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Sampling effects and the robustness of quantitative and qualitative food-web descriptors

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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 10 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.

Keywords: Connectance; Food-web structure; Information theory; Link importance; Omnivory; Sampling effect; Trophic links

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 behavior when analysed over a number of webs with differing species richness fostered the postulation of generalities such as scale-invariance (e.g. Pimm, 1982; Cohen, 1989; Briand and Cohen, 1984; Cohen and Briand, 1984; 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

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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 aforementioned 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 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 (1997) approach to test the performance of our newly defined quantitative descriptors on 10 well-defined web compilations.

We consider the effect of sampling effort on the qualitative and quantitative properties by examining the behavior 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, p. 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 (sdG), standard deviation in vulnerability (sdV). For each of these 14 properties, the customary qualitative version, as well as the unweighted quantitative and the weighted quantitative versions are analysed. 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. Data set

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, unpublished), 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, unpublished). 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 analysed 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 $p_{ij} = b_{ij}/b_j$.

Species richness for the webs analysed 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: $0.5{*}L, L, 2{*}L, \ldots, 64{*}L$. 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 ($\mathbf{p}' = [p'_{ij}]$). The resulting number of hits per link for a given predator is multiplied by the respective predator's inflow sum ($p'_{ij}{*}b_j$). 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 $\bar{z}'$ 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 $\bar{z}'/z$. Second, we calculated the overall accuracy of a property as the median of each percentage of agreement over the 10 webs analysed. 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 10 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 10 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 it that the shape of the distribution of link magnitude affects the properties' performance, with highly uneven distributions likely to yield less robust estimates. Consequently, we compare the equitability of link magnitude per web with the quality of prediction of the analysed 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 ($|\bar{z}' - z|/z$). The quality of prediction is calculated for each of the 10 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 ($\%B + \%I + \%T = 1$, $C = LD/s$, $\%T{-}B + \%T{-}I + \%I{-}I + \%I{-}B = 1$) 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 behavior of each property with increasing sampling effort in 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 good 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 presented in Table 1 specify the degree of dispersion between the results for the 10 individual webs. Among-web spreading of values is inferior or equal to that of the respective qualitative version for all weighted

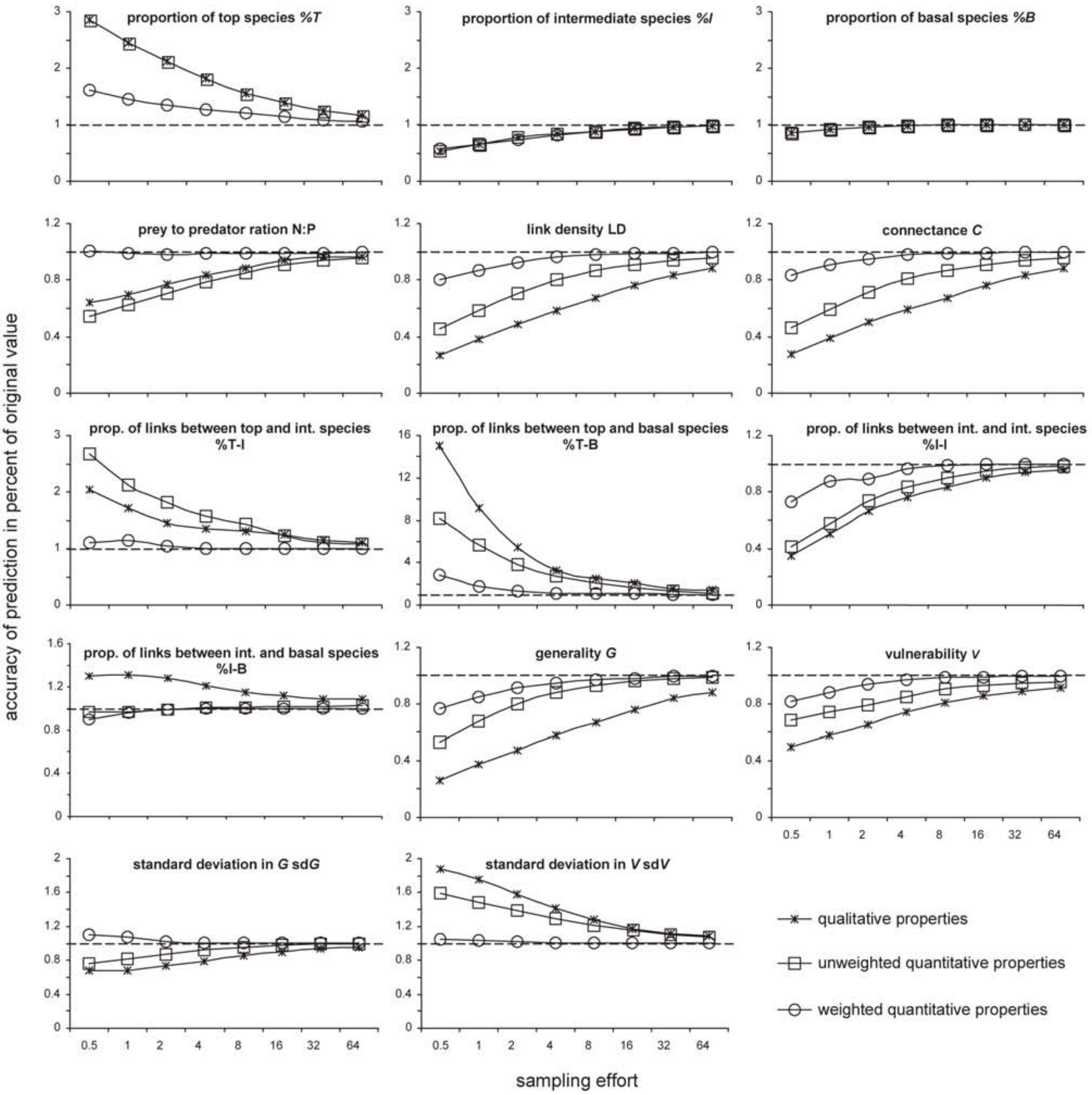

Fig. 1. Accuracy of the qualitative and quantitative properties with increasing sampling effort. Accuracy is measured in percent of the original values (broken line). Given are the median values of accuracy for the 10 examined food webs; accuracy within a food web is measured as the mean percentage deviation 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 10 food webs are given in Table 1.

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 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

Table 1
Mean quartile ranges for the food-web properties over the 10 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, sdG	0.126	0.028	0.043
Standard deviation in V, sdV	0.241	0.197	0.021

observe 8000 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 10 food webs for each property is presented in Fig. 2. Most CV-functions decline smoothly with increasing sampling effort; only $\%T$, $\%T-I$, and $\%T-B$ show a more erratic behavior. This feature can again be attributed to the very small means of these properties. For the individual webs analysed, 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 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 $\%B$, and the link

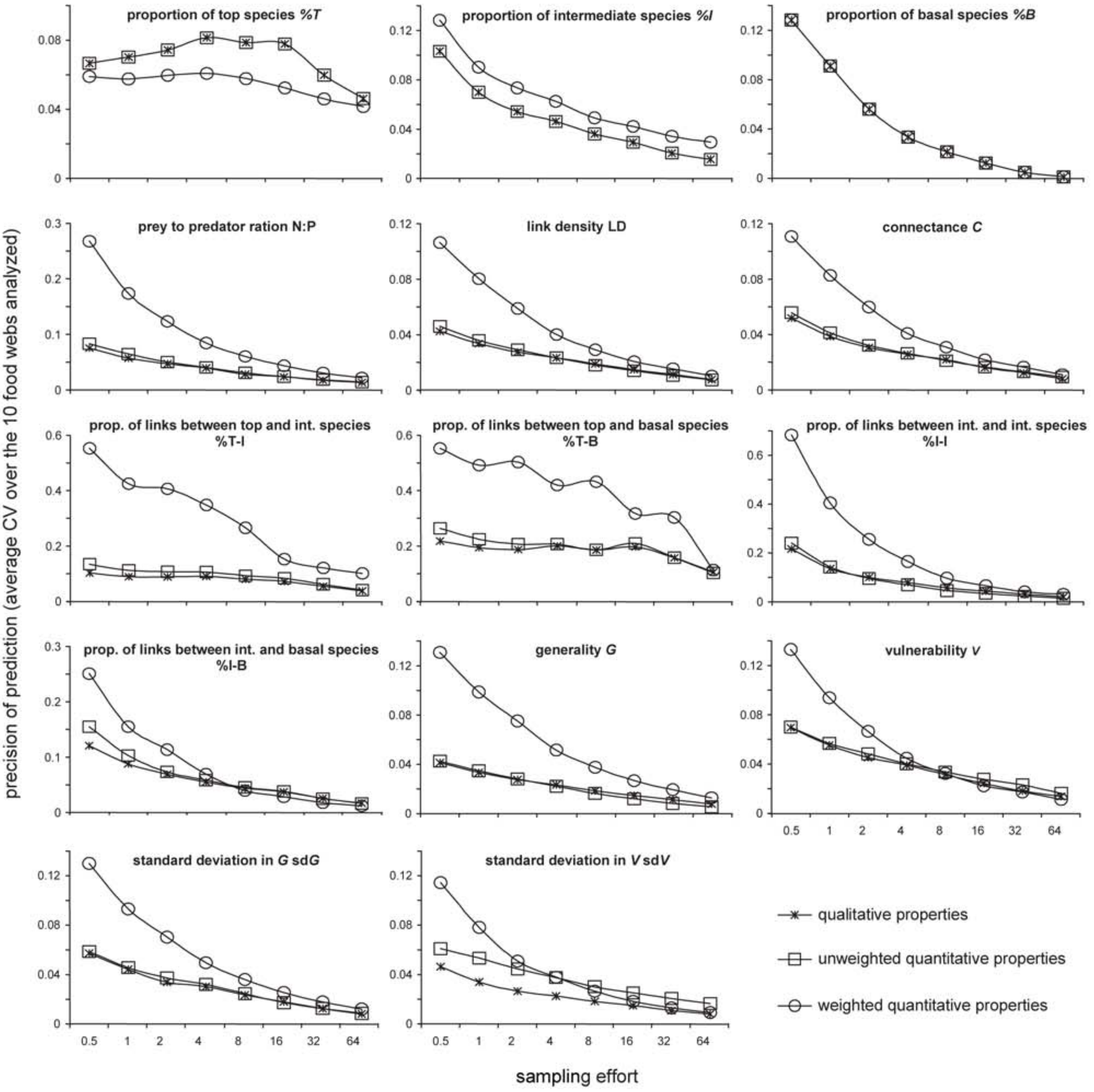

Fig. 2. Within-web precision of the qualitative and quantitative properties with increasing sampling effort. Precision is measured as the average coefficient of variation for the 10 examined food webs at each sampling intensity. Sampling effort is given as a multiple of the total number of trophic links in each food web.

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 behavior of the link density LD was affected by sampling effort: intrinsically scale-dependent collections of food webs appeared scale-invariant when sampling was 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

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

Property	Qualitative		Unweighted quantitative		Weighted quantitative	
	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, sdG	**−0.879**	**0.001**	−0.345	0.328	0.018	0.960
Standard deviation in V, sdV	**−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.

properties analysed 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, 1988; 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. 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, 1992, 2002; 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). 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 behavior 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.

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