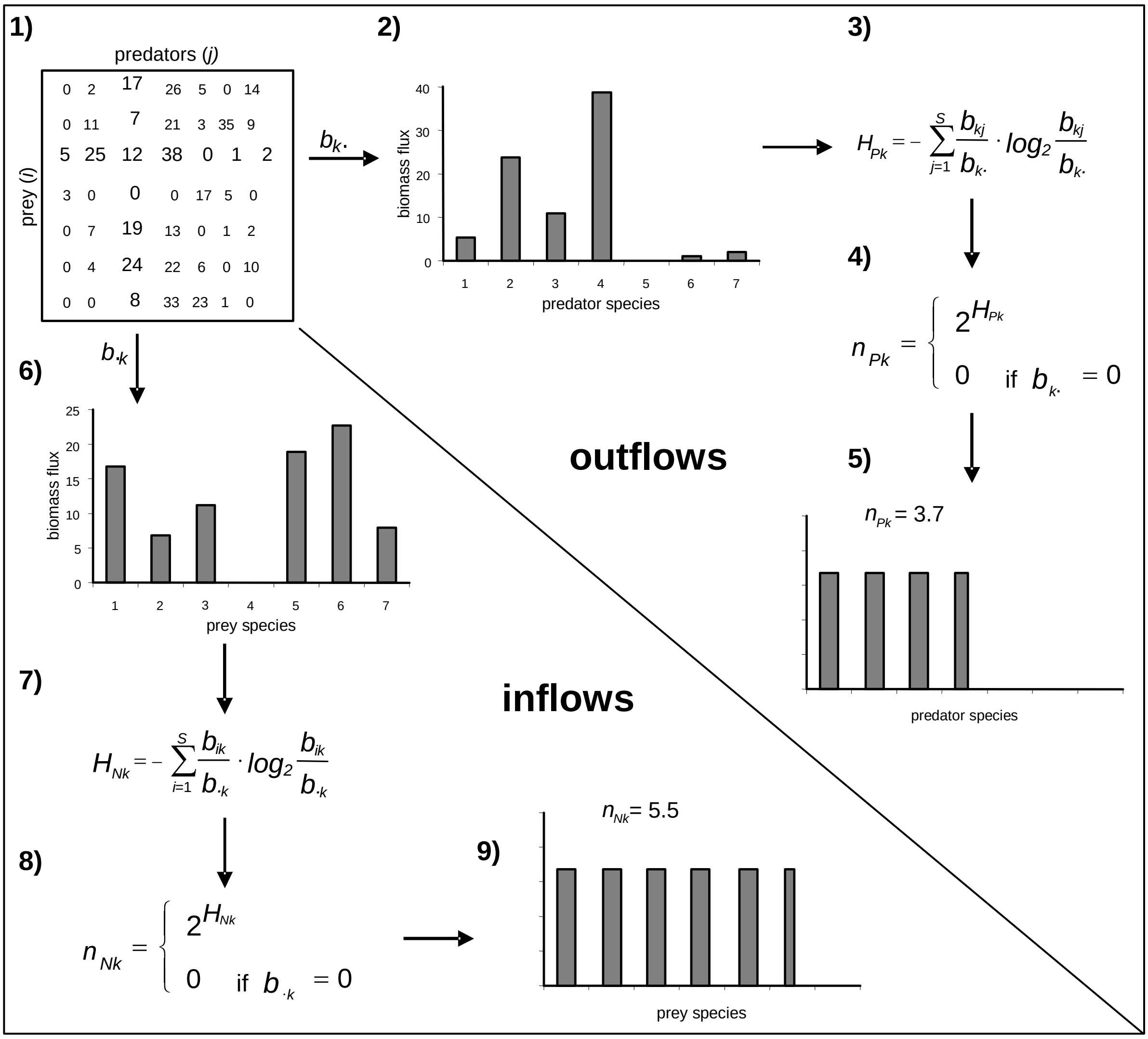
$$LD'_q = \frac{1}{2}\left(\sum_{i=1}^{S}\frac{1}{S}\cdot n_{P\,i} + \sum_{j=1}^{S}\frac{1}{S}\cdot n_{N\,j}\right) \tag{1}$$

This approach does not account for the fact that species vary in the amount of biomass transferred by them, and we thus refer to LD'_q as the "unweighted" quantitative link density. To include varying amounts of biomass transfer, $1/S$ in equation (1) is substituted by the quotient of each species' biomass output and total outflow over all species ($b_{i.}/b_{..}$). In other words, the effective number of predators for species i is weighted by i's contribution to total outflow. The same is done for inflow and the "weighted" quantitative link density LD_q is obtained by averaging over both equations:

$$LD_q = \frac{1}{2}\left(\sum_{i=1}^{S}\frac{b_{i\cdot}}{b_{\cdot\cdot}}\cdot n_{P\,i} + \sum_{j=1}^{S}\frac{b_{\cdot j}}{b_{\cdot\cdot}}\cdot n_{N\,j}\right). \tag{2}$$

For any given food web, LD'_q will always be smaller or equal to LD. This difference is an expression of the degree to which biomass flow in the system departs from a uniform distribution. The difference between LD'_q and LD_q in turn is attributable to the variation between species with respect to the partitioning of total biomass flowing in the system.

Species at high trophic levels are typically characterized by low biomass and consequently little in- and outflow, while greater biomass and more extensive biomass flux is generally a feature of



0	2	17	26	5	0	14
0	11	7	21	3	35	9
5	25	12	38	0	1	2
3	0	0	0	17	5	0
0	7	19	13	0	1	2
0	4	24	22	6	0	10
0	0	8	33	23	1	0

Fig. 2 Process of finding a quantitative definition of link density. Biomass in- and outflow for species *k* are considered separately in the lower left and the upper right half of the figure, respectively. 1) Arbitrarily assembled quantitative food web matrix, highlighting the feeding interactions of species *k*. 2) Distribution of species *k*'s biomass outflows; $b_{k.}$ = total biomass output from species *k*. 3) Shannon formula applied to species *k*'s biomass outflows; H_{Pk} = diversity of species *k*'s biomass outflows. 4) Reciprocal of H_{Pk}; n_{Pk} is the equivalent number of predators for species *k*. 5) Distribution of n_{Pk} outflows equal in magnitude, which yield the same value of H_{Pk}. 6-9) Analogous to 1) to 5), for biomass inflows to species *k*. $b_{.k}$ = total biomass input to species *k*, H_{Nk} = diversity of *k*'s biomass inflows, n_{Nk} = equivalent number of prey for species *k*.

species at low trophic levels. Therefore, trophodynamical constraints (Lindeman 1942) have a determining influence on the value of LD_q.

We examined the effect of increasing sampling effort on qualitative, unweighted quantitative, and weighted quantitative link density for 10 extensively documented quantitative webs (Banašek-Richter et al. 2004). Both quantitative versions were found to be much more robust against variable sampling effort than their qualitative counterpart. This increase in accuracy is accomplished at the cost of a slight decrease in precision as compared to the qualitative link density. Conversely, the quantitative versions also proved less sensitive to differences in evenness in respect to the distribution of link magnitude. In sum, quantitative properties are not only useful as bearer of ecological information, they also represent a much more robust description of weighted matrices.

Scaling behaviour of the link density – Results and discussion

The scaling behaviour of the conventional qualitative link density and its newly defined quantitative counterparts is compared for a collection of height seasonal food webs from the southern shore of Lake Neuchâtel near the village of Chabrey in Switzerland (see Cattin et al. 2003). These arthropod-dominated webs were collected in early summer and early fall of 2001. For each season there are two webs from a *Schoenus nigricans* dominated, and two from a *Cladium mariscus* dominated vegetation zone. Of these, one web is from an area with mowing treatment, one from a control area without mowing. Species richness spans a range of 118 to 202 species.

The relation between link density and scale for the Chabrey collection is depicted in Fig. 3. Qualitative link density (LD) is scale dependent due to the increase in exploitable resources with species richness. Concurrently, the linear regression slopes for the two versions of quantitative link density are not significantly different from zero, thus indicating (moderate) scale-invariance for both properties. These results lead us to infer that in comparison to systems with low species richness, the distribution of in- and outflows within species-rich systems is more inequitable, which counteracts the increase in qualitative link density.

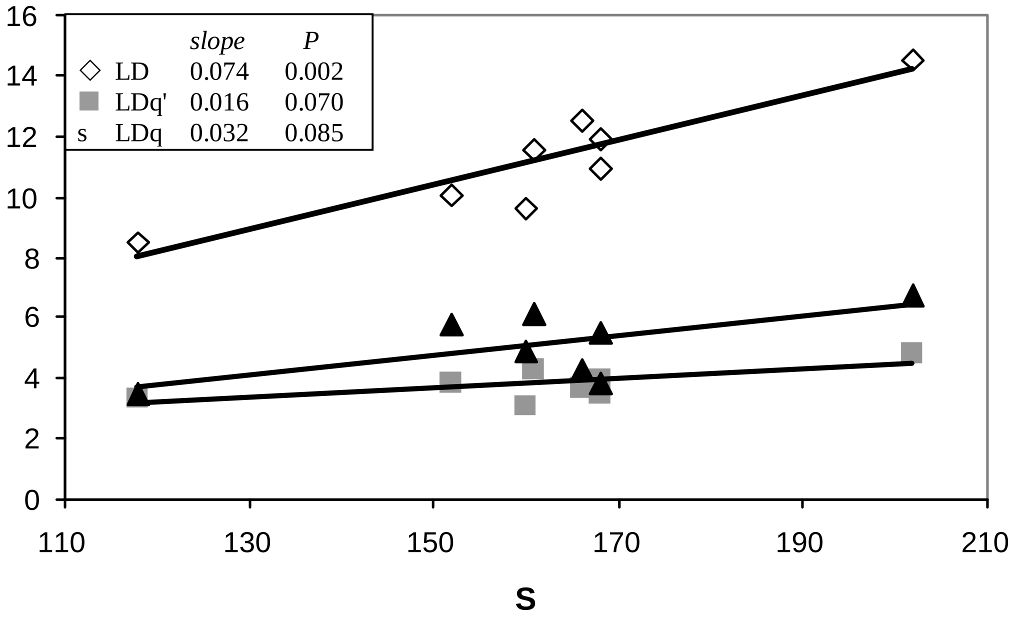


Fig. 3 Data and least-squares regressions (solid lines) of quantitative link density (◇), unweighted quantitative link density (■), and weighted quantitative link density (▲) for eight seasonal food webs from wet meadows on the southern shore of Lake Neuchâtel (Switzerland).

The invariance observed for this collection is however superseded by moderate scale-dependence when the Chabrey data set is supplemented by four other collections of community food-webs spanning a range of 14 to 173 species (Banašek-Richter et al., in prep.). The non significant results for the Chabrey data may be due to insufficient statistical power within the collection. Since both quantitative versions of link density were found to be largely insensitive to variable sampling effort (Banašek-Richter et al. 2004), we can rule out the possibility that this source of variability has influenced the results when pooling data over five community food web collections (Bersier et al. 1999; Winemiller et al. 2001). The scale-dependence observed implies that linkage complexity increases with species richness even when considered quantitatively. Using an approach developed by Ulanowicz (2002) to infer the dynamical behaviour of food webs from their static quantitative structure, we find that species rich food webs fall in the unstable region of parameters space. These food webs are so complex that they will not be stable according to May's (1974) stability criterion. It remains that we observe them without sign of strong instability, which portends that the mechanisms preventing them to collapse are still to be uncovered.

References

Banašek-Richter, C., M.F. Cattin and L.F. Bersier. (2004) Sampling effects and the robustness of quantitative and qualitative food-web descriptors. *J. Theor. Biol.* 226:23-32.

Bengtsson, J. (1994) Confounding variables and independent observations in comparative analyses of food webs. *Ecology* 75:1282-1288.

Bersier, L.F., and G. Sugihara. (1997) Scaling regions for food-web properties. *Proc. Natl. Acad. Sci. USA* 94:1247-1251.

Bersier, L.F., P. Dixon and G. Sugihara. (1999) Scale-invariant or scale-dependent behavior of the link density property in food webs: A matter of sampling effort? *Am. Nat.* 153:676-682.

Briand, F., and J.E. Cohen. (1984) Community food webs have scale-invariant structure. *Nature* 307:264-267.

Cattin, M.F., G. Blandenier, C. Banašek-Richter and L.F. Bersier. (2003) Effects of mowing on the spider. (Araneae) community as management practice in wet meadows. *Biol. Conserv.* 113:179-188.

Cohen, J.E., R.A. Beaver, S.H. Cousins, D.L. DeAngelis, L. Goldwasser, K.L. Heong, R. Holt, A.J. Kohn, J.H. Lawton, N. Martinez, R. Omalley, L.M. Page, B.C. Patten, S.L. Pimm, G.A. Polis, M. Rejmánek, T.W. Schoener, K. Schoenly, W.G. Sprules, J.M. Teal, R.E. Ulanowicz, P.H. Warren, H.M. Wilbur and P. Yodzis. (1993) Improving Food Webs. *Ecology* 74:252-258.

Cohen, J.E., and F. Briand. (1984) Trophic links of community food web. *Proc. Natl. Acad. Sci. USA* 81:4105-4109.

Cohen, J.E., F. Briand and C.N. Newman. (1990) Community Food Webs: Data and Theory. Springer-Verlag, Berlin.

Cohen, J.E., and C.M. Newman. (1984) The stability of large random matrices and their products. *Annals of Probability* 12:283-310.

Deb, D. (1995) Scale-dependence of food web structures: Tropical ponds a paradigm. *Oikos* 72:245-262.

Gardner, M., and W. Ashby. (1970) Connectance of large dynamic. (cybernetic) systems : critical values for stability. *Nature* 228:784.

Goldwasser, L., and J. Roughgarden. (1993) Construction and Analysis of A Large Caribbean Food Web. *Ecology* 74:1216-1233.

Goldwasser, L., and J. Roughgarden. (1997) Sampling effects and the estimation of food-web properties. *Ecology* 78:41-54.

Havens, K.E. (1992) Scale and Structure in Natural Food Webs. *Science* 257:1107-1109.

Havens, K.E. (1997) Unique structural properties of pelagic food webs. *Oikos* 78:75-80.

Kenny, D., and C. Loehle. (1991) Are Food Webs Randomly Connected? *Ecology* 72:1794-1799.

LINDEMAN, R.L. (1942) The trophic-dynamic aspect of ecology. *Ecology* 23:399-418.

MARTINEZ, N.D., B.A. HAWKINS, H.A. DAWAH and B.P. FEIFAREK. (1999) Effects of sampling effort on characterization of food-web structure. *Ecology* 80:1044-1055.

MAY, R.M. (1974) Stability and Complexity of model ecosystems. Princeton University Press, Princeton.

MAY, R.M. (1983) The structure of food webs. *Nature* 301:566-568.

PAINE, R.T. (1988) Food web: road maps of interactions or grist for theoretical development? *Ecology* 69:1648-1654.

PIMM, S.L., J.H. LAWTON and J.E. COHEN. (1991) Food web patterns and their consequences. *Nature* 350:669-674.

POLIS, G.A. (1991) Complex trophic interactions in deserts: an empirical critique of food-web theory. *Am. Nat.* 138:123-155.

POLIS, G.A., and S.D. HURD. (1996) Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *Am. Nat.* 147:396-423.

REAGAN, D.P., and R.B. WAIDE. (1996) The food web of a tropical rain forest. The University of Chicago Press, Chicago.

REJMÁNEK, M., and P. STARY. (1979) Connectance in real biotic communities and critical values for stability of model ecosystems. *Nature* 280:311-313.

SCHOENER, T.W. (1989) Food webs from the small to the large. *Ecology* 70:1559-1589.

SCHOENLY, K., R.A. BEAVER and T.A. HEUMIER. (1991) On the trophic relations of insects: A food-web approach. *Am. Nat.* 137:597-638.

SHANNON, C.E. (1948) A mathematical theory of communications. *Bell System Technical Journal* 27:379-423.

SUGIHARA, G., K. SCHOENLY and A. TROMBLA. (1989) Scale invariance in food web properties. *Science* 245:48-52.

ULANOWICZ, R.E. (2002) The balance between adaptability and adaptation. *BioSystems* 64:13-22.

ULANOWICZ, R.E., and W.F. WOLFF. (1991) Ecosystem flow networks: loaded dice? *Math. Biosci.* 103:45-68.

WARREN, P.H. (1989) Spatial and temporal variation in the structure of a freshwater food web. *Oikos* 55:299-311.

WARREN, P.H. (1990) Variation in food-web structure: the determinants of connectance. *Am. Nat.* 136:689-700.

WINEMILLER, K.O. (1990) Spatial and temporal variation in tropical fish trophic networks. *Ecol. Monogr.* 60:331-367.

WINEMILLER, K.O., E.R. PIANKA, L.J. VITT and A. JOERN. (2001) Food web laws or niche theory? Six independent empirical tests. *Am. Nat.* 158:193-199.

YODZIS, P. (1980) The connectance of real ecosystems. *Nature* 284:544-545.

Abstract.

Food webs are highly complex and variable, but nevertheless possess regularities. First compilations revealed that food webs have scale-invariant structure, i.e., that descriptors of their structure remain constant for webs spanning a wide range in species richness. More highly resolved datasets however, did not uphold these scaling laws. This search for regularities rested on qualitative food webs, thus disregarding the partly huge disparity in the magnitude of biomass flow between trophic links. Moreover, qualitative food web properties were found to be sensitive to the amount of sampling effort devoted to the collection of data in the field. Both problems can be solved if the quantitative nature of food webs is taken into consideration. For this purpose, we devised quantitative descriptors based on information theoretical indices, and exemplify here the derivation of quantitative analogues for link density, a descriptor expressing

linkage complexity. Two quantitative counterparts are proposed, one giving the same weight to each species, and one weighing each species by the amount of biomass emanating from, and flowing into it. We demonstrate these quantitative descriptors to be less affected by varying levels of sampling effort. Furthermore, we compare them with respect to their scaling behaviour with qualitative link density for an original data set consisting of eight (non-independent) quantitative food webs from wet meadows, spanning 118 to 202 species. The conventional qualitative version is found to increase with the number of species, while both quantitative counterparts remain largely scale-invariant. However, preliminary analyses of new data sets reveal both quantitative versions of link density to increase with the number of species in the webs. Thus, linkage complexity is likely to increase with species richness in quantitative food webs as well, which would have important implications for our understanding of their dynamical behaviour.

SUMMARY

The basis of this thesis is the work of Bersier et al. (2002, Chapter II), who propose a quantitative unweighted and a quantitative weighted counterpart for a suite of conventional qualitative food web properties derived from the Shannon-Wiener index. This index measures the diversity of a biological system in terms of species richness and species abundance. In the context of the pursued quantitative approach, this corresponds to the number of flows (or links) and the magnitude of the flows. For qualitative properties, binary data is drawn on, which gives information only on the number of flows (the elements of a qualitative matrix take on values either of 0 if there is no link, or 1 if a link exists). The quantitative unweighted version further includes information on the magnitude of these flows; the difference between the two versions being due to non-zero elements in the quantitative matrix that differ from 1. Expanding this version even further, weighted quantitative descriptors additionally consider each species' contribution to total flow in the system: each taxon is weighed by the amount of incoming and outgoing flows. The difference between the quantitative weighted and unweighted version is thus attributable to unequal row and column sums for the quantitative matrix.

In view of the fact that qualitative properties were criticized for their sensitivity to variable sampling effort, 14 weighted and unweighted quantitative descriptors are initially tested regarding their accuracy and precision in this respect (Chapter III). Under the premise that the most important links in reference to the associated biomass flux are the ones most likely to be sampled first, quantitative descriptors prove more robust against variable sampling effort and thus more accurate than their qualitative counterparts. The pursuit of a quantitative approach thus makes it possible to comprise much of the information on feeding interactions at an early stage of sampling. The increase in accuracy is achieved at the cost of a moderate loss in precision due to highly variable in- and outflows, which are only accounted for quantitatively. On the other hand, quantitative properties have the desirable feature of being less sensitive to variable levels of evenness in the distribution of link magnitude. In brief, these results indicate that the use of information theoretical indices is a promising possibility of taking the importance of trophic links into account and that the so obtained quantitative food web properties are suitable for between-web comparisons. The second part of this thesis is consequently dedicated to a quest for quantitatively perceivable generalizations with the aid of Bersier et al.'s quantitative descriptors.

The quantitative properties tested with respect to their sensitivity to sampling effort are evaluated on the basis of data from quantitative food web collections (Chapters IV – VI). To discern potential regularities, their behaviour with variable species richness is considered, with a special emphasis on the property of link density. The analysis within each of seven food web

collections rendered scale-dependent link density for the qualitative version as opposed to largely scale-invariant quantitative versions (Chapter IV). Following an approach by Ulanowicz (2002), the results for qualitative and quantitative unweighted link density are used to express the "edge of chaos" based on May's stability criterion (May 1972). Surprisingly, a majority of the 58 food webs considered fall into the unstable region of parameters' space (Chapter IV). A number of May's assumptions can be challenged to explain why these systems can still be observed. As yet, such criticism was based on model predictions (e.g. DeAngelis 1975, Cohen & Newman 1984, McCann et al. 1998, Kondoh 2003). The empirical evidence presented in its support in this thesis could thus aid in making progress on the matter of stability and complexity.

With regard to the search for regularities in food web structure, the result of scale-invariant link density would be of extreme relevance were it not put into perspective by deviating results obtained from an assessment of link density's scaling behaviour between the seven collections (Chapter V). These latter findings predicate of linkage complexity to increase with species richness in quantitative food webs, a notion with strong implications for the stability-complexity debate as well. Under the assumption that stability generally decreases with increasing complexity (e.g. Gardner & Ashby 1970, May 1972, 1973, DeAngelis 1975) it indicates that complex systems should possess a special structure to remain stable. Conveniently, the later idea can also be brought into line with more recent advances that assume complexity to give rise to stability without necessarily being the driving force behind this effect (McCann 2000). Instead, communities are presumed to depend on special structures (species) capable of differential response to maintain stability.

In the vast majority of cases, the other 13 properties under consideration are also found to depend on species richness for both the unweighted and the weighted version when food webs from various collections are compared (Chapter V). The predictions of constant connectance (Martinez 1992, 1993, 1994), or alleged "laws" of scale-invariance (Briand & Cohen 1984, Cohen & Briand 1984, Cohen & Newman 1985) are thus contradicted. Furthermore, the comparison of different food web collections quantitatively serves to uncover special features of food-web structure that cannot be discerned when data is analysed solely qualitatively. The three different versions of each property are built one on the other, all depending on the same data but by definition differing with respect to the amount and type of information they incorporate. To interpret the behaviour of the unweighted quantitative properties, the behaviour of the corresponding qualitative properties must thus be considered, and concurrently to disentangle the feature or features responsible for a quantitative weighted properties' value the results of the other versions of the property must be compared. For the data sets analysed, this procedure reveals the number of prey species per predator to increase with scale, while the largest portion of the biomass outflow in species-rich systems is attributable to only few prey species. These systems are thus distinguished by a highly asymmetric distribution of in- and outflows: uneven outflows coincide with more evenly distributed inflows. Large systems additionally appear to be dominated by species with a highly diverse diet (or with highly diverse predators) that outweigh the others with respect to the amount of associated biomass inflow (or outflow). Accordingly, within the range of species richness considered (analysed webs consist of between 13 and 202 species) there is no support of the contention that predators are limited in the number of different prey items they can consume (Schoener 1989). Instead, predators appear to take advantage of a broader range of resources wherever possible.

A final analysis explores differences between webs from aquatic as opposed to terrestrial environments that are manifest independent of the possible effect of scale. Quantitative properties aptly discern such differences and expose features pertaining to biomass flux that remain imperceptible to qualitative scrutiny.

Requisite to the derivation of new food web regularities based on the approach pursued in this thesis is the collection and analyses of more high-quality quantitative food web data. This could serve to substantiate and supplement the obtained results, as well as to ascertain patterns in food-web structure pertaining to biomass flux which sensibly complement the results of qualitative analyses.

Moreover, the development of new quantitative models of food-web structure may benefit from the approach taken in this thesis since the observed regularities represent the patterns that such models should reproduce. Only recently, Cattin et al. (2004) introduced the niche-hierarchy-model to predict food web topology with high accuracy. The question of how to integrate quantitative information into such a model remains to be explored nonetheless.

REFERENCES

Bersier, L.F., Banašek-Richter, C., Cattin, M.F., 2002. Quantitative descriptors of food-web matrices. Ecology 83: 2394-2407.

Briand, F., Cohen, J.E., 1984. Community food webs have scale-invariant structure. Nature 307: 264-267.

Cattin, M.F., Bersier, L.F., Banašek-Richter, C., Baltensperger, R., Gabriel, J.P., 2004. Phylogenetic constraints and adaptation explain food-web structure. Nature 427: 835-839.

Cohen, J.E., Briand, F., 1984. Trophic links of community food webs. Proceedings of the National Academy of Sciences of the United States of America 81: 4105-4109.

Cohen, J.E., Newman, C.M. 1985. A stochastic theory of community food webs: I. Models and aggregated data. Proceedings of the Royal Society of London B 224: 421-448.

——— 1985. A stochastic theory of community food webs: I. Models and aggregated data. Proceedings of the Royal Society of London B 224: 421-448.

DeAngelis, D.L., 1975. Stability and connectance in food web models. Ecology 56: 238-243.

Gardner, M.R., Ashby, W.R., 1970. Connectance of large dynamic (cybernetic) systems: Critical values for stability. Nature 228: 784.

Kondoh, M., 2003. Foraging adaptation and the relationship between food-web complexity and stability. Science 299: 138-139.

Martinez, N.D., 1992. Constant connectance in community food webs. American Naturalist 139:1208-1218.

——— 1993. Effects of scale on food web structure. Science (Washington DC) 260:242-243.

——— 1994. Scale-dependent constraints on food-web structure. American Naturalist 144:935-953.

May, R.M., 1972. Will a large complex system be stable? Nature 238: 413-414.

——— 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton.

McCann, K.S., 2000. The diversity-stability debate. Nature 405: 228-233.

McCann, K.S., Hastings, A., and Huxel, G.R., 1998. Weak trophic interactions and the balance of nature. Nature 395: 794-798.

Curriculum vitae

Personal details

Date of birth: 13.07.1972
Place of birth: Unna, Germany
Nationality: German
Marital status: married, one daughter.

Education

08/78 – 04/81	Nikolai Schule Unna (elementary school).
04/81 – 07/84	Worthington Elementary School, due to my father's transfer to Ohio (USA).
09/84 – 06/85	Worthingway Middle School in Ohio (USA).
09/85 – 06/91	Pestalozzi-Gymnasium Unna (grammar/high school). Majors: English, Mathematics. Graduation, final Grade: 1,7 (on a scale from 1 to 6).

University studies

11/91 – 10/93	Undergraduate studies in Biology at the University of Bayreuth (Germany). Intermediate examination, average grade: 1,7.
11/93 – 05/98	Graduate studies in Biology. Major: Animal Ecology, minors: Plant physiology, Environmental Economy.
08/94 – 06/95	Graduate studies in Biology at the University of Delaware in Newark, Delaware (USA) as scholarship holder. Average grade: A-.
05/97 – 05/98	Diploma thesis at the University of Mainz (Germany). Subject: Examinations on the dietary ecology of magpies (*Pica pica* L.) and carrion crows (*Corvus corone* L.) in Rhineland-Palatinate. Commissioned by the Ministry for Environment and Forestry of Rhineland-Palatinate.
05/98	Diploma in Biology. Final grade: 2,0.
10/98	Speaker at the annual assembly of the German Ornithology Society (DOG) in Jena (Germany). Subject: Dietary spectrum of magpies (*Pica pica*) and carrion crows (*Corvus corone*) in Rhineland-Palatinate.
05/99 – 06/04	Ph.D. thesis at the department of Ecology and Ethology of the Université de Neuchâtel (Switzerland). Research focus: Qualitative and quantitative aspects of food webs. Area of responsibility: field work, empirical data analysis, microscopic arthropod-determination, programming in SPSS and C++ to simulate ecological models, statistical evaluation, development of theoretical principles.
08/02	Speaker at the annual assembly of the Ecological Society of America (ESA) in Tucson, Arizona (USA). Subject: Quantity defies quality – a new approach to food web analysis.
11/03	Speaker at the 3. international "Food Web Symposium" in Giessen (Germany). Subject: Food web complexity: from scale invariance to scale dependence, and back again?
02/00 – 06/03	Correspondence degree course at the AFW Academy of Economics (Bad Harzburg, Germany). Course of studies: Conservation Management including Eco-Audit. Cumulative grade of study assignments: very good.
01/02	Certificate as environmental auditor "RKW".
06/03	Diploma in Conservation Management. Grade of final exam: very good (highest mark possible).

Professional experience

09/91	Vintage in Dijon (France).
02 – 03/93	Research assistant at the Genetics faculty of the University of Bayreuth.
09 – 10/95	Internship for the society “Jordsand e.V.”: Public relations work, field research about bird migration on the Greifswalder Oie (Baltic Sea).
03/96	Internship for the society “Aktion Fischotterschutz e.V.” near Hannover (Germany): Field research on the otter.
04/96	Internship for the “Biological Station” of the district of Unna (Germany): Stock registration of the lapwing.
05/97 – 05/98	Freelance at the Zoological Institute of the University of Mainz: Research on magpie and carrion crow.
06 – 12/98	Part-time employment at the Lurgi AG Holding (Frankfurt, Germany) in the department of personal development / education and training.
10 – 12/98	Internship for the tropical forest foundation “OroVerde” (Frankfurt): Public relations work, marketing, project management.
01 – 04/99	Biologist in the “Gemeinschaftspraxis für Pathologie” (Institute for Pathology, Frankfurt): Reception and macroscopic preparation of material.
05/99 – 08/03	Research assistant at the "Institut de Zoologie" of the Université de Neuchâtel (Switzerland) within the framework of a doctoral thesis.
starting 06/04	Research assistant at the Technische Universität Darmstadt (Germany). Research focus: Diversity and stability of complex ecosystems in space and time.

Social Engagement

04/93	Social work as volunteer in the refugee camp of Veli Losinj (Croatia).
11/93 – 01/00	Founding and committee member of “pro humanitate e.V.”. Charity purpose: Organization of humanitarian aid for the former Yugoslavia.
06/96 – 11/97	President of pro humanitate e.V.: e.g. organization and undertaking of relief transports to Bosnia and Croatia, implementation of scholarship programs for refugee students in co-operation with the World University Service (WUS) and the German society for technical co-operation (GTZ).

Linguistic proficiency

English:	fluent in written and spoken form,
French:	advanced knowledge,
Spanish:	basic knowledge.

Knowledge in computer processing

Windows, Macintosh, MS-Office, SPSS 7.5 for Windows, WinStat 3.1, Internet, Programming experience in SPSS and C++.

Hobbies

Photography, singing, swimming (competition experience), snorkeling, literature.