

# Connectance in stream food webs

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## Summary

1. The properties of food webs are important both in theoretical ecology and environmental management, yet remain elusive. Here, we examined 12 new stream food webs of higher taxonomic resolution and completeness than any previously published data set and combined them with other 10 published stream webs.

2. Compared with most previously published food webs, these stream communities (containing between 22 and 212 species) had more feeding links per species, a higher fraction of intermediate species (0.78–0.88) and lower fractions of top (0.04–0.09) and ‘basal’ species (0.07–0.15).

3. The exponent of the log link-log species relationship ( $S^{1.3}$ ) differed significantly (ANCOVA:  $P < 0.001$ ) from the link-species ‘law’ ( $S^1$ ) and the constant connectance hypothesis ( $S^2$ ). Based on these results, the link scaling law and the constant connectance hypothesis must be rejected for food webs in stream systems.

4. Connectance was markedly lower than previously reported and decreased with web size. We attribute this to the body-size disparity of organisms at the top and the bottom of the web, flow disturbance and to the high physical heterogeneity and complexity of the sedimentary habitat. All these may reduce the fraction of possible feeding links that are realized.

*Key-words:* connectance, macrofauna, meiofauna, stream food webs, taxonomic resolution.

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## Introduction

The food web concept is central to community ecology and continues to stimulate debate among scientists searching for general patterns and ecological ‘laws’. Reliable descriptions of food web topology should facilitate comparisons between communities (e.g. in terms of web size, number of links, chain length) as well as yielding insight into their organization. The identification of structural patterns is fundamental to the interpretation of general or specific processes (e.g. significance of predation, degree of dietary specialization). The detection of patterns is challenging because they are not only a consequence of ecological processes but also themselves influence such processes (Winemiller & Polis 1996).

One broad generalization, examined by Martinez (1992) and Hall & Raffaelli (1993) is the link-species scaling law, in which the number of links ( $L$ ) increases linearly with the number of ‘trophic species’ ( $S$ ) and is independent of the number of species in the web (Cohen & Newman 1985). The link-species scaling law predicts two predator–prey interactions per species across all values of  $S$  (Winemiller *et al.* 2001). These webs included no food chains that counted the same species twice (i.e. feeding loops where  $a$  eats  $b$  eats  $c$  eats  $a$ ). A linear relationship between  $S$  and  $L$  is a basic assumption of the trophic cascade model of Cohen, Newman & Briand (1985) and some analyses suggest that small size webs fit such a pattern well (Solow 1996). Alternatively, under the constant connectance model (Martinez 1992), the exponent of  $S$  in the log link-log species relationship is equal to 2. If the number of predator–prey interactions per species increases as the square of  $S$  then connectance is constant (Williams & Martinez 2000).

Web properties are sensitive to taxonomic resolution, sampling effort and selective sampling (see Winemiller & Polis 1996).

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Simplified webs do not describe real communities adequately, because they depict too few species, too few links between species, little omnivory and cannibalism and, often, lack of feeding loops (Winemiller & Polis 1996). Bias associated with the functional aggregation of species is likely to be as great or greater than that associated with focusing on trophic interactions between higher level taxa (Winemiller *et al.* 2001), and is frequently biologically unrealistic (Hall & Raffaelli 1993).

Even food webs containing all the species in a community may still be an inadequate description of trophic relations, however, unless their realized diets are known with more confidence and analysed more realistically (Polis 1991). Benthic organisms usually reveal strong ontogenetic size-dependent predation (Schmid & Schmid-Araya 1997; Woodward & Hildrew 2002) and, because their diet also changes seasonally, the impact of such shifts on food web structure should not be ignored. For instance, in one acid stream there was a seasonal shift from a web dominated by links between numerous intermediate species to one with most links from intermediate to basal species (Schmid-Araya *et al.* 2002).

In common with other habitats, data obtained from streams and rivers have previously been very variable, based on an uneven taxonomic resolution, and mainly lacking information on small organisms < 300 ( $\mu\text{m}$ ) (Hildrew, Townsend & Hasham 1985; Closs & Lake 1994; Lancaster & Robertson 1995; Tavares-Cromar & Williams 1996; Woodward & Hildrew 2001). In general, webs from sedimentary environments, such as the soil and the aquatic benthos, have major detrital compartments, including organisms that have usually been lumped or even ignored in food webs compilations. These organisms show a high degree of omnivory, however, so that estimates of predator/prey ratio, or even a meaningful value of connectance, are debatable (Wardle *et al.* 1995).

Only recently has a more resolved and complete data set been reported for a stream food web (Schmid-Araya *et al.* 2002) and this paper takes advantage of this background and of new, hitherto unpublished, data from further stream systems to search for general patterns in natural food webs. We examine the relationship between web size and the total number of links, connectance and the fraction of basal, intermediate and top species for stream communities. We used lotic data that comprised: (a) 10 published webs of moderate taxonomic resolution in which known taxonomic species were not lumped but from which meiofaunal-sized organisms were excluded, and (b) an additional 12 highly resolved webs that included algae, micro-meiofauna and macroinvertebrates.

## Methods

### THE DATA

Webs of medium resolution included non-aggregated data from published webs of the following rivers/

streams: the Rheidol (Jones 1949a, 1950), Clydach and Sawdde (Jones 1948, 1949b), Dee (Badcock 1949), Cam (Hartley 1948), Morgan Creek (Minshall 1967) and Wharfe (Percival & Whitehead 1929). Also, previous depictions of the Broadstone Stream food web by Hildrew *et al.* (1985), Lancaster & Robertson (1995) and Woodward & Hildrew (2001) were included.

Highly resolved webs comprised new data sets from the Broadstone stream (accounting for five webs, Schmid-Araya *et al.* 2002) and single webs from seven other low-order streams. The latter corresponded to one temporary and six permanently flowing low-order (1–3) streams that had variable sediment type and hydraulic conditions. These streams were located in four areas: the Ashdown Forest (south-east England, UK, four streams), the upper Tywi (Mid-Wales, UK, one stream), central Europe (Germany and Austria: one stream each) and the Hainault Forest (south-east England: one stream).

In the Ashdown Forest (south-east England), the second-order Broadstone Stream (51°04'N, 0°03'E) and Lone Oak (51°04'36"N, 0°04'00"E) both drain acidic heath and deciduous woodland. Their mean daily discharge ranges between 0.001 and 0.11  $\text{m}^3 \text{s}^{-1}$  (Lancaster & Hildrew 1993). The two other streams in the area, Maresfield (50°59'45"N, 0°05'35"E) and Marsh Green (51°04'45"N, 0°04'45"E), were of third-order and flow through deciduous woodland and agricultural land with a mean daily discharge between 0.017 and 0.39  $\text{m}^3 \text{s}^{-1}$  (Lancaster & Hildrew 1993).

The stream in Mid-Wales (Mynydd Traswnant, 52°07'N, 3°43'W: site LI7 of Dobson 1990) is of first order and circumneutral, draining moorland, with a substratum characterized by shales and mudstones and a mean daily discharge of 0.034  $\text{m}^3 \text{s}^{-1}$ . The Breitenbach in Hessen (Germany, 50°4'N, 09°45'E) is a small first-order stream (4 km length) with a discharge between 0.004 and 0.20  $\text{m}^3 \text{s}^{-1}$  and a stream bed consisting of 'Bunter sandstones' of varying grain-sizes (Wagner *et al.* 1993). The Oberer Seebach (Lower Austria, 47°51'N, 05°04'E) is a second-order, calcareous stream with a range of discharge between 0.19 and 15  $\text{m}^3 \text{s}^{-1}$  and a stream bed of medium to coarse gravel sediments (median: 23.1 mm). The temporary, first-order Hainault stream (south-east England, 51°37'N, 0°07'E) was characterized by a sandy stream bed surface with a median grain size < 1 mm.

In Broadstone Stream, samples were taken in July/August and November 1996 and in February and May 1997, whereas all other study sites (elsewhere in the UK and in Central Europe) were visited between May and July 1997 and, again, between October and December 1997. In order to achieve greater standardization and accuracy, the sampling procedure was the same in all streams and, on each occasion, we selected sites randomly within 300 m stream stretches, avoiding any anoxic areas. At each stream 10 quantitative samples were collected randomly using a modified Hess sampler (surface area, 0.01  $\text{m}^2$ : mesh size, 40  $\mu\text{m}$ ). These

**Table 1.** Food web properties derived from medium and highly resolved lotic food webs. *N* is the number of webs, *B*, *I* and *T* are fractions of basal, intermediate and top species (see text for explanation) and *C* is directed connectance ( $C = L/S^2$ ; Martinez 1991)

Source	<i>N</i>	Web size, <i>S</i> Range (mean)	<i>B</i> Range (mean)	<i>I</i> Range (mean)	<i>T</i> Range (mean)	<i>C</i> Range (mean)
(a) Medium resolution						
Percival & Whitehead (1929), Jones (1948, 1949a,b, 1950), Hartley (1948), Badcock (1949), Minshall (1967), Hildrew <i>et al.</i> (1985), Lancaster & Robertson (1995), Woodward & Hildrew (2001)	10	24–92 (46.2)	0.05–0.30 (0.17)	0.38–0.91 (0.69)	0.03–0.47 (0.15)	0.033–0.156 (0.080)
(b) High resolution						
Schmid-Araya <i>et al.</i> (2002)	5	54–128 (84.4)	0.07–0.15 (0.11)	0.78–0.88 (0.82)	0.04–0.09 (0.07)	0.044–0.082 (0.057)
This study	7	22–212 (101.0)	0.05–0.20 (0.15)	0.67–0.85 (0.74)	0.07–0.17 (0.11)	0.026–0.122 (0.060)

samples were kept cool and transported to the laboratory, where they were carefully sieved to separate the (500 µm and > 500 µm size fractions). The larger fraction was immediately preserved with 4% formalin for later sorting, while identification and counting of organisms (500 µm was performed on the live material).

For food web analyses, specimens from these quantitative samples were supplemented where necessary with extra individuals. A minimum of 50 individuals was collected of each meio- and macrofaunal species (size > 500 µm) whose mean abundance exceeded 0.5 individuals per 0.01 m<sup>2</sup> (Schmid-Araya *et al.* 2002). More macroinvertebrate individuals were collected as required with pond nets (300 µm mesh net) and meio-invertebrates with a 100-µm net. Predators were anaesthetized with carbonated water, to reduce regurgitation of prey, and later preserved in 4% formalin.

We compiled five different webs (four seasonal and one single summary web) for Broadstone Stream (Schmid-Araya *et al.* 2002). Summary webs were constructed for Lone Oak, Maresfield, Marsh Green, L17, Breitenbach and Hainault stream. The summary web for the Oberer Seebach was compiled from the data of Schmid & Schmid-Araya (1997) and from the two sampling occasions reported here.

Using this standardized sampling regime, we incorporated algae, micro-, meio- and macrofauna but did not include taxa such as bacteria, birds and other vertebrates. In all the streams examined, the meiofauna (size range < 500 µm) comprised between 60% and 81% of the species present.

#### WEB PROPERTIES

Feeding interactions were determined by gut content analyses of > 50 specimens of each invertebrate species found during the sampling period, following Schmid-Araya *et al.* (2002). Links were determined as interactions between predators and prey established on the basis of direct, empirical analysis rather than relying on the literature. The total number of links was estimated

for each web based on the respective food web matrix. Species were categorized as *top* species, having prey but no predators, *intermediate* species, with both prey and predators, or *basal* 'species', that have predators but no prey (Martinez 1991). Directed connectance ( $L/S^2$ ) is the proportion of directed links that is realized (including cannibalism and mutual predation; Martinez 1991).

#### Statistical analyses

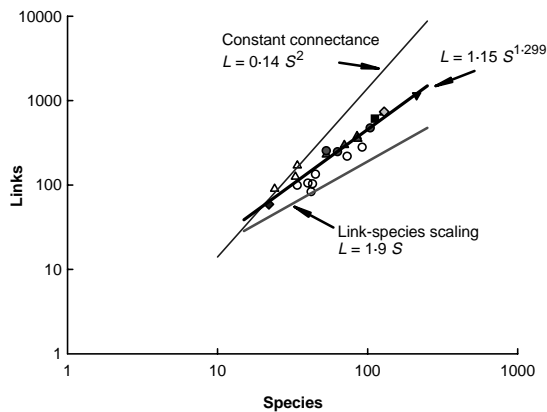
To examine whether the number of links, proportion of species (in the top, intermediate and basal categories) and connectance were related to species richness, we used ordinary least-squares regressions (OLS). For comparison, the proportions of species in the three categories were also examined with logistic regressions (LOGIT) using the maximum likelihood method (McCullagh & Nelder 1989; Murtaugh 1994).

We used ANCOVA (Sokal & Rohlf 1981) to compare regression slopes obtained from log-transformed data of the relationship between the number of links and species richness. In particular, we tested whether the scaling exponent observed for stream food webs differed from that of the link-species scaling 'law' (exponent of *S* equals 1) and constant connectance model (exponent equals 2).

#### Results

The number of taxonomic species in the webs ranged between 22 and 212. Not surprisingly, highly resolved webs including the meiofauna and algae had a distinctly higher mean number of species, 101, than those from webs of medium resolution, with a mean of 46.2 (Table 1).

In these stream communities, the relationship between links (*L*) and species (*S*) was well described by the equation  $L = 1.15 S^{1.299}$  (regression ANOVA:  $F_{1,20} = 438.18$ ;  $P < 0.001$ ; Fig. 1). The exponent of *S*,  $\beta = 1.3$  ( $SE_{\text{slope}} = 0.07$ ), differs significantly from the link-species



**Fig. 1.** Hypotheses and data on the relationship between species ( $S$ ) and links ( $L$ ) in stream communities. [Published compilations (see Methods): open circles, moderately resolved webs for Broadstone stream (Hildrew *et al.* 1985; Lancaster & Robertson 1995; Woodward & Hildrew 2001): open triangles, well-resolved webs for Broadstone stream: shaded triangles, Lone Oak, Marsh Green and Maresfield: shaded circles, Oberer Seebach: shaded upside-down triangle, Breitenbach: shaded square, L17 Mid-Wales: open diamond and Hainault stream: shaded diamond]. Regression equation  $L = 1.15 S^{1.299}$  ( $R^2 = 0.956$ ,  $P < 0.001$ ;  $SE_{\text{slope}} = 0.066$ ,  $t$ -test:  $P < 0.001$ ).

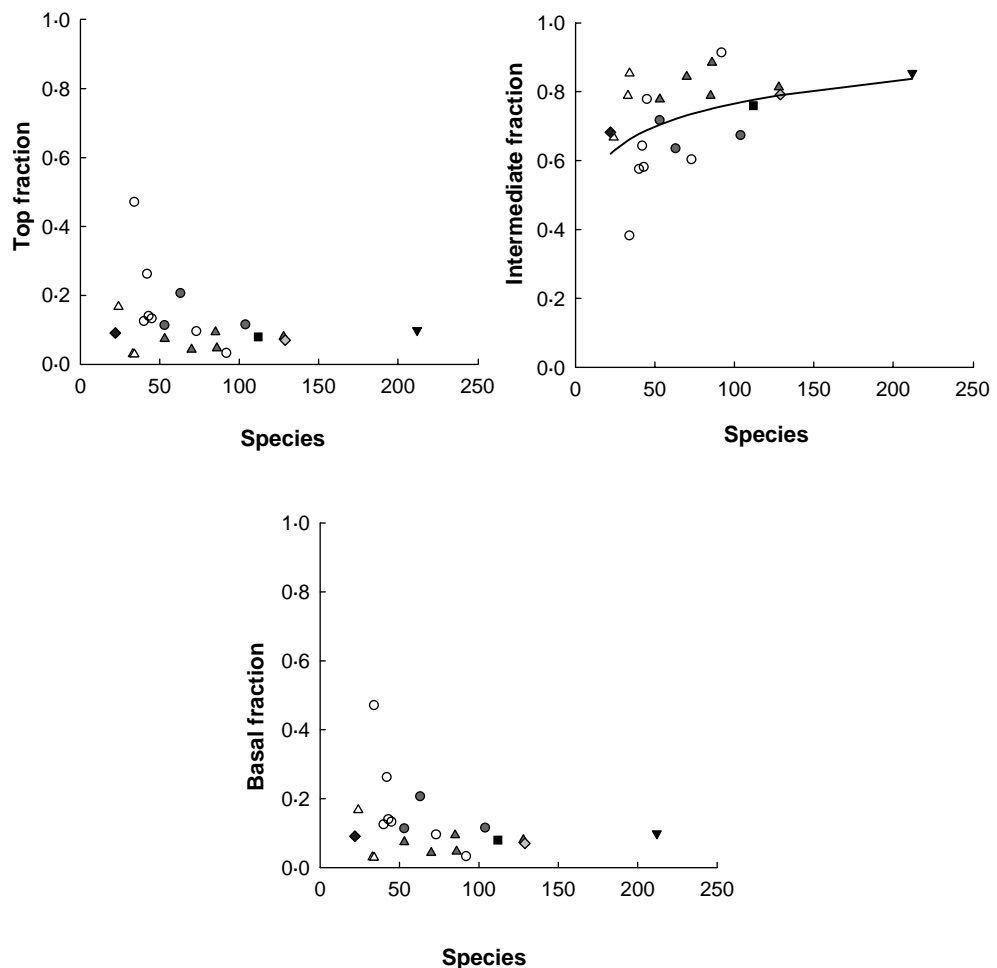
scaling law Cohen & Newman (1985) ( $L = 1.9 S^1$ ; ANCOVA  $F_{1,40} = 965.33$ ,  $P < 0.001$ ) and from the constant connectance hypothesis of Martinez (1992) ( $L = 0.14 S^2$ ; ANCOVA  $F_{1,40} = 133.09$ ,  $P < 0.001$ ).

Based on linear regression the fraction of intermediate species increased with web size ( $P = 0.031$ , Fig. 2), although logistic regression did not show a significant relationship ( $P = 0.071$ ). For communities with more than 50 species, the predicted fraction of intermediate species remained between 0.70 and 0.80 (Fig. 2). Neither maximum likelihood logistic (LOGIT) regression nor ordinary least square (OLS) methods showed any significant relationship between the fraction of 'basal' species ( $P_{OLS} = 0.091$ , Fig. 2;  $P_{LOGIT} = 0.114$ ) and top species ( $P_{OLS} = 0.222$ , Fig. 2;  $P_{LOGIT} = 0.075$ ) and species richness in these webs.

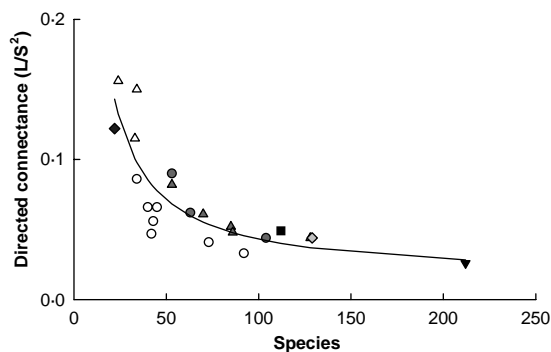
Connectance declined markedly with increasing species richness but remained relatively similar at web sizes above 70 species (Fig. 3).

## Discussion

Most reported patterns in food webs have been based on webs containing variable aggregations of trophic



**Fig. 2.** The fraction of species in (a) basal, (b) intermediate and (c) basal categories as a function of  $S$  in stream communities. Regression equation  $I = 0.323 + 0.098 \ln S$  ( $R^2 = 0.213$ ,  $P = 0.031$ ;  $SE_{\text{slope}} = 0.042$ ,  $t$ -test:  $P = 0.030$ ). Stream identities as in Fig. 1.



**Fig. 3.** Directed connectance ( $L/S^2$ ; Martinez 1991) as a function of  $S$  in stream communities. Regression equation  $L/S^2 = 0.015 + 2.818/S$ ; ( $R^2 = 0.723$ ,  $P < 0.001$ ;  $SE_{\text{slope}} = 0.390$ ,  $t$ -test:  $P < 0.001$ ).

species and far less on highly resolved data sets. The stream communities reported here were characterized by more feeding links per species, a higher fraction of intermediate species and a lower fraction of top and 'basal' species than most stream webs previously (e.g. Cohen *et al.* 1985).

The power-law relationship between links and web size ( $L = \alpha S^\beta$ ) not surprisingly confirmed that the number of links increases with web size, but we obtained an exponent ( $\beta$ ) of  $S$  of 1.3, a value that differs significantly from the link-species scaling 'law' ( $\beta = 1$ ) and the constant connectance hypothesis ( $\beta = 2$ ). In addition, connectance (the proportion of directed links realized out of the maximum number of possible links, including cannibalism and mutual predation) decreased with increasing web size.

Despite the fact that the total number of links in a food web increases with the number of species, the rate of this increase is not well established in the literature (Pimm, Lawton & Cohen 1991). Analysing webs with variable degrees of aggregation ( $n = 113$ ), Cohen, Briand & Newman (1986) calculated an exponent  $\beta$  of 1.36 but argued that their allometric model  $L = 0.671 S^{1.356}$  did not differ significantly from a linear model  $L = 1.999 S$ . Over a range of web sizes, the true exponent  $\beta$  must lie between 1 and 2 (Martinez 1992). However, while his analysis of 163 webs (a data set including many of the webs cited by Cohen & Newman 1985) yielded an estimate of  $\beta$  of 1.5, the exclusion of webs with less than 10 taxa yielded  $\log L$ - $\log S$  regressions with  $\beta = 2.0$ . Hall & Raffaelli (1991) also reported a  $\beta$  of 1.34 in the relationship between  $L$  and  $S$  for the large and well-resolved Ythan food web. Warren (1990) argued that the total number of links in a web should increase as  $S^2$ . Warren's biological explanation for this was that consumers exploit a constant fraction of the prey available, this fraction being estimated by the parameter  $\alpha$  in the power-law relationship  $L = \alpha S^2$  and thus being equal to the directed connectance. For any particular kind of habitat, Warren (1990) suggested that connectance would not change with  $S$  and would be high in freshwater webs that consist of trophic generalists.

Values of connectance in these lotic systems were lower than reported for most published food web, with the exception of a few cases (the Ythan estuary, Huxham *et al.* 1996; parasitoid communities, Memmot *et al.* 2000). Controversy persists on whether  $C$  is independent of  $S$  (Martinez 1992), increases with  $S$  (Winemiller 1989) or decreases with  $S$  (Rejmánek & Starý 1979). It is likely that any relationship is obscured by the variability in documenting links (Hall & Raffaelli 1993). Nevertheless, from our data it appears that the observed decline in connectance with increasing  $S$  in food webs indicates that species are exploiting a declining fraction of the total 'prey' available (Warren 1990).

There are several possible and related explanations for the pattern of declining connectance with increasing species richness. First, a preponderance of non-predatory species (herbivores/detritivores) places a constraint on the maximum number of links per species (Closs & Lake 1994), as non-predators by definition can consume only basal species. In general the position and/or proportion of species in the different trophic categories must determine limits to the total number of links in food webs.

Lotic food webs contain many species (60–80% of total community) in the meiofaunal size range (50–500  $\mu\text{m}$ ), and the proportion of these species in the intermediate category increases with better and more even resolution (Schmid-Araya *et al.* 2002). Most organisms < 500  $\mu\text{m}$  have been categorized hitherto as basal in more 'lumped' compilations and, regrettably, in aggregating different types of organism, some studies may have overlooked important and different patterns in web subsets (Polis 1991; Murtaugh & Kollath 1997).

Our results demonstrated that the fraction of intermediate species increased with web size ( $S$ ), similar to other webs (Martinez 1994), the fraction of intermediate species remained between 0.7 and 0.8 for stream communities with more than 50 species. There was no significant relationship between the fraction of top and 'basal' species and  $S$ . Changes in one or more of the trophic fractions with  $S$  have been reported before (Schoenly *et al.* 1991; Martinez 1994), while Murtaugh & Kollath (1997) argued that the nature of the relationships of the trophic categories to  $S$  should vary among habitat types. Unfortunately, these web properties are extremely sensitive to the level of resolution and a variety of conclusion have been reached previously.

A second, related explanation for the decline in connectance with  $S$  is that a high number of species in stream food webs is accompanied by an increase in the total range of body sizes in the community. This increased size disparity may render direct trophic links less likely between species at the two extremes, contributing to a decline in connectance (Hildrew 1992). High body size disparity between meiofauna and macrofauna in the stream bed could also decrease encounter rate, and thus the fraction of realized food web links, because the former are more likely to be interstitial and the latter epibenthic (Ward *et al.* 1998).

Thirdly, in streams, spatial heterogeneity plays an important role in the coexistence of species (Tokeshi 1999) and should promote complex, multispecies webs. Keitt (1997) demonstrated that the introduction of spatial heterogeneity in simulated food webs also changes the relationship between food web connectance, interaction probabilities and species richness. He speculated further that the inverse relationship between web connectance and species richness suggests that the product of this relationship may govern the stability of real, finite webs.

The higher connectance reported for lentic systems could be a consequence either of not including 'smaller taxa' and their food items or because a greater fraction of realized linkages occurs in the water column than in the complex, labyrinthine sediments of streams that provide refugia from predation (Schmid 2000). It is also likely that different hydraulic preferences between predators and prey in running waters reduces the encounter or attack rates between them (Hansen, Hart & Merz 1991) and therefore reduces web connectance. Finally, low connectance in stream communities may also be attributable to the more frequent and intense physical disturbance regime of streams, limiting the realized links between species.

This analysis of stream food webs indicates that their structure differs from previously published studies. We found that an increase in taxonomic resolution resulted in: (a) an increase in the number of interacting species, (b) an increase in  $L$  with  $S$ , although at a lower rate than suggested previously and indicated by a  $\beta$  value of 1.3 and (c) a consequent decline in connectance with increasing  $S$ . We conclude, therefore, that our results refute both the link-scaling law and the constant connectance hypothesis. Values of connectance between 0.026 and 0.122 suggest that stream webs are less connected than many other natural systems studied previously. Candidate explanations for the decline in connectance include the body size of species and environmental variables such as disturbance regime, habitat type and habitat heterogeneity. Finally, further generalizations about the rate of increase of the number of links with species richness and the pattern of connectance need to consider the contribution of the trophic categorization of species. The question remains of whether streams are unique in their properties or whether these are shared by other communities of sedimentary environments (soil, lake, marine benthos). Unfortunately, there are very few comparable data for other systems.

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