Estimating trophic link density from quantitative but incomplete diet data

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Abstract

The trophic link density and the stability of food webs are thought to be related, but the nature of this relation is controversial. This article introduces a method for estimating the link density from diet tables which do not cover the complete food web and do not resolve all diet items to species level. A simple formula for the error of this estimate is derived. Link density is determined as a function of a threshold diet fraction below which diet items are ignored (''diet partitioning function''). Furthermore, analytic relationships between this threshold-dependent link density and the generality distribution of food webs are established. A preliminary application of the method to field data suggests that empirical results relating link density to diversity might need to be revisited.
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1. Introduction

It is already 33 years ago that, based on numerical results of Gardner and Ashby (1970), May (1973) gave an analytic argument that there should be an upper limit to the *link density*—the ratio of the number of trophic links (L) to the number of species (S)—in stable ecological communities, and it is still controversial if the argument applies or not. Such a limit would imply an inverse relationship between the ''complexity'' $C = L/S^2$ of stable communities and their ''diversity'' S, or a loss stability with increasing diversity at fixed complexity, somewhat against the intuition that many ecological communities are highly diverse and complex.

Large efforts have been made to either verify the original prediction (the ''link-species scaling law'') or to establish other scaling laws relating the number of species to the number of links (e.g. Rejmánek and Stary, 1979; Yodzis, 1980; Cohen and Briand, 1984; Sugihara et al., 1989; Schoener, 1989; Warren, 1989, 1990; Cohen et al., 1990; Winemiller, 1990; Pimm, 1991; Havens, 1992; Deb, 1995; Banašek-Richter et al., 2005). However, problems remain. In the earlier works, the food webs considered were probably too small. Recently, larger food webs have been recorded and analysed, but often it is unclear if these can be consistently compared, because the methods used to obtain the data vary between data sets. Also, some data sets do not distinguish between possible links (''A can eat B'') and realized links (''A does eat B here'', see Kondoh, 2003).

In a recent work, Banašek-Richter et al. (2005), who give a more detailed account of the debate than space permits here, make use of two new measures of link density that take differences in the strength of links explicitly into account. Rather than simply computing the link density as the number of links per species L/S, their measure is based on the Shanon entropy index of the links of individual species. Taking link strengths into account is important, because most links are comparatively weak (Berlow et al., 2004, and references therein), and the measured number of links depends sensitively on some implicit or explicit link-strength threshold above which links are considered as present. In fact, Banašek-Richter et al. demonstrate that the correlations between link density and web size become

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smaller and statistically insignificant when the new measures are applied.

A problem that has remained unsolved is that, in empirical data sets, species are often aggregated to *trophic species* such as "small spiders" or "benthic phytoplankton". Such lumping is known to affect the link density (Sugihara et al., 1989; Martinez, 1991, 1993; Hall and Raffaelli, 1991). Since May's argument can be understood as a generalization of the principle of competitive exclusion (the broader the diets the more do niches overlap, resulting in tougher competition), and the ecological unit of competitive exclusion is the species, the link density relevant for May's argument should be defined based on unlumped species alone.

Here, we present a method to estimate link density in this sense from data sets that do not fully resolve all species. Typical data for such an analysis are diet tables of representative species in a food web. Such data are widely available from the literature and large databases of diet data are now being developed (e.g. Potier et al., 2005). Thus, we expect that our method can contribute to understanding the relationships between species number, link number, and stability.

Link density is closely related to another concept of community ecology, the trophic niche breadth. Link density can be understood as a measure for the average trophic niche breadth in a community. However, it is important to distinguish the niche breadth relative to the total variability of available resource items from the breadth in terms of the number of prey species, which is of interest here. Methods to determine the former can utilize stable isotope analysis (Bearhop et al., 2004) or principle component analysis of diet data (de Crespin de Billy et al., 2000). A number of measures for the latter kind of niche breadth have also been proposed, most of them taking the highly uneven partitioning of diets into account (e.g. Levins, 1968; Hurlbert, 1978; Ulanowicz and Wolff, 1991; Bersier et al., 2002; Banašek-Richter et al., 2005). However, since it is not a priori clear which of these measures is the ecologically most significant, we do here compute the niche breadth as a function of a parameter θ, specifically, we compute the number of diet items that contribute a fraction larger than θ to the diet. From this unifying measure, most other measures of niche breadth can be derived. The food-web average of this function we call the *diet partitioning function* (DPF). For each value of θ, the DPF gives the density of links above this threshold. Although DPFs obtained from empirical (Winemiller and Layman, 2006) or simulated (Drossel et al., 2004; Quince et al., 2005) data can occasionally be found in the literature, there has, to our knowledge, been no work so far on the systematic analysis of the concept or a comparison of DPFs from different sources.

By establishing analytic relationships between the DPF and the distribution of generality (the number of prey species of a single consumer species), we obtain a formula for the sampling error of our link-density estimator which takes phylogenetic correlations between resource species into account, and can be computed from the sampled diet data alone. This is important, because collections of diet- and food-web data sets are rarely homogeneous enough to justify the computation of variances (and the *p*-values for scaling laws) from the variability *across* data sets.

The formula for the sampling error decomposes the error into components from different sources, and thus helps to plan future empirical work. In particular, we find that, rather than a high quantitative accuracy of the diet data (which is not easy to achieve, Smith et al., 2004), the number of sampled species is important. Using the formula, the sampling effort required to obtain a given accuracy can be estimated.

The method we introduce here is an example showing that better and more accurate characterizations of food-web structure do not always require complete food-web data sets, acquisition of which is laborious and expensive. Careful sub-sampling of a web and statistical data processing will often be sufficient for an accurate description and theory building.

In the following, we give a precise definition of the DPF (Section 2) and then discuss some of its properties and conceivable interpretations in Section 3. The method we propose for estimating the DPF and its error from incomplete diet data is explained in Section 4, and is applied to some examples in Section 5. Section 6 closes with some final remarks. Analytic calculations to derive our results can be found in the Appendices.

2. The diet partitioning function

2.1. Traditional link density

The link-density Z in a food web is defined as the ratio

$$Z := \frac{L}{S} \qquad (1)$$

of the number of (directed) trophic links L and of the number of species S in a food web. One finds values for Z spread widely and cover the range from 1 to 20 in the literature.

Counting the number of links L is a delicate business, because, as explained above, there are many more weak links than strong links (Berlow et al., 2004). Thus, results depend strongly on the choice of the cutoff in link strength below which links are not counted.

To some extent, a similar ambiguity exists also for the number of species S. Usually there are just a few abundant species and many rare species. Furthermore, most ecosystems are open, and somewhat arbitrary criteria have to be introduced to decide which species to include. For now, we shall assume that the pool of species to be included in the analysis, and hence S, has already been determined. Then the dependence of L on the threshold translates directly into a dependence of Z. Later, in Section 4.1, we shall argue that, using an adequate measure of link density, the

precise criterion for the exclusion or inclusion of species will not strongly affect the result.

2.2. Measuring link strength

Various measures of trophic link strength have been used in the literature (Berlow et al., 2004). The measure most frequently used in the empirical literature is probably the fraction a resource contributes to the diet of a consumer, where the contribution can be measured in units of energy, mass, or volume. Most commonly, mass fractions are cited. Methods to determine diet fractions include gut content analysis, forced regurgitation, direct observation of feeding behavior, or analysis of feces. As measures of link strength, diet fractions might sometimes be misleading. For example, a link from an abundant consumer to a rare resource may be weak, even though the resource's abundance is fully controlled by the consumer, if the consumer has other resources that dominate its diet. A theoretically more satisfactory measure of link strength might be the specific consumption rate, i.e. the biomass flow from the resource to the consumer per total biomass of resource and consumer. However, this and many other measures of link strength are more difficult to determine empirically than diet fractions. And, in numerical or analytic food-web models that incorporate the concept of energy- or mass conservation, diet fractions are easily computed. Thus, diet fractions seem to be the measure of link strength for which a comparison of theory and observation is most easy, and this is why we shall formulate our results in terms of diet fractions here. However, most results apply very similarly also to other measures of link strength.

Let species j contribute the mass m_{jk} to the diet (e.g. the gut content) of consumer species k on the average. Then, following, e.g. Drossel et al. (2004), the link strength from j to k in terms of diet fractions is given by

$$l_{jk} := \frac{m_{jk}}{\sum_h m_{hk}}, \qquad (2)$$

where the sum runs over all species.

2.3. Consumer link density

For bottom species k (i.e. autotrophs and detrivorous), l_{jk} is undefined since the denominator in Eq. (2) is zero. We decided to exclude bottom species from the analysis rather than setting $l_{jk} = 0$ in this case. The link density can then be defined as the *consumer link density*

$$Z_c := \frac{L}{S_c}, \qquad (3)$$

where L is the number of links with $l_{jk} \geqslant \theta$ for some threshold θ, and S_c is the number of non-bottom species (but S_c includes consumers for which all diet fractions happen to be below the threshold). When the fraction $B = 1 - S_c/S$ of bottom species in a food web is known, the link density in the conventional form (1) can be obtain from Z_c as

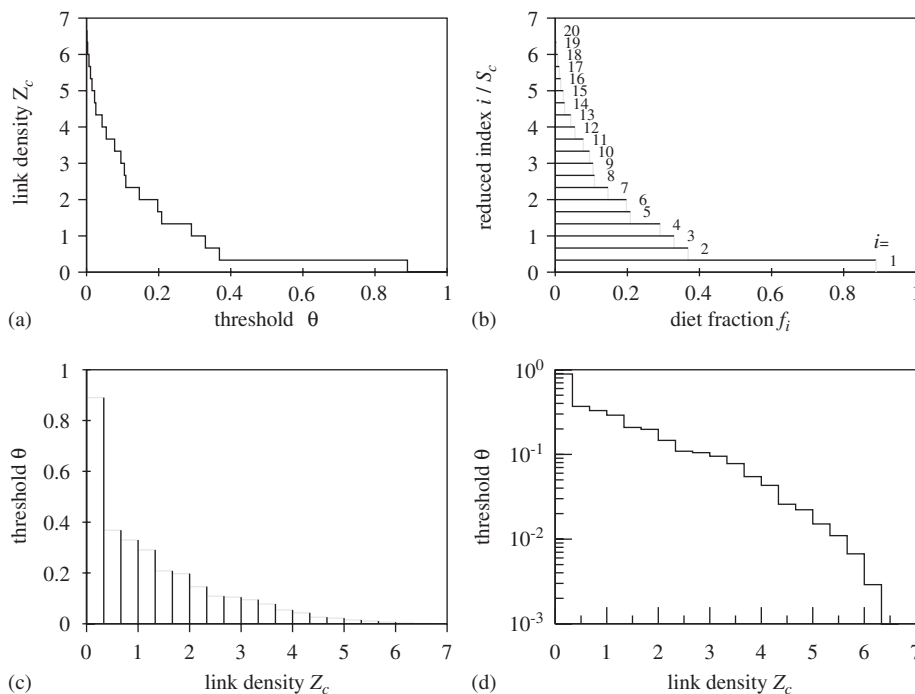$$Z = (1 - B) Z_c. \qquad (4)$$

Fig. 1. Concept and construction of the diet partitioning function: (a) the link density Z_c decreases with increasing link-strength threshold θ. (b) This piecewise constant function $Z_c(\theta)$ can be constructed from the sorted diet fractions. (c) Following general conventions, we exchange the axis and (d) draw θ logarithmically.

For typical empirical data sets $B \lesssim 0.25$, thus Z_c and Z are of the same order of magnitude.

2.4. Definition and construction of the DPF

When all link strengths l_{jk} are given, Z_c can be computed for any threshold θ $(0 \leqslant \theta \leqslant 1)$. Z_c increases as θ decreases, for example, as shown in Fig. 1a. As an efficient way to obtain $Z_c(\theta)$, first make a list of the values of all link strength l_{jk} and sort it in decreasing order so that the ith strongest link has strength l_i. Then, as illustrated in Fig. 1b,

$$Z_c(\theta) = \frac{i}{S_c} \quad \text{for } l_i \geqslant \theta > l_{i+1}. \tag{5}$$

Set $Z_c(\theta) = 0$ for $\theta > l_1$. In view of conventions adopted for graphs of similar relations such as rank-abundance plots, we shall, in the following, exchange Z_c and θ axis (Fig. 1c) and draw θ logarithmically (Fig. 1d). We call the function $Z_c(\theta)$ the DPF of a food web. When clear from the context, this term is used also for the inverse function $\theta(Z_c)$.

2.5. Examples of DPF ignoring species lumping

Ignoring, for now, the fact that some "species" in food-web data sets are actually aggregates, Fig. 2a shows the DPF for six data sets that have been published in the standard SCOR data format (Ulanowicz, 1999). The basic characteristics of these curves can be found also for other data: $\theta(Z_c)$ decays approximately exponentially for intermediate Z_c. For $Z_c \lesssim 1$ there are deviations from exponentiality due to the normalization in Eq. (2): all curves have to go through $\theta(0) = 1$. For large Z_c, there is a cutoff which may or may not be a measurement artifact.

Link densities in these six food-web data sets are correlated with S (the number of "living compartments" given in the SCOR files). For example, Fig. 2b shows Z_c values at $\theta = 0.01$ vs. S for the six data sets considered. A comparison of the rank ordering of S and Z_c is sufficient to

identify significant correlations (Spearman test, $r_s = 0.94$, d.f. = 4, $p < 0.01$, two-sided). However, in Section 5 we shall argue that this conclusion does not withstand a more careful analysis. The following two sections give the necessary theoretical background.

3. Some properties of the DPF

In the following, we discuss some properties of the DPF derived in Appendix A, which help in understanding and interpreting this characterization of food webs.

3.1. Normalization and probability interpretation

The DPF always satisfies the normalization condition

$$\int_0^1 Z_c(\theta)\, d\theta = 1. \tag{6}$$

Yet, neither $Z_c(\theta)$ nor $\theta(Z_c)$ have a direct interpretation as probability densities. Instead, the following holds: the probability $p(f)\Delta f$ that a consumer has a link with link strength in the small interval $[f, f + \Delta f]$ is given by the first derivative of $Z_c(f)$:

$$p(f) = -Z_c'(f). \tag{7}$$

3.2. DPF and generality distributions

For a given threshold θ, or for the corresponding link density $Z_c(\theta)$, the *cumulative generality distribution* (Camacho et al., 2002a,b) $P_{gen}(Z_c; n)$ can be defined as the probability that a consumer has n or more links to resources above the threshold. Given $P_{gen}(Z_c; n)$ and $Z_c(\theta)$, the probability $p_n(f)\Delta f$ that the strength of the nth strongest link of a consumer is in the small interval $[f, f + \Delta f]$ can be computed as

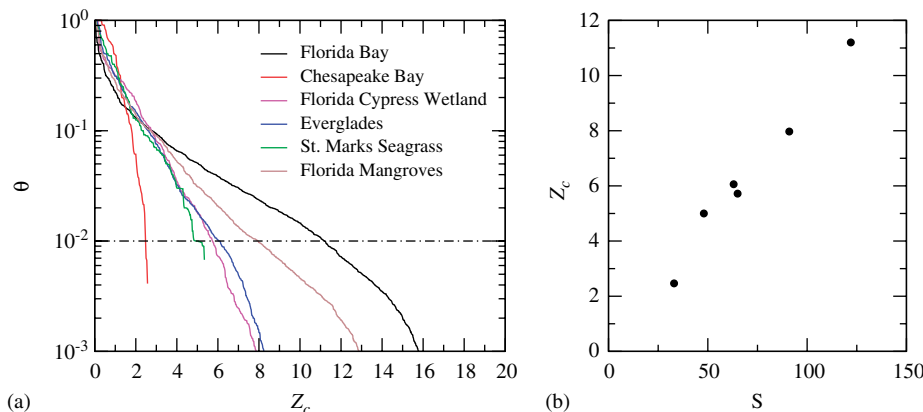$$p_n(f) = -\frac{dP_{gen}(Z_c(f); n)}{dZ_c} Z_c'(f). \tag{8}$$

Fig. 2. (a) The DPFs corresponding to six empirical food webs, without distinguishing between species and aggregates (Florida Bay: Ulanowicz et al., 1998, Chesapeake Bay: Baird and Ulanowicz, 1989, Florida Cypress Wetland: Ulanowicz et al., 1997, Everglades: Ulanowicz et al., 2000, St. Marks Seagrass: Christian and Luczkovich, 1999, Florida Mangroves: Ulanowicz et al., 1999). (b) The corresponding relation between the diversity (the number of "living compartments" in the data sets) and the link-density at $\theta = 0.01$.

Empirical food-web data (Camacho et al., 2002a,b; Stouffer et al., 2005) and theoretical considerations on food-web evolution (Rossberg et al., 2006b) suggest that there is a single family of distributions $P_{gen}(Z_c; n)$ that describes a large number of food webs over a large range of Z_c (see Eq. (A.12)). By the connection between the DPF and the generality distribution established in Eq. (8), this universality can be used to derive further general properties of the DPF.

3.3. Normalized ranks and their distribution

If l_i is the ith strongest link in a food web, then i is its rank. We call $z = i/S_c$ its *normalized rank*. By Eq. (5), $z = Z_c(l_i)$. By construction, normalized ranks are evenly distributed on the z-axis with density one.

Intuitively, one might expect that the normalized rank z_n of the nth strongest link of a consumer, i.e. $Z_c(l_n)$ if l_n is its nth largest diet fraction, is somewhere near n. In fact, one finds that for networks with link strengths assigned randomly between all species pairs, z_n has the expectation value n and the standard deviation $n^{1/2}$. But for food webs with the universal generality distributions of Camacho et al. (2002a), z_n scatters over a very broad range and its expectation value diverges.

The reason is that the normalized ranks of the links of a given consumer tend to cluster. Specifically, one can define the probability $\pi(z_1, z_2)\Delta z_1$ of finding (for a given consumer) a link with a normalized rank in the small interval $[z_1, z_1 + \Delta z_1]$, if another link with normalized rank z_2 has been found already. Using Eq. (8), we derive an approximation of $\pi(z_1, z_2)$, which depends only on the ratio z_1/z_2 (see Eq. (A.25)). As shown in Fig. 3, finding z_1 near z_2 is particularly likely. Through the interpretation of the generality distributions by Rossberg et al. (2006b), this can be traced back to phylogenetic correlations between link strengths.
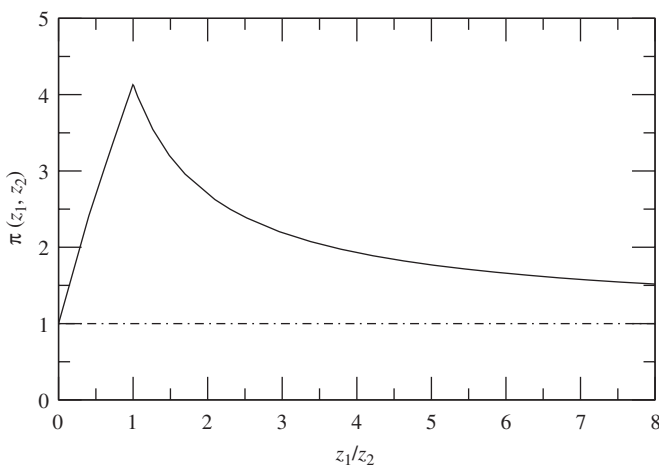

Fig. 3. Maximum entropy estimate of the two-point density $\pi(z_1, z_2)$ of the normalized rank assuming the family of degree distributions (A.12). The dash-dotted line is the asymptote for large or small z_1/z_2.

4. Estimating the DPF from incomplete information

4.1. Incomplete sampling of consumers

The value of Z_c can be estimated also if, rather than the diets of all consumers, only the diets of a representative sub-sample of consumers are available. This estimate of Z_c is given by Eq. (3), however, with S_c now representing the number of consumer species sampled, and L the number of their above-threshold links to resources.

When interpreting the DPF as a food-web average that can be estimated by sub-sampling, it becomes clear that the problem of determining the boundaries of an ecosystem or the question of the inclusion or exclusion of rare consumers will not affect Z_c much—provided we do account for all above-threshold diet items of those consumers that are included, irrespective if the resources are considered to be part of community or not.

4.2. Incomplete resolution of diets

To obtain a consistent estimator of the link density even when not all resource species are resolved in dietary data, we shall assume the following:

> The probability of lumping a species together with other species into a single diet category does not depend on the size of the species' diet fraction.

Of course, many scenarios of data acquisition are conceivable where this assumption is violated. But for the most frequently cited reason for lumping species, that they are too similar to be distinguished, there are no obvious reasons why lumping should be more likely for either abundant or rare species. We denote the probability for a species not to be lumped together with one or many other species by p.

Now, consider the list of those diet fractions that refer to resolved resource species in an empirical data set. Rank order the list and denote the jth largest diet fraction by l'_j. This list can be thought of as being obtained from the unknown true list l_i of the diet fractions of these consumers with consistent single-species resolution by eliminating those entries that have been lumped, i.e. any entry from the true list is contained in the list of known link strengths with probability p. The jth fraction in the empirical list corresponds to the ith fraction in the true list with $j \approx ip$.

Thus

$$Z_c(l_i) = \frac{i}{S_c} \tag{9}$$

can be approximated as

$$Z_c(l'_j) \approx \frac{j}{pS_c}. \tag{10}$$

The probability p can be estimated as

$$p \approx \hat{p} := \frac{\sum_k l'_k}{\sum_i l_i} = \frac{\sum_k l'_k}{S_c} \qquad (11)$$

if none of the diet fractions dominates the sums. (Typically this is the case when $l'_1 \ll \sum_i l'_i$.) The last equation follows from the fact that l_i values from each consumer species in the sample add up to one, so that the sum over all l_i is S_c. Finally, by combining (10) and (11), one obtains the estimator

$$\hat{Z}_c(\theta) = \frac{j}{\sum_k l'_k} \qquad \text{for } l'_j \geqslant \theta > l'_{j+1}. \qquad (12)$$

It is easily verified that $\int \hat{Z}_c(\theta) \, d\theta = 1$ just as in Eq. (6).

Note that estimator (12) does not depend explicitly on the number of consumer species included in the analysis. Neither does the inclusion or exclusion of extremely weak links ($l_i \approx 0$) affect the estimator, nor the inclusion or exclusion of consumers for which not a single diet item has been resolved at species level.

4.3. Error estimate

In Appendix B we derive an estimate of the error when using the empirical $\hat{Z}_c(\theta)$ as an approximation of some true $Z_c(\theta)$. For not too small $\hat{p}S_c$ we find that $Z_c(l'_j) = \hat{Z}_c(l'_j) \pm (RV)^{1/2} \hat{Z}_c(l'_j)$, with the relative variance consisting of two main components $RV = RV_{samp} + RV_{meas}$. The first component is the variance due to sampling errors

$$RV_{samp} = \frac{5}{3 S_c} + \frac{1}{j} + \frac{1 - \hat{p}}{\hat{p}^2 S_c^2} \sum_{i=1}^{\infty} l_i'^2 - \frac{2(1 - \hat{p})}{j \hat{p} S_c} \sum_{i=1}^{j} l'_i. \qquad (13)$$

Typically, the largest contribution here comes for the first addend, which is directly obtained as an integral over the increased conditional density of normalized ranks $\pi(z, z')$ (Section 3.3) due to clustering, and can be interpreted as an effect of phylogenetic correlations.

The contribution RV_{meas} is due to errors in measuring the diet fractions. When the error for each l'_i is normally distributed with standard deviation σ_i, this is

$$RV_{meas} = \frac{\sum_{i=1}^{\infty} q_i(1 - q_i)}{j^2} + \frac{1 - \hat{p}}{\hat{p}^2 S_c^2} \sum_{i=1}^{\infty} \sigma_i^2 \quad \text{where}$$

$$q_i = \frac{1}{2} \left[1 - \text{erf} \left(\frac{|l'_i - l'_j|}{\sigma_i \sqrt{2}} \right) \right]. \qquad (14)$$

As we shall see below, this contribution is typically small compared to RV_{samp}.

5. Examples of DPF using the new estimator for the link density

5.1. Typical DPF and their dependence on S

To illustrate the use of estimator (12) for the DPF and its error formulae (13), (14), we come back to the data sets analysed in Section 2, but now taking information

regarding species lumping (from the descriptions of the compartments in the SCORE files and Ulanowicz et al., 2003) into account. The requirement that $\hat{p}S_c$ should be large (Sections 4.3, B.1) is satisfied at best for Florida Bay ($\hat{p}S_c = 6.8$) and Chesapeake Bay ($\hat{p}S_c = 4.3$); for all other data $\hat{p}S_c$ is below two. But for illustrative purposes, we shall nevertheless proceed with a quantitative evaluation of all data.

Fig. 4 shows the estimated DPF for four exemplary data sets, assuming 30% relative errors in the diet fractions. Compared to Fig. 2a, there are considerable changes. For example, the estimate of $Z_c(0.01)$ for the Everglades increased from about 6 to more than 17.

Fig. 5 shows values of $Z_c(0.01)$ estimated by linear interpolation of $\hat{Z}_c(\theta)$ between the nearest θ points. Due to insufficient resolution (see Fig. 4), the data set for Chesapeake Bay was excluded. The changes compared to Fig. 2b are obvious. In particular, there is no significant
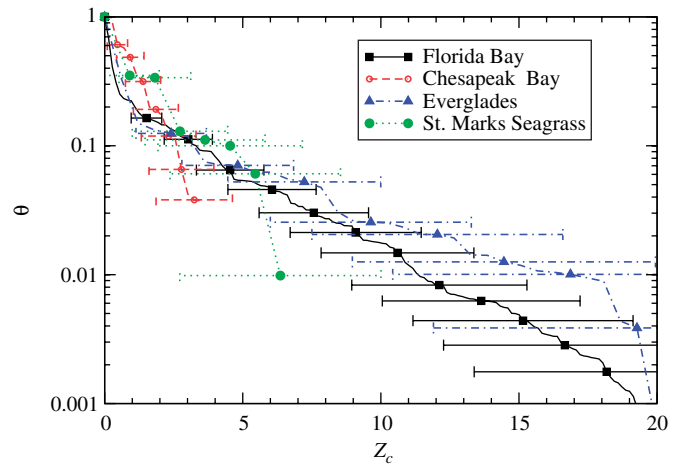

Fig. 4. (a) The DPFs corresponding to four of the six empirical food webs of Fig. 2, now corrected for species lumping, $\pm$ one standard deviation as given by Eqs. (13), (14). Note, that not for all computed points error bars are drawn.
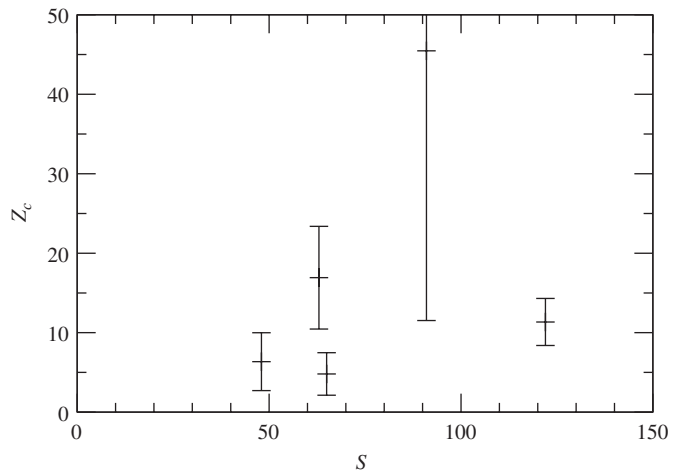

Fig. 5. $Z_c(0.01)$ estimated from various data sets $\pm$ one standard error against the number of "living compartments" S in the data sets.
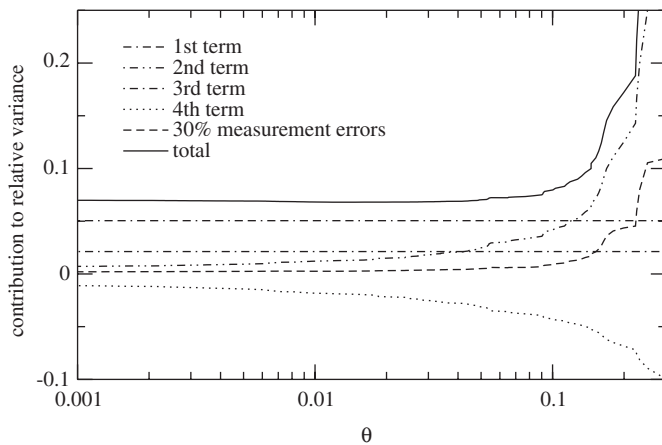
Fig. 6. The error structure for the estimated DPF of Florida Bay: contributions to the relative variance by Eq. (13) (first to fourth term) and by Eq. (14), assuming 30% relative errors, as well as the total relative variance.

positive correlation between Z_c and S anymore ($r = 0.54$, data points weighted by variance; $p = 0.24$, one-sided, from bootstrap permuting S). This suggests that the correlation between Z_c and S found at the end of Section 2 was an artifact of not taking species lumping into account. It is not clear to us in how far such artifacts also affected the conclusions that have been drawn from more systematic investigations of larger food-web collections in the past.

The weighted mean of the five values for $Z_c(0.01)$ is 8.2. The data appear to be compatible with the hypothesis that there is only a single, universal value of $Z_c(0.01)$ (sum of squares$= 6.0$, $p = 0.20$ assuming normal distributions, one-sided). If so, the standard error for our estimate of $Z_c(0.01)$ is 2.8, i.e. the 95% confidence interval for $Z_c(0.01)$ is approximately [2.6, 13.8].

5.2. Error structure

As a typical example for the error structure of the estimated DPF, Fig. 6 shows the contributions of the four terms of Eq. (13) and the contribution by Eq. (14) assuming 30% Gaussian errors for the diet fractions, as well as the resulting total relative variance of $\hat{Z}_c$ (solid line). Even though rather large measurement errors were assumed, their contribution (simple dashes) is nearly always negligible. The largest contribution comes from the phylogenetic correlations described by the first term in Eq. (13). The total relative variance—and hence the relative error—has a shallow minimum at $\theta \approx 0.01$, where correlated errors from the numerator and the denominator of (12) partially cancel each other.

6. Conclusions

In this work we proposed the DPF as a characterization of trophic link density. A detailed discussion of the mathematical properties of the DPF was provided. We introduced an estimator to obtain the DPF from empirical data and an error formula for this estimator.

It turns out that errors in measuring the diet fractions affect the result only weakly, while the sample size S_c and its completeness p strongly affect the accuracy (see Eq. (13)). This general observation is important for planning future empirical work to correlate food-web complexity with other properties, such as diversity or invadibility.

When measuring the link density in food webs for the purpose of relating it to food-web stability, lumping of species cannot be ignored. Our method takes lumping explicitly into account. But there is another problem for which no satisfactory solution appears to exist, yet, which is spatial coupling: assume that A eats only B in habitat I and A eats only C in habitat II. If the populations of A are isolated in the two habitats, the trophic niche breadth of A, as relevant for May's (1973) argument, is 1 in both habitats. If, on the other hand, the populations are coupled well enough that they are effectively identical, then the trophic niche breadth of A has to be taken as 2 for stability considerations. It is obvious that the spatial coupling affects stability: in the first case B and C do not compete, while in the second case A mediates an indirect competition between the two resource species. In reality, the effective niche breath of A would be somewhere between 1 and 2. A future theory should tell how to incorporate the effects of spatial coupling into the analysis of link density.

Finally, we caution to interpret the quantitative results obtained here using the SCORE data files with care. Not only because of the rather low accuracy we could achieve, but also because this data had not been assembled for the kind of analysis we did. For example, the diet of dolphins in Florida Bay has been recorded as consisting to 98% of fish and 2% of invertebrates, based on literature data (Ulanowicz et al., 2003). All fish species were then apportioned to the dolphin diet in proportions of their abundances. Preferences of dolphins for particular fish species were not taken into account. It is clear that such procedures can lead to a systematic overestimation of Z_c.

Acknowledgements

Appendix A. Derivation of properties of the DPF and related concepts

A.1. Normalization

To verify the normalization Eq. (6), first note that, by Eq. (5), Z_c is piecewise constant. Thus the integral (6)

equals

$$\sum_i Z_c(l_i)(l_i - l_{i+1}) = \sum_i \frac{i}{S_c}(l_i - l_{i+1}) = \frac{1}{S_c}\sum_i l_i = 1.$$

(A.1)

Using standard calculus, Eq. (6) can also be expressed in terms of the inverse DPF,

$$\int_0^\infty \theta(z)\,\mathrm{d}z = 1.$$

(A.2)

A.2. DPF and generality distribution

We go over to a stochastic setting. Assume that, for some fixed environmental conditions, there is a probability density $p(f_1, f_2, f_3 \ldots)$ to obtain the sorted list of diet fractions f_i for *one* randomly chosen consumer species ($\sum_i f_i = 1$, $f_1 \geqslant f_2 \geqslant f_3 \geqslant \cdots$, and $f_m = 0$ if the consumer has less than m resources). Integrating out all but the nth fraction ($n \in \mathbb{N}$) leads to the probability density $p_n(f)$ of finding the link strength f for the nth strongest link.

The cumulative distributions

$$P_n(\theta) := \int_\theta^1 p_n(f)\,\mathrm{d}f$$

(A.3)

have the following interpretation: with the threshold for link assignment θ fixed, $P_n(\theta)$ is the probability that the nth link exists, i.e. the probability that the consumer has n or more links. Hence, with $p_{gen}(\theta; k)$ denoting the probability that a consumer has exactly k resources with link strength above threshold θ—the "generality" k—one gets

$$P_n(\theta) = \sum_{k=n}^\infty p_{gen}(\theta; k).$$

(A.4)

That is, $P_n(\theta)$ is the cumulative distribution of the generality of consumers. The average number of links per consumer, Z_c, is

$$Z_c(\theta) = \langle k \rangle = \sum_{k=0}^\infty k p_{gen}(\theta; k) = \sum_{n=1}^\infty P_n(\theta).$$

(A.5)

The last equation can be used to determine Z_c from a given cumulative generality distribution even if the particular value of θ to which it applies is unknown. Thus, even without knowledge of the DPF, we can define the threshold-dependent family of cumulative generality distributions $P_{gen}(Z_c, n)$. Once a DPF is given, one has

$$P_n(\theta) = P_{gen}(Z_c(\theta), n).$$

(A.6)

Differentiating Eq. (A.5) with respect to θ yields

$$-Z_c'(\theta) = \sum_{n=1}^\infty p_n(\theta).$$

(A.7)

That is, the slope of the DPF $p(f) := -Z_c'(f)$ is the probability density for some link of a randomly chosen consumer to have strength f (because generally consumers have more than one link, $p(f)$ is not normalized). Eq. (A.7)

decomposes this density into the contributions from the strongest link $p_1(\theta)$, from the next strongest link $p_2(\theta)$, etc. These individual components can be computed according to Eq. (8), which follows from combining Eqs. (A.3) and (A.6).

A.3. The univariate distributions of normalized ranks

The probability $p_n(f)\Delta f$ for finding a link strength in the small interval $[f; f + \Delta f]$ equals the probability $\pi_n(z)\Delta z$ of finding a normalized rank in the small interval $[z; z + \Delta z]$ if $z = Z_c(f)$ and $\Delta z/\Delta f = |Z_c'(f)| = -Z_c'(f)$. Thus, the probability density $\pi_n(z)$ for the normalized rank of the nth strongest link of a consumer is given by

$$\pi_n(z) = -\frac{p_n(\theta(z))}{Z_c'(\theta(z))} = \frac{\mathrm{d}P_{gen}(z; n)}{\mathrm{d}z}$$

(A.8)

with the use of Eq. (8). By combining Eq. (A.7) and (A.8), one gets

$$\pi(z) := \sum_{n=1}^\infty \pi_n(z) = 1$$

(A.9)

for all z as expected from the definition of z.

A.3.1. Random networks

We consider first the application of Eq. (A.8) to Erdös–Renyi-type random networks: assume that all trophic link strengths are assigned randomly and independently from some given distribution. Then the number k of prey items of a consumer above a given threshold follows a Poisson distribution $p_{gen}(\theta; k) = Z_c(\theta)^k \exp[-Z_c(\theta)]/k!$. By Eq. (A.4),

$$P_{gen}(Z; n) = \sum_{k=n}^\infty \frac{Z^k}{k!}\,\mathrm{e}^{-Z} = 1 - \frac{\Gamma(n; Z)}{\Gamma(n)}$$

(A.10)

and

$$\pi_n(z) = \frac{\mathrm{d}P_{gen}(z; n)}{\mathrm{d}z} = \frac{z^{n-1}}{(n-1)!}\,\mathrm{e}^{-z}.$$

(A.11)

(For the verification of some results here and later on, symbolic algebra software can be helpful.) These distributions correspond to normalized ranks which are independently[1] scattered with constant density along the z-axis: the probability $\pi_n(z)\Delta z$ of finding the rank of the nth link in the small interval $[z, z + \Delta]$ is the Poisson distributed probability of finding $n - 1$ links below z times the probability Δz of finding a link in the small interval. From Eq. (A.11) one obtains expectation value and standard deviation of z as given in Section 3.3.

A.3.2. Food webs

Camacho et al. (2002b) showed that the family

$$P_{gen}(Z; n) = \exp\left(-\frac{n}{2Z}\right) - \frac{n}{2Z}E_1\left(\frac{n}{2Z}\right),$$

(A.12)

---

[1]Independent up to the artificial dependencies that result from rank ordering the links.

with $E_1(x) := \int_x^\infty t^{-1} \exp(-t)\,dt$ denoting the exponential integral function, describes the generality distributions of empirical food-web data well. Eq. (A.12) is valid when Z is large (cf. Rossberg et al., 2006b), and thus the predicted fraction of bottom species $B = 1 - P_{gen}(Z; 1)$ is small and we may then approximate $Z = Z_c$. To be consistent with this approximation, sums over n such as in Eq. (A.5) should be approximated by integrals $\int_0^\infty dn$. Eq. (A.12) is remarkable also because not all data sets it describes are based on the same criteria for link assignment.

Inserting Eq. (A.12) into Eq. (A.8) yields

$$\pi_n(z) = \frac{n}{2z^2} E_1\left(\frac{n}{2z}\right). \tag{A.13}$$

Up to normalization, the distribution of the normalized rank depends only on n/z. For all n, the mean normalized rank $\int_0^\infty z\pi_n(z)\,dz$ and all higher moments are infinite.

A.4. The two-point density of normalized ranks

A.4.1. Definition

The conditional density of the normalized rank $\pi(z_1, z_2)$ defined in Section 3.3 has an equivalent interpretation as the two-point density of normalized ranks $\pi(z_1, z_2)\pi(z_2) = \pi(z_1, z_2)$. That is, it gives the probability $\pi(z_1, z_2)\Delta z_1 \Delta z_2$ of finding, among the resources of one consumer, one with a link strength with normalized rank in the small range $[z_1, z_1 + \Delta z_2]$ and another in the small range $[z_2, z_2 + \Delta z_2]$.

A.4.2. Maximum entropy estimation

For a given family of rank distributions $\pi_n(z)$ we compute the maximum entropy estimate (Jaynes, 1957) of $\pi(z_1, z_2)$. For simplicity, we shall first ignore the constraint that the diet fractions of a consumer have to add up to one, but comes back to it further below.

Consider first the following general problem: let $g(z_1, z_2)$ be the density of ordered pairs (z_1, z_2) of numbers $0 < z_1 \leqslant z_2 < \infty$. Let the density of z_2 alone be

$$g_2(z_2) := \int_0^\infty g(z_1, z_2)\,dz_1, \tag{A.14}$$

and the distribution of z_1 alone be

$$g_1(z_1) := \lim_{\zeta \to \infty} \frac{\int_0^\zeta g(z_1, z_2)\,dz_2}{\int_0^\zeta g_2(z_2)\,dz_2} \tag{A.15}$$

be given. We seek an estimate for $g(z_1, z_2)$. The formula for $g_1(z_1)$ is expressed as a limit $\zeta \to \infty$ to include the case that $g_2(z_2)$ is not normalizable (and it cannot be interpreted as a probability density). In fact, the problem simplifies considerably under the assumption that g_2 is non-normalizable but g_1 is normalized to $\int g_1(z_1)\,dz_1 = 1$, and we shall make this assumption hereafter.

Using standard functional analysis and Lagrangian multiplier techniques, one finds that the density $g(z_1, z_2)$ satisfying Eqs. (A.14) and (A.15) and $g(z_1, z_2) = 0$ for $z_1 > z_2$ and maximizing the entropy $H = -\int\int g \log$

$g\,dz_1\,dz_2$ has the general form

$$g(z_1, z_2) = h_1(z_1)h_2(z_2)\Theta(z_2 - z_1), \tag{A.16}$$

where $\Theta(\cdot)$ is the Heaviside step function and h_1 and h_2 are some real-valued functions. It is straightforward to verify that the function

$$g(z_1, z_2) = \frac{g_1(z_1)g_2(z_2)}{\int_0^{z_2} g_1(z)\,dz}\,\Theta(z_2 - z_1) \tag{A.17}$$

satisfies all three conditions (A.14)–(A.16) and is thus the desired maximum entropy estimator.

To use this result for the estimation of $\pi(z_1, z_2)$, let

$$g_1(z_1) = \pi_n(z_1) \tag{A.18}$$

be the rank distribution of the nth link of a random consumer, and

$$g_2(z_2) = \sum_{k=n+1}^\infty \pi_k(z_2) \tag{A.19}$$

be the density of the normalized ranks of those links weaker than the nth. Since each distribution $\pi_k(z_2)$ is normalized to one, $g_2(z_2)$ is non-normalizable as required. Eq. (A.17) yields an estimate for the joint densities of ordered pairs (z_1, z_2) of normalized ranks under the condition that z_1 is the rank of the nth link. This last condition can be relaxed by summing over all n, giving

$$\hat{\pi}(z_1, z_2) := \sum_{n=1}^\infty \frac{\pi_n(z_1)}{P_{gen}(z_2; n)} \sum_{k=n+1}^\infty \pi_k(z_2)\Theta(z_2 - z_1), \tag{A.20}$$

where Eq. (A.8) has been used to evaluate the integral. Finally, the two-point density of unordered pairs (z_1, z_2) is obtained as

$$\pi(z_1, z_2) = \hat{\pi}(z_1, z_2) + \hat{\pi}(z_2, z_1). \tag{A.21}$$

A.4.3. Random networks

For Erdös–Renyi networks as discussed above, Eqs. (A.20) and (A.21) evaluate simply to $\pi(z_1, z_2) = 1 = \pi(z_1) \cdot \pi(z_2)$. The ranks of two randomly chosen links of a random consumer are uncorrelated. This is the expected result for Erdös–Renyi networks, confirming the validity of our method.

A.4.4. Food webs

In order to evaluate Eq. (A.20) for the generality distribution (A.12) in a consistent form, sums over n are again replaced by integrals, giving

$$\hat{\pi}(z_1, z_2) \approx \int_0^\infty dn\, \frac{\pi_n(z_1)}{P_{gen}(z_2; n)} \int_n^\infty dk\,\pi_k(z_2)\Theta(z_2 - z_1) \tag{A.22}$$

$$= j(z_1/z_2)\Theta(z_2 - z_1) \tag{A.23}$$

with

$$j(x) := \frac{1}{4x^2} \int_0^\infty v E_1\left(\frac{v}{2x}\right) \times \left(v + \frac{4}{2 - v\exp(v/2)E_1(v/2)}\right) dv, \tag{A.24}$$

and

$$\pi(z_1, z_2) = j\left[\min\left(\frac{z_1}{z_2}, \frac{z_2}{z_1}\right)\right]. \tag{A.25}$$

A.4.5. Corrections for small z

We shall now discuss the effect of the constraint that the diet fractions of a consumer have to add up to one. By Eqs. (A.2) and (A.9) this constraint is satisfied on the average ($\int_0^\infty \theta(z)\pi(z)\,dz = 1$), but it should also be satisfied in each case. In particular, the expectation value of the sum of the diet fractions should be one also when the normalized rank z_1 of one diet fraction is already known, i.e.

$$\int_0^\infty \theta(z_2)\pi(z_1, z_2)\,dz_2 + \theta(z_1) = 1. \tag{A.26}$$

The estimated density (A.21) does not generally satisfy this condition. Adding Eq. (A.26) to the prerequisites for the maximum likelihood estimation is possible but awkward. Instead, we note here that the integral over z_2 in Eq. (A.26) has contributions only from small z_2, where $\theta(z_2) = \mathcal{O}(1)$ (assuming exponentially decaying $\theta(z)$). Thus, it will affect $\pi(z_1, z_2)$ mostly for small z_2 and, by symmetry, for small z_1 (there typically leading to lower densities than (A.21)). For other values of z_1 and z_2, Eq. (A.21) should be a good approximation.

Appendix B. Derivation of an error estimator for empirically determined DPF and link densities

Here, formulae (13) and (14) of the error of estimator (5) for the DPF (or the link density for a fixed threshold) are derived.

It is assumed that there is a "true" DPF $Z_c(\theta)$ of some sort, e.g. the expectation value for some specific class of food webs or the DPF of a single web from which a comparatively small number of links l_j' has been sampled. Errors due to the finite sample size are evaluated in Section B.1, errors due to inaccurate measurement of the l_j' in Section B.2.

B.1. Sampling errors

Define the *sampling function* $s(z)$ in the following way: divide the z-axis into small intervals of width Δz and set $s(z) = 1/\Delta z$ in the intervals into which $Z_c(l_j')$ falls for at least one of the sampled diet fractions l_j', and otherwise set $s(z) = 0$.

To lowest order in Δz, the expectation value of the sampling function is

$$\langle s(z) \rangle = \frac{1}{\Delta z} p S_c \pi(z) \Delta z = p S_c \tag{B.1}$$

and its second moment

$$\langle s(z_1)s(z_2) \rangle$$
$$= \begin{cases} p^2 S_c[\pi(z_1, z_2) + (S_c - 1)] & \text{if } z_1 \text{ and } z_2 \text{ are in different intervals,} \\ p S_c/\Delta z & \text{if } z_1 \text{ and } z_2 \text{ are in identical intervals,} \end{cases} \tag{B.2}$$

where $\pi(z_1, z_2)$ is the two-point density of normalized ranks defined in Section A.4.1. The expression for the case of different intervals takes into account that, while there are considerable correlations between the link strength to the resources of one consumer, such correlations are weak between different consumers (Rossberg et al., 2006a).

Now, take the limit $\Delta z \to 0$. The covariance of $s(z)$ then becomes

$$\text{cov}(s(z_1), s(z_2)) = \langle s(z_1)s(z_2) \rangle - \langle s(z_1) \rangle \langle s(z_2) \rangle$$
$$= p S_c\{p[\pi(z_1, z_2) - 1] + \delta(z_1 - z_2)\}, \tag{B.3}$$

with $\delta(\cdot)$ denoting Dirac's δ-functional.

Using the sampling function $s(z)$, estimator (12) can be rewritten as

$$\hat{Z}_c(\theta_0) = \frac{\int_0^{Z_c(\theta_0)} s(z)\,dz}{\int_0^\infty \theta(z)s(z)\,dz}, \tag{B.4}$$

where $\theta(\cdot)$ denotes the true inverse DPF, i.e. $Z_c(\theta(z)) = z$.

The variance of the numerator integral $N := \int_0^{Z_c} s(z)\,dz$ in Eq. (B.4) (we suppress the argument θ_0 from here on) is given by

$$\text{var}\, N = \int_0^{Z_c} \int_0^{Z_c} \text{cov}(s(z_1), s(z_2))\,dz_1\,dz_2$$
$$= p^2 S_c \int_0^{Z_c} \int_0^{Z_c} (\pi(z_1, z_2) - 1)\,dz_1\,dz_2 + p S_c Z_c. \tag{B.5}$$

For not too small Z_c, contributions from small z_1 or small z_2 are negligible over the full range $[0, Z_c] \times [0, Z_c]$ of the last integral, and we may rely on Eqs. (A.24) and (A.25) for $\pi(z_1, z_2)$. The last double integral then evaluates to $5Z_c^2/3$. Since the expectation value of N is $p S_c Z_c$ by Eq. (B.1), the relative variance of the numerator integral N is

$$\frac{\text{var}\, N}{\langle N \rangle^2} = \frac{1}{p S_c}\left(\frac{5}{3}p + \frac{1}{Z_c}\right). \tag{B.6}$$

For the denominator integral $D = \int_0^\infty \theta(z)s(z)\,dz$ in Eq. (B.4) one obtains

$$\frac{\text{var}\, D}{\langle D \rangle^2} = \frac{p \int_0^\infty \int_0^\infty \theta(z)\theta(z')(\pi(z, z') - 1)\,dz'\,dz + \int_0^\infty \theta(z)^2\,dz}{p S_c} \tag{B.7}$$

$$= \frac{(1 - p)\int_0^\infty \theta(z)^2\,dz}{p S_c} \tag{B.8}$$

with the help of Eqs. (A.2) and (A.26), independent of the particular form of $\pi(z_1, z_2)$.

The relative variance of D is small ($\ll 1$) if $p S_c \gg 1$. We shall assume this in the following. It is then straightforward to verify that the expectation value of $\hat{Z}_c = N/D$ equals Z_c to lowest order in $1/p S_c$, i.e. the estimator is asymptotically

unbiased. Using the standard error-propagation law, one obtains the relative variance of $\hat{Z}_c$

$$\frac{\operatorname{var}\hat{Z}_c}{\langle\hat{Z}_c\rangle^2} = \frac{\operatorname{var} N}{\langle N\rangle^2} + \frac{\operatorname{var} D}{\langle D\rangle^2} - 2\frac{\operatorname{cov}(N,D)}{\langle N\rangle\langle D\rangle}, \tag{B.9}$$

with the last term evaluating to

$$\begin{aligned}
\frac{\operatorname{cov}(N,D)}{\langle N\rangle\langle D\rangle} &= \frac{1}{pS_cZ_c}\left[p\int_0^{Z_c}\int_0^\infty \theta(z')(\pi(z,z')-1)\,\mathrm{d}z'\,\mathrm{d}z \right. \\
&\quad \left. + \int_0^{Z_c}\theta(z)\,\mathrm{d}z \right] \\
&= \frac{(1-p)\int_0^{Z_c}\theta(z)\,\mathrm{d}z}{pS_cZ_c}, \tag{B.10}
\end{aligned}$$

again using Eqs. (A.2) and (A.26).

Putting Eqs. (B.6), (B.7), and (B.10) into Eq. (B.9) and replacing $p \to \hat{p}$ (see Eq. (11)), $\int \to \sum$, $z \to i/\hat{p}S_c$, $\theta(z) \to l'_i$, and $pS_cZ_c \to j$ yields the estimator (13) for the relative variance of $\hat{Z}_c$.

B.2. Measurement errors

Assume that the measurement standard errors σ_i for all l'_i have been estimated by other methods. These errors contribute to the variance of the numerator integral N if fractions with (true) normalized rank $z < Z_c$ are erroneously thought to have a rank $> Z_c$ and are thus not included in the integral or vice versa. Let q_i be the probability for the rank of the ith diet fraction to be on the wrong side of $Z_c(\theta_0)$ due to measurement errors. For example, for Gaussian errors,

$$q_i = \frac{1}{2}\left[1 - \operatorname{erf}\left(\frac{|l'_i - \theta_0|}{\sigma_i\sqrt{2}}\right)\right]. \tag{B.11}$$

Since N just counts the number of diet fractions with rank below Z_c, each fraction contributes a variance $q_i(1-q_i)$ to the variance of N. The total contribution to the relative variance of N is thus given by the first term in Eq. (14).

Measurement errors in the l'_i also affect D, the sum over all l'_i in the denominator. The contribution to the relative variance of D is given by the second term in Eq. (14), where the factor $(1-\hat{p})$ accounts for correlations between the diet fraction due to the normalization in Eq. (2), assuming uncorrelated errors for the diet masses m_{ik}.

Since, as exemplified in Section 5.2, the effect of measurement errors is generally small, correlations of the last two kinds of errors with other errors are not considered here.

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