

Structure, dynamics and stability of a Mediterranean river food web

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Abstract. We present the results of a study of the food web of a Mediterranean river in the four seasons of the year. A high-resolution taxonomic description has been produced to characterise the different community components. We have also determined the trophic relationships among organisms by analysing their gut contents. From the network topology, we extracted several descriptors of structural complexity of the community in terms of number of nodes and links. We found a positive relationship between connectance and diversity (both biological and functional). Moreover, we developed and applied a quantitative approach to estimate the link strength, which showed that not all links constituting the network are equally important. In the present paper, we show that the strength of the food-web links vary over time, but there is a natural tendency to keep a small set of strong links throughout the year. However, the existence of two consecutive strong links is not common, meaning that trophic cascades are not promoted.

Additional keywords: biological diversity, freshwater, functional diversity, link density, macroinvertebrate community, nodes, omnivory, trophic web.

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Introduction

Ecological network models are an approach to understanding the functioning of ecosystems in which species interactions have a role that is as important as that of community composition (Bascompte 2009). Among these, one of the most popular network models is food webs, which can be defined broadly as a map that describes the interaction network among organisms in which some eat others (Pimm *et al.* 1991). In fact, food-web models have been proposed as fundamental for describing and quantifying ecosystem complexity (May 1972; Pimm 1984; Montoya *et al.* 2006), with food-web studies advancing considerably in recent years (Thompson *et al.* 2012a). Generating food-web models requires knowledge of the structural architecture and the temporal dynamics of the ecosystem because these factors are important in determining the characteristics of the study community. Complexity measures of structural architecture incorporate the number of nodes (taxa and trophic resources) and links (interactions among nodes) in the network (Thompson *et al.* 2012b). There are several methods for quantifying a community's structural complexity, but the most frequently used are the calculation of connectance (the connectance ($C = L/S^2$) relates the number of links (L) with the square of the number of nodes (S^2)), link density (L/S) and

omnivory degree (omnivorous nodes ratio, being omnivorous all those nodes that consume resources from more than one trophic level). Moreover, structural knowledge of these networks and their assembly over time is of interest not only in basic ecology, but may also be crucial to carrying out successful conservation and restoration strategies (Neutel *et al.* 2007).

Food-web models, in comparison with other ecological network models, are relatively small with respect to number of nodes and their structure shows a high proportional linkage density, giving them high connectance values (Dunne *et al.* 2002). Knowledge of link distribution (structure) and dynamics of food webs is fundamental to understanding the persistence and stability of ecosystems (Sánchez-Carmona *et al.* 2013). However, since food-web models were first used (May 1972), the way in which complexity is related to stability has been frequently debated (Allesina and Pascual 2008). Another factor related to stability is diversity. It has been observed in both aquatic and terrestrial communities that stability is positively correlated with taxonomic diversity (McGrady-Steed *et al.* 1997; Naeem and Li 1997) and potentially has a stronger relationship with functional diversity (i.e. the diversity of functional groups) (Huston 1997; Tilman *et al.* 1997; Thompson and Starzomski 2007). An understanding of how food-web

architecture varies over time will help inform an understanding of how food-web complexity relates to community diversity (both functional and taxonomic) and indirectly relates to community stability.

The strength of network linkages varies within food webs; of all the links that make up a food web, there are usually only a few strong links nested within a network of weak links (McCann *et al.* 1998; Neutel *et al.* 2002; Bascompte *et al.* 2005). The non-random arrangement of these strong links in ecosystems, which have been studied previously, seems to be another determinant of stability at the community level (Bascompte *et al.* 2005; O’Gorman and Emmerson 2009). In fact, experimental removal of a few strong interaction nodes can result in a dramatic collapse of the ecosystem (O’Gorman and Emmerson 2009). In this sense, components linked by strong links can be viewed to operate analogously to key species in ecosystems because their disappearance from the ecosystem (for instance, as a result of extinction) has disproportionately large effects in relation to their abundance (see Moore and de Ruiter 2012). However, weak links, which can be formed more easily and disappear over time, could also play an important role in maintaining the stability of the community (McCann and Yodzis 1998), through supporting the strong links. If they attenuate very strong interactions by increasing the number of alternative trophic resources for a given consumer (e.g. alternative prey for a predator), they would help limit the excessive consumption of those resources, and this would reduce the likelihood of trophic cascades (Bascompte *et al.* 2005). Thus, the quantitative study of the abundance of each node and the interaction forces between nodes is of great interest.

Although network models are rooted in concepts imported from physics and mathematics (Bascompte 2009), reliability and predictability critically depend on the biological and ecological knowledge that we have of the community under study. It is not enough to identify taxa that form the food web, it is also important to analyse the identity of trophic interactions and the rate at which they occur (Ulanowicz 2004), for which more refined units of reporting are required (Cohen *et al.* 1993). However, this is a difficult task because many of the properties of the proposed food-web models may be the result of artefacts caused by the limitations of the data on which they are based (Polis 1991; Cohen *et al.* 1993; Winemiller *et al.* 2001). This could be a consequence of several factors. First, the level of taxonomic knowledge of many biological communities (Mayr 1997), with many researchers studying trophic networks forced to work at higher taxonomic levels. Consequently, networks tend to be composed of nodes (tropho-species) the relationships of which with others, and with basal resources (e.g. detritus), are generalised from the literature. For instance, Thompson and Townsend (2000) demonstrated how taxonomic resolution clearly affects the value of connectance. Second, most studies focus on structural factors in food webs, describing structure at one point in time, missing completely the temporal component; for example, many studies ignore the existence of ontogenetic variations in diets throughout life cycles. Finally, there are few studies that quantitatively measure the strength of links among components of the network. In fact, it has been shown that this ‘link-strength’ can be affected by the abundance of the different nodes (Vázquez *et al.* 2007).

The present study describes the food web and trophic relationships of a macroinvertebrate assemblage of a permanent Mediterranean river. This information is then used to calculate descriptors of network complexity in terms of connectance, linkage density and degree of omnivory. The relationships between diversity (biological and functional) and complexity are then analysed with the distribution of strong and weak links, and their permanence over time, identified.

Materials and methods

The study was conducted in the Castril River, a permanent limestone river in the Guadalquivir basin (southern Spain). This river flows ~40 km from an altitude of 1600 to 650 m above sea level (ASL). The sampling area (1220 m ASL, 37°52’37’’N, 2°45’26’’W) is within the Natural Park of the Sierra de Castril. The study reach is surrounded by forest composed mainly of *Pinus nigra* and *P. halepensis*, with some *Quercus ilex* and *Salix* spp. The riparian vegetation is low-growing vegetation *Scirpus holoschoenus*, with some herbaceous Ranunculaceae (particularly the genus *Ranunculus*), Umbelliferae and Compositae. The channel in the study area has low canopy cover and varies in width between 7 and 18.5 m, with a maximum depth of more than 0.5 m, and with a bed composed mainly of gravel, cobbles and boulders.

Samples were collected on four occasions over a 12-month period, each coinciding with the central month of a season: July (summer), October (autumn), January (winter) and April (spring). At each sample occasion, spot measurements of water-quality parameters including oxygen concentration, conductivity, pH and flow were taken. The values of oxygen (mg L^{-1}) and percentage saturation, conductivity ($\mu\text{S cm}^{-1}$) and pH were obtained using a VWR sympHony multiparameter probe (VWR International Eurolab S.L., Barcelona, Spain). Discharge ($\text{m}^3 \text{s}^{-1}$) was estimated by measuring the width of the channel and the average depth of the section with a tape measure, and the velocity of the water with a Global Water digital flowmeter (Global Water Instrumentation, Rancho Cordova, CA, USA). Finally, temperature was obtained by placing a probe (iBCod, Leiria, Portugal, accuracy = 0.5°C) in the riverbed, which measured this parameter every hour throughout the study period.

Macroinvertebrates were sampled quantitatively using a Surber sampler (EFE & GB NETS, Cornwall, UK, 0.1-m² area and 250- μm mesh size). To have a proper representation of the community, six samples were collected covering all microhabitats of the study area (i.e. rapid flow, slow flow, gravels, sands, proximal zones to shore and vegetated areas). Macroinvertebrates were preserved in 70% ethanol, identified to the lowest possible taxonomic level and counted in the laboratory. Except Diptera, all orders of insects were identified to genus level (~66% of nodes). Diptera were identified to tribe level for Tanytarsini (family Chironomidae) and Simuliini (family Simuliidae) (~5% of nodes), subfamily level for Tanypodinae, Prodiamesinae, Orthocladiinae (family Chironomidae) and Clinocerinae (family Empididae) (~10% of nodes) and family level for Limoniidae, Tabanidae, Ceratopogonidae and Stratiomyidae (~10% of nodes). Finally, non-insect macroinvertebrates were identified to genus level for *Eisenella* spp. (Oligochaeta; ~3% of nodes), to family level for Lumbriculidae (Oligochaeta; ~3% of nodes) and class level for Hirudinea (~3% of nodes).

Gut contents of individuals of all the collected taxa were studied using the transparency method of Bello and Cabrera (1999), as in other articles on macroinvertebrate feeding (e.g. Peralta-Maraver *et al.* 2012; Bottová *et al.* 2013; Vannucchi *et al.* 2013). For this, when it was possible, 30 individuals of the same taxon from each date were used to account for possible changes in diet with time. These individuals were introduced into a vial with Hertwig's liquid and heated in an oven at 65°C for a period of 6–24 h. For large organisms, for example, some Perlidae, we opted for the dissection and removal of the gut contents. Subsequently, individuals or their gut contents were placed on a slide with a coverslip and were examined under the microscope. First, at 40× magnification, the total percentage of food contents in the gut was determined. Later, at 400× magnification, the relative percentage of each type of food (prey, detritus, diatoms, fungi or coarse particulate organic matter (CPOM), pollen or other) was identified. For Tabanidae, Hirudinea and *Orectochilus* spp. (whose fluidophagous feeding mechanism did not allow us to identify their gut contents by the previous method), we used the trophic information reported by Tachet *et al.* (2010).

The data obtained from gut-content analysis were used in two ways; initially, data were used to assign each taxon to their respective functional feeding group (FFG) according to the classification of Merritt and Cummins (1996; collectors, shredders, scrapers, filterers and predators). Second, information from gut contents informed diet composition, the percentages of the various resources consumed by each individual taxon, allowing construction of the actual food web for each date; and, from this, the connectance value, omnivory degree and linkage density were extracted. Tabanidae, *Orectochilus* spp. and Hirudinea were not included in the food web. Finally, from density values of identified taxa, taxonomic and functional-diversity values on each date were calculated. Two measures of diversity were then calculated; taxonomic diversity was calculated using density values of the different taxa identified and functional diversity was calculated using density values of the different FFGs. Taxonomic diversity and functional diversity were calculated using both the Shannon–Wiener index (using \ln , which measures diversity in nits per individual) and the probability of interspecific encounter ($1 - D$, complementary of the Simpson index, without units; Hurlbert 1978) indexes were used.

As indicated by Vázquez *et al.* (2007), both resource and consumer abundance can affect the link strength between them. Given this, the following index was used to quantify the interaction strength (I) that occurred between different nodes of the network:

$$I = [Pres \div Pcon] \times \%Di$$

where $\%Di$ is the average of the resource in the consumer gut tract (e.g. percentage of detritus in the gut content of *Caenis* spp.), $Pres$ is the proportion of resource in the environment (e.g. 0.516 in the case of detritus) and $Pcon$ is the proportion of consumers in the community (e.g. 0.157 in the case of *Caenis* spp. in October).

The proportion of each consumer on different dates was extracted from the density of each captured taxon divided by the total density of all the organisms in the community for each date. For basal resources (detritus, diatoms, coarse particulate organic

matter (CPOM), fungi and pollen), the proportion cannot be determined in the same way as for consumers. Thus, for the index proposed, an ordinal scale was used in which each resource was assigned a value based on its relative estimated abundance with respect to the rest of the resources, following a geometric progression with a factor of 2. Thus, the scarcest resource, pollen, was assigned a value of 1, the next resource in abundance, fungi, was assigned 2 ($=1 \times 2$), the next 4 ($=2 \times 2$), and so on, to the most abundant resource, detritus, which was assigned a value of 16. To transform these values into proportions, the value assigned to each resource was divided by the sum of total values assigned to all resources (31), whereby the following ratios for detritus, diatoms, CPOM, fungi and pollen were obtained: 0.516, 0.258, 0.129, 0.065 and 0.032 respectively. In our model, we assume that the proportion of resources remains stable over time, although it is probable that there is slight seasonal variation.

Following Bascompte *et al.* (2005), links from each date were classified into four-quartile classes according to their interaction strength, with links in the top quartile defined as strong links. The 'high interaction scaffold' was defined as the set of strong links in the food web as well as the nodes linked by them. Finally, the variability of the total foodweb and the variability of the high-interaction scaffold were analysed between different pairs of sampling dates. For this, the variability of the total food web and the variability of the high-interaction scaffold were compared in terms of density of taxa, presence or absence of links and link strength. The Bray–Curtis dissimilarity index was used to compare the density of taxa across the community among sampling dates. Link patterns among sampling dates (for both the total food web and the high-interaction scaffold) were captured by building matrices for each date using the presence or absence (1 or 0) and interaction strength (I) of links. In this manner, we compared both qualitatively through a Sørensen similarity matrix, and quantitatively (using the interaction strength of each link) with a Bray–Curtis dissimilarity matrix. To facilitate the interpretation of results, dissimilarity matrices were transformed into similarity matrices ($1 - \text{Bray-Curtis dissimilarity matrix}$). Diversity values and similarity matrices were computed using the Vegan package (Okansen *et al.* 2013) whereas for graphical representation of food web and high interaction scaffold Cheddar package (Hudson *et al.* 2015) was used, both within the R software platform (R Foundation for Statistical Computing, Vienna, Austria, see <http://www.R-project.org/>, accessed 5 April 2016). For the structural descriptor calculation Network 3D computer software for Windows was used (Yoon *et al.* 2014; Williams 2010).

Results

The water-quality parameters of pH and conductivity showed little variation over the study period, whereas temperature and discharge displayed more pronounced variations (Table 1). In the case of discharge, maximum peaks were recorded in the rainy season (spring), whereas minimum levels occurred in summer. Dissolved oxygen could be recorded only in 3 months and so no clear trend could be obtained.

Across the four sampling periods, a total of 22 767 individuals belonging to 38 taxa was collected. Most taxa were present during the whole study period and had a reasonably

high abundance (Table 2). The highest densities were found for *Baetis* spp., *Epeorus* spp., *Ecdyonurus* spp., *Micrasema* spp., *Metalype* spp., *Hydropsyche* spp., and Limoniidae, whereas *Ephemera* spp., *Helichus* spp., *Onychogomphus* spp., Stratiomyidae and Hirudinea never exceeded 8 individuals m^{-2} (Table 2). Although there was some species turnover throughout the study (some taxa appeared and others disappeared), the total number of taxa remained constant, peaking in January, with a minimum in July (Table 2).

The FFG composition of the community at each sampling date changed throughout the study (Fig. 1). Scrapers were always the dominant group, whereas the proportion of other groups depended on the time of year. Collectors were the second-most abundant group in July, January and April, but they were outscored in abundance by shredders in October, possibly reflecting an increase in the delivery of leaf litter to the stream during the autumn. Predators usually had less abundance than did the other groups; however, they increased in July, becoming more abundant than shredders. Filterers (*Simuliini* and *Hydropsyche* spp.) were always the scarcest group. Moreover, the FFG to which each taxon belonged was almost the same throughout the year. However, *Rhyacophila* spp., which was one of the most important predators in the community, behaved more as a scraper in spring (consuming mainly diatoms). Finally, *Simuliini* were always dominantly filter feeders, but in July and April they showed a small percentage of prey in their guts (very little individuals of *Tanytarsini* on July and *Prodiamesinae* on April).

Taxonomic- and functional-diversity values changed throughout the year, following the same pattern for the two diversity indices used (Table 3). The highest values of taxonomic and functional diversity were obtained in July and April, and the lowest values occurred in January (Table 3).

Fig. 2 shows the number of nodes and the link pattern of the food web of the Castril River community for each sampling date, as well as the high-interaction scaffold of each sampling date. The number of nodes in the food web for each date ranged from a maximum of 36 nodes in January to a minimum of 29 nodes in July (Table 3, Fig. 2). The total number of links in the community varied little among July, October and January, but increased slightly in April (Table 3). Values of connectance and linkage density showed a tendency similar to those of taxonomic and functional diversity, whereas the omnivory degree reached its maximum in July and October (Table 3). The Bray–Curtis dissimilarity index for density of taxa and link strength, both for the total food web and the high-interaction scaffold, showed

considerable variation among different dates (1 – Bray–Curtis index almost always below 0.5; Table 4), i.e. the abundance of different taxa varied considerably over time. By contrast, the qualitative analysis of the link pattern both for the total food web and the high-interaction scaffold (Sørensen similarity index always <0.75 , Table 4) showed that there was less variation in the link pattern among sampling dates. Finally, the Bray–Curtis dissimilarity index for link strength showed that there was a large variation over time; both if we studied the link set of the total food web and if we focussed on the high-interaction scaffold, all values were very close to zero (Table 4).

Discussion

Composition of the community and trophic function of macroinvertebrates

There were some evident trends in community diversity throughout the study period. The more favourable light environment favoured the development of diatoms (Allan and Castillo 2007), an abundant, easily assimilated resource (Hall *et al.* 2001). Collectors were the next-most abundant group, with abundance peaking in spring and being only slightly exceeded by shredder abundance in autumn. Detritus, which collectors feed on, is less energy rich than are diatoms (Giller and Malmqvist 1998); however, it is an abundant resource in lotic ecosystems around the world because of its multiple sources (such as e.g. leaf debris, remains of dead organisms, faeces; Cummins and Klug 1979; Allan and Castillo 2007). The increased density of shredders in autumn possibly reflects the contribution of leaves from deciduous vegetation around the river (Peralta-Maraver *et al.* 2011). Similar patterns in macroinvertebrate FFG composition throughout a year has been shown in other well-lit Mediterranean rivers (Sánchez-Carmona *et al.* 2012; Vannucchi *et al.* 2013). Finally, predators and filter feeders were the scarcest groups in our study site. The low proportion of predators in relation to other FFGs fits Elton's pyramid (Elton 1927), which is common for most ecosystems (not only freshwater ecosystems), whereas the low abundance of filterers reflects the low levels of suspended organic particles in our study sites, with high loads of suspended organic particles known to be important for filter feeders (Hynes 1970).

Structure and complexity of the total food web

The similarity analysis suggested that the community composition of the food web varied over time. Over the 12-month study, variation was observed (both qualitatively and quantitatively), both in terms of abundance of organisms that form the community and in the link pattern of the associated foodweb (Table 4). This variation reflects the natural variation in benthic communities that is itself a reflection of complexity and variability of rivers as ecosystems (Lancaster *et al.* 1990). In lotic environments, the temporal variability in benthic macroinvertebrate community composition, as measured by taxonomic diversity, partly reflects the extraordinary diversity of life-history strategies (e.g. hatching periods, stages duration, emergence period) existing in lotic systems and the influence of a wide range of environmental variables (Lancaster and Downes 2013). Variations observed in the diversity of FFG reflect the ontogenetic changes in the feeding habits of many stream

Table 1. Principal physico-chemical parameters recorded in the Castril River during the sampling period

Oxygen could be recorded only in 3 months (see Materials and methods)

Parameter	N	Mean	s.d.	Max	Min
O ₂ (mg L ⁻¹)	3	8.77	1.14	9.70	7.50
O ₂ (%)	3	80.33	8.14	86.00	71.00
Conductivity (μS cm ⁻¹)	12	220.38	11.20	243.00	209.10
pH	12	8.69	0.12	8.87	8.44
Temperature (°C)	9032	11.57	2.54	20.00	7.00
Discharge (m ³ s ⁻¹)	12	1.71	1.48	4.51	0.41

Table 2. Density and functional feeding groups of the macroinvertebrate taxa present in the Castril River for each sampling date

C, collectors; F, filterers; FFG, functional feeding group; P, predators; Sc, scrapers; Sh, shredders

Taxon	July		October		January		April	
	Density (individuals m ⁻²)	FFG (%)	Density (individuals m ⁻²)	FFG (%)	Density (individuals m ⁻²)	FFG (%)	Density (individuals m ⁻²)	FFG (%)
<i>Baetis</i> spp.	392	0.90 Sc; 0.07 C; 0.03 Sh	540	0.82 Sc; 0.12 C; 0.06 Sh	1625	0.80 Sc; 0.14 C; 0.06 Sh	303	0.78 Sc; 0.20 C; 0.03 Sh
<i>Serratella</i> spp.	282	0.79 Sc; 0.15 C; 0.05 Sh; 0.01 Pr	0	—	310	0.52 Sc; 0.39 C; 0.09 Sh	62	0.47 C; 0.45 Sc; 0.08 Sh
<i>Ephemera</i> spp.	0	—	3	0.55 C; 0.45 Sc	2	0.55 C; 0.45 Sc	2	0.55 Sc; 0.45 C
<i>Cuatis</i> spp.	0	—	142	0.49 C; 0.38 Sc; 0.13 Sh	17	0.54 C; 0.32 Sc; 0.15 Sh	0	—
<i>Epeorus</i> spp.	0	—	142	0.67 Sc; 0.26 C; 0.07 Sh	567	0.72 Sc; 0.24 C; 0.04 Sh	8	0.65 Sc; 0.31 C; 0.04 Sh
<i>Ecdyonurus</i> spp.	27	0.61 Sc; 0.22 C; 0.17 Sh	563	0.60 Sc; 0.24 Sh; 0.16 C	428	0.40 Sc; 0.36 C; 0.24 Sh	45	0.39 C; 0.39 Sc; 0.22 Sh
<i>Rhitrogena</i> spp.	0	—	0	—	128	0.68 Sc; 0.25 C; 0.07 Sh	10	0.67 Sc; 0.33 C
<i>Onychogomphus</i> spp.	0	—	2	1 Pr	0	—	0	—
<i>Perla</i> spp.	50	0.94 Pr; 0.03 Sc; 0.02 Sh; 0.01 C	75	0.48 Sc; 0.35 Sh; 0.10 Pr; 0.07 C	65	0.89 Pr; 0.11 C	45	0.91 Pr; 0.05 C; 0.03 Sh; 0.01 Sc
<i>Dinocras</i> spp.	27	0.98 Pr; 0.02 C	30	0.98 Pr; 0.02 C	87	0.91 Pr; 0.07 C; 0.02 Sh	63	1 Pr
<i>Leuctra</i> spp.	8	0.61 Sc; 0.37 C; 0.02 Sh	8	0.63 C; 0.30 Sc; 0.07 Sh	0	—	13	0.77 C; 0.20 Sc; 0.03 Sh
<i>Micrasema</i> spp.	250	0.83 Sc; 0.10 C; 0.07 Sh	3843	0.56 Sc; 0.28 Sh; 0.16 C	16400	0.62 Sc; 0.20 Sh; 0.18 C	560	0.52 Sc; 0.28 Sh; 0.20 C
<i>Lasiocephala</i> spp.	0	—	27	0.84 Sc; 0.35 Sh; 0.10 Pr; 0.07 C	8	0.95 Sc; 0.03 C; 0.02 Sh	253	0.48 Sh; 0.40 Sc; 0.07 Pr; 0.05 C
<i>Sericostoma</i> spp.	12	0.56 Sh; 0.27 Sc; 0.13 C; 0.04 Pr	70	0.42 Sh; 0.32 Sc; 0.23 C; 0.02 Pr	73	0.74 Sh; 0.18 C; 0.08 Sc	207	0.76 Sh; 0.14 Sc; 0.08 C; 0.02 Pr
<i>Oreochilus</i> spp.	0	—	18	1 Pr ^A	98	1 Pr ^A	2	1 Pr ^A
<i>Metatype</i> spp.	50	0.61 Sc; 0.23 C; 0.16 Sh	1398	0.65 Sc; 0.18 Sh; 0.17 C	1965	0.51 Sc; 0.29 C; 0.20 Sh	3	0.68 Sc; 0.28 Sh; 0.04 Sh
<i>Hydropsyche</i> spp.	28	0.58 Sc; 0.16 C; 0.16 F; 0.9 Sh; 0.01 Pr	743	0.50 Sc; 0.32 Sh; 0.06 C; 0.06 F; 0.06 Pr	387	0.35 Sc; 0.28 Sh; 0.022 Pr; 0.07 C; 0.07 F	43	0.36 Sc; 0.35 Pr; 0.19 Sh; 0.05 F; 0.05 C
<i>Rhyacophila</i> spp.	50	0.95 Pr; 0.05 Sc	18	0.82 Pr; 0.16 Sc; 0.02 C	140	0.92 Pr; 0.08 Sc	12	0.55 Sc; 0.33 Pr; 0.09 C; 0.03 Sh
<i>Limnius</i> spp. (adult)	23	0.66 Sc; 0.21 C; 0.13 Sh	2	0.52 Sc; 0.38 C; 0.10 Sh	7	0.40 Sc; 0.35 C; 0.25 Sh	7	0.53 Sc; 0.37 C; 0.10 Sh
<i>Limnius</i> spp. (larva)	60	0.91 Sc; 0.05 C; 0.04 Sh	93	0.81 Sc; 0.11 C; 0.09 Sh	123	0.53 Sc; 0.44 C; 0.04 Sh	47	0.62 Sc; 0.25 C; 0.13 Sh

(Continued)

Table 2. (Continued)

Taxon	July		October		January		April	
	Density (individuals m ⁻²)	FFG (%)	Density (individuals m ⁻²)	FFG (%)	Density (individuals m ⁻²)	FFG (%)	Density (individuals m ⁻²)	FFG (%)
<i>Elmisp</i> spp. (adult)	57	0.60 Sc; 0.20 Sh; 0.20 C	25	0.59 Sc; 0.25 C; 0.15 Sh	5	0.60 Sc; 0.25 C; 0.15 Sh	3	0.60 Sc; 0.25 C; 0.15 Sh
<i>Elmisp</i> spp. (larva)	127	0.85 Sc; 0.14 C; 0.01 Sh	250	0.86 Sc; 0.08 C; 0.06 Sh	267	0.81 Sc; 0.14 C; 0.05 Sh	25	0.69 Sc; 0.17 Sh; 0.14 C
<i>Esolus</i> spp. (adult)	47	0.96 Sc; 0.04 C	27	0.90 Sc; 0.10 C	20	0.48 Sc; 0.27 C; 0.25 Sh	27	0.75 Sc; 0.20 C; 0.05 Sh
<i>Esolus</i> spp. (larva)	102	0.96 Sc; 0.03 C; 0.01 Sh	307	0.93 Sc; 0.05 C; 0.02 Sh	165	0.92 Sc; 0.05 C; 0.03 Sh	95	0.91 Sc; 0.09 C; 0.01 Sh
<i>Helichius</i> spp.	0	–	0	–	2	0.40 Sh; 0.30 Sc; 0.30 C	0	–
Sf. Tanypodinae	333	0.75 Pr; 0.24 C; 0.01 Sh	15	0.67 C; 0.33 Pr	8	0.75 C; 0.22 Pr; 0.03 Sh	0	–
Sf. Prodiamesinae	135	0.95 C; 0.03 Sh; 0.02 Sc	112	0.84 C; 0.10 C; 0.04 Sc	270	0.71 C; 0.19 Sh; 0.10 Sc	93	0.83 C; 0.13 Sh; 0.04 Sc
Sf. Orthocladinae	0	–	20	0.98 C; 0.01 Sc; 0.01 Sh	7	0.94 Sh; 0.06 C;	0	–
Tr. Tanytarsini	275	0.80 Pr; 0.13 Sh; 0.07 Sc	48	0.40 C; 0.35 Sc; 0.25 Sh	3	0.40 C; 0.35 Sc; 0.25 Sh	2	0.4 Sh; 0.25 C; 0.25 Sc
Limoniidae	90	0.96 C; 0.02 Sh; 0.02 Sc	198	0.98 C; 0.01 Sc; 0.01 Sh	223	0.99 C; 0.01 Sc	318	0.98 C; 0.01 Sh; 0.01 Sc
Tabanidae	3	0.75 Pr; 0.25 Sh ^A	5	0.75 Pr; 0.25 Sh ^A	0	–	0	–
Ceratopogonidae	18	0.94 C; 0.06 Sc	278	0.95 C; 0.05 Sc	142	0.98 C; 0.02 Sc	245	0.92 C; 0.08 Sc
Tr. Simuliini	18	0.96 F; 0.04 Pr	15	1 F ^A	0	–	5	0.99 F; 0.01 Pr
Sf. Clinocerinae	7	1 C	17	0.65 C; 0.34 Sc; 0.01 Sh	2	–	32	0.68 C; 0.28 Sc; 0.02 Pr; 0.02 Sh
Stratiomyidae	0	–	0	–	2	1 C	2	1 C
<i>Eisenella</i> spp.	0	–	2	0.80 C; 0.15 Sc; 0.05 Sh	8	0.93 C; 0.06 Sc; 0.01 Sh	0	–
Lumbriculidae	0	–	0	–	35	0.99 C; 0.01 Sc	0	–
Hirudinea	2	1 Pr ^A	0	–	8	1 Pr ^A	2	1 Pr ^A

^AFunctional feeding groups were extracted from Tachet *et al.* (2010).

organisms (Anderson and Cummins 1979), and this process (metaphoetesis) produces variability in the link pattern throughout time. This also results in a fluctuation of complexity descriptors throughout the year. It is interesting to compare our results with those obtained by Thompson and Townsend (2005) in a previous study. These authors conducted an exhaustive study of the food webs in 18 different streams in New Zealand, taking samples at a point in time in each site. They studied the determinants of the food-web structure, with a particular reference to energy availability, spatial heterogeneity and ecosystem size. They found that well-lit rivers, in which there is an increased production of algae, had higher connectance and link-density values than did forested rivers. In that study, connectance and link density reached respective maximum values of 0.18 and 9.03 for well-lit streams, and respective minimum values of 0.06 and 1.56 for forested streams. The temporal study of the food web in Castril River showed that the connectance and link-density values fluctuate (Table 3) inside the range obtained by Thompson and Townsend (2005). This highlighted the importance of temporal resolution when assessing the web structure of food webs. This idea was also supported by the results of Tavares-Cromar and Williams (1996). These authors studied the food web of an entire macroinvertebrate riffle

community in one small river in eastern-central Canada, addressing the temporal dynamic. They sampled the complete community at seven times throughout one year, assessing trophic relations throughout a detailed gut analysis, and quantified the importance of trophic links. As in the Castril River, Tavares-Cromar and Williams (1996) showed fluctuation of the complexity descriptors with time (connectance ranged from 0.09 to 0.11, whereas link density ranged from 3.14 to 4.29).

Finally, we could not determine a statistical relationship between the various complexity descriptors (connectance, link density and omnivory degree) and biological and functional diversity because of the low number of cases. However, the general pattern of higher taxonomic and functional diversity concurred with higher connectance and link-density values (Table 3). From a descriptive perspective, the food-web complexity observed throughout the year in our study area showed a positive trend compared with both measures of diversity. According to McCann (2000), the periods of the year in which diversity values are lower can be interpreted as moments in which a simplification of the community occurs (lower complexity), so the stability of the network will be lower. This was the case in January, when an increase in the density of *Baetis* spp., *Micrasema* spp. and *Metalype* spp. occurred, and these dominated the rest of the community. Nonetheless, we observed the same tendency in the complexity of the network both with taxonomic diversity and functional diversity, so we cannot affirm that complexity was associated more strongly with one or the other kind of diversity. It has been proposed that greater taxonomic diversity increases the probability that any of the organisms that compose the community respond differently to the rest under varying conditions or disturbances, promoting the community's persistence (see Hooper et al. 2005); furthermore, greater taxonomic diversity allows a functional redundancy in communities that are formed by species that can functionally replace others (greater functional diversity; Naeem and Li 1997; Naeem 1998).

Permanence of high-interaction scaffold along time and stability implications

In the case of the high-interaction scaffold proposed, the similarity indices suggested that, as occurred with the total food web, both density of consumer nodes and link strength differed greatly among different sampling dates (Table 4). Nonetheless, the link pattern of the high-interaction scaffold was less different among sampling dates (Table 4). This implies that, over time, certain nodes of the high-interaction scaffold remained

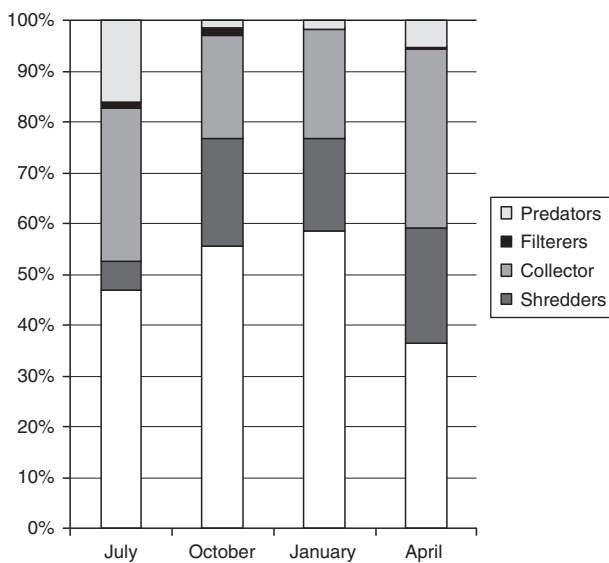


Fig. 1. Percentage of functional feeding groups (FFGs) at each sampling date during the study period in the Castril River.

Table 3. Structural and complexity descriptors (without units) of the studied food webs for each date and values of biological and functional diversity calculated with the Shannon–Wiener index (H , measured in nits individual⁻¹) and the probability of interspecific encounter ($1 - D$, without units)

Trophic web	Nodes (trophospecies) (S)	Links (L)	Connectance (L/S ²)	Links density (L/S)	Omnivory (%)	Biological diversity		Functional diversity	
						H	$1 - D$	H	$1 - D$
July	29	120	0.14	4.03	0.27	2.68	0.91	1.23	0.66
October	35	130	0.11	3.71	0.26	2.10	0.78	1.10	0.61
January	36	130	0.10	3.61	0.17	1.35	0.50	1.03	0.58
April	33	143	0.13	4.33	0.24	2.53	0.89	1.25	0.69

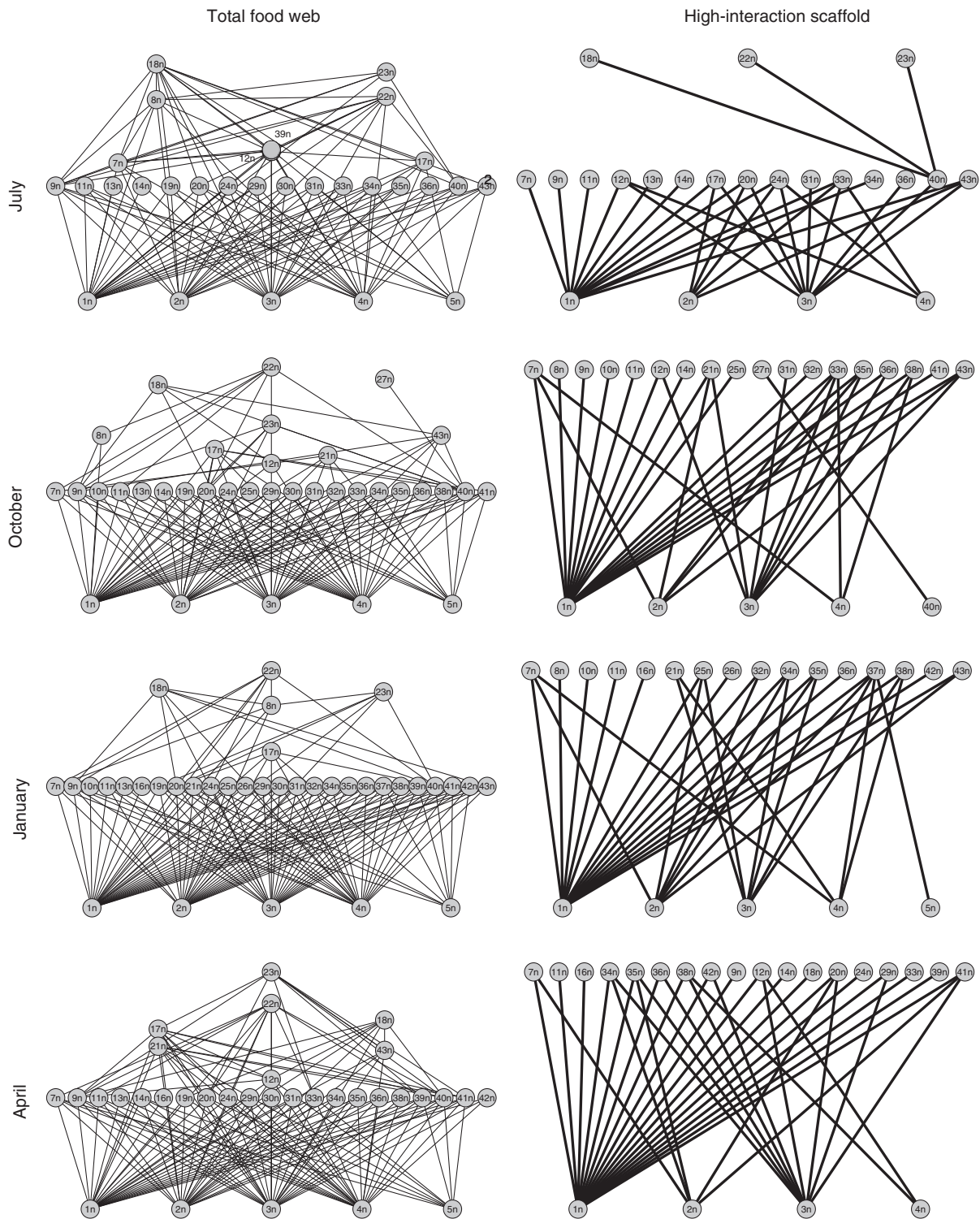


Fig. 2. Graphical representation of the total food web of the Castril River on each sampling date (left) and the high interaction scaffold on each date (right). 1n, detritus node; 2n, coarse particulate organic matter (CPOM) node; 3n, diatoms node; 4n, fungi node; 5n, pollen node; 7n, Tanytarsini node; 8n, Tanytopodinae node; 9n, Prodiamesinae node; 11n, Limoniidae node; 12n, Simuliini node; 13n, Ceratopogonidae node; 14n, Clinocerinae node; 16n, Stratiomyidae node; 17n, *Hydropsyche* spp. node; 18n, *Rhyacophila* spp. node; 19n, *Micrasema* spp. node; 20n, *Metalyse* spp. node; 21n, *Lasiocephala* spp. node; 22n, *Perla* spp. node; 23n, *Dinocras* spp. node; 24n, *Ecdyonurus* spp. node; 27n, *Onychogomphus* spp. node; 29n, *Elmis* spp. (larvae) node; 30n, *Esolus* spp. (larvae) node; 31n, *Limnius* spp. (larvae) node; 33n, *Leuctra* spp. node; 34n, *Elmis* spp. (adult) node; 35n, *Limnius* spp. (adult) node; 36n, *Esolus* spp. (adult) node; 38n, *Ephemera* spp. node; 39n, *Serratella* spp. node; 40n, *Baetis* spp. node; 41n, *Epeorus* spp. node; 42n, *Rhitrogena* spp. node; 43n, *Sericostoma* spp. node.

Table 4. Similarity matrices at different dates for density of nodes, number of links and link strength

	July	October	January	April
Similarity values for density of nodes of the total food web (1 – Bray–Curtis index)				
July	1.00			
October	0.26	1.00		
January	0.13	0.49	1.00	
April	0.48	0.33	0.15	1.00
Similarity values for density of nodes of the high-interaction scaffold (1 – Bray–Curtis index)				
July	1.00			
October	0.57	1.00		
January	0.13	0.34	1.00	
April	0.28	0.36	0.44	1.00
Similarity values for the qualitative link pattern of the total food web (Sørensen index)				
July	1.00			
October	0.70	1.00		
January	0.69	0.68	1.00	
April	0.74	0.77	0.69	1.00
Similarity values for the qualitative link pattern of the high-interaction scaffold (Sørensen index)				
July	1.00			
October	0.54	1.00		
January	0.16	0.46	1.00	
April	0.45	0.50	0.43	1.00
Similarity values for the link strength of the total food web (1 – Bray–Curtis index)				
July	1.00			
October	0.06	1.00		
January	0.02	0.16	1.00	
April	0.04	0.00	0.00	1.00
Similarity values for the link strength of the high-interaction scaffold (1 – Bray–Curtis index)				
July	1.00			
October	0.03	1.00		
January	0.01	0.16	1.00	
April	0.03	0.00	0.00	1.00

connected by the same links. This organisation of the food webs into subgroups of taxa, in which many strong interactions occur ‘within’ the subgroups, compared with a few weak interactions ‘among’ the subgroups, may lead to network compartmentalisation (Krause *et al.* 2003; Teng and McCann 2004). In recent studies, which have quantitatively analysed the linkage strength of food webs, compartmentalisation has been proposed to be a stabilising agent of communities (Stouffer and Bascompte 2011). However, too much compartmentalisation (strong links are maintained invariably and the weak links disappear) can lead to network instability (Pimm 1979) because, as Guimerà *et al.* (2010) proposed, it can potentially cause ecosystem fragmentation. We found that, qualitatively, the link pattern of the high-interaction scaffold was reasonably similar among some sampling dates (the same links between some nodes are maintained), whereas, quantitatively, the link strength of the high-interaction scaffold differed greatly among sampling dates (the strength of these links vary, even belonging to the category of strong links); so, probably, the compartmentalisation would be scarce and, thus, this would not lead to instability.

It is important to note that we assumed that diatoms constituted a unique resource and the broad diatom group was not taxonomically resolved. Diatoms as a group, therefore, appear as a single strong link and not as several links, and as was discussed by Thompson and Townsend (2000), this could affect some of the parameters calculated in the present study. A similar

argument can be made for detritus, which is a group that could be further subdivided.

As expected, the high-interaction scaffold described on each date was constituted by only a small part of the total links that built the food web (Fig. 2). This pattern has already been described in terrestrial (e.g. Neutel *et al.* 2002), marine (e.g. Bascompte *et al.* 2005) and freshwater ecosystems (e.g. Layer *et al.* 2010). In lotic systems, Layer *et al.* (2010), in a study of food webs in 20 Atlantic rivers (from United Kingdom and Ireland), found that a higher pH promoted a greater number of strong links, particularly between primary consumers and algae and between fish and invertebrates. Thus, the high-interaction scaffold may be variable, depending on environmental conditions and temporal variation.

However, more than two consecutive connected levels were not usually found in the scaffold structure of our study, with only one exception in July. The existence of strong links along consecutive levels promotes the appearance of trophic cascades (Carpenter and Kitchell 1996; Pace *et al.* 1999), which may have strong implications for destabilisation of a community (Strong 1992). Contrary to what was observed in our study, the existence of potential trophic cascades has been widely suggested in aquatic ecosystems, such as lakes and streams (Strong 1992; Pace *et al.* 1999). However, most of these studies have not quantified interaction strength between the nodes that were part of the network.

In the case of the macroinvertebrate community in the Castril River, by quantifying link strength, we could see that there were very few consecutive strong links, and when there were such links, they were accompanied by a high percentage of omnivory. In our study, three consecutive chains of strong interaction appeared only in July, where *Perla* spp., *Dinocras* spp. and *Rhyacophila* spp. were strongly connected to a primary consumer (*Baetis* spp.); we also found the highest percentage of omnivory (Table 3). In fact, these three top macroinvertebrate predators were generalists and omnivores because their diets consisted of basal resources as well as other consumers of different levels. These results agree with those obtained in previous studies of feeding where the same methodology was used, and where both *Perla* spp. and *Dinocras* spp. in the Castril River (Bo et al. 2008) and *Rhyacophila* spp. in another Mediterranean river (Bello and Alba-Tercedor 2004) preferentially consumed Baetidae, followed by a wide range of trophic resources. Thus, weak links resulting from the omnivorous behaviour of some predators had an important role in community stability, allowing the existence of strong links along the high-interaction scaffold, without giving rise to the occurrence of trophic cascades.

Conclusions

In streams and rivers where the channel is well lit, diatoms are abundant and easy to assimilate as a resource; in this manner, the organisms specialised in using this resource become dominant. Phenomena such as the diversity of life strategies of organisms or ontogenetic diet changes promote variability of food-web architectures, which result in oscillations of values of structural complexity. The variation in these values seems to relate positively to the taxonomic and functional diversity of communities and, by extension, to their stability.

The quantitative study of link strengths of our food web revealed that there was a small group of strong links within many weak links. Among the links that constituted this high-interaction scaffold, the existence of two consecutive strong links was not common, which means that the appearance of trophic cascades was not promoted. Studying the temporal dynamics showed that the strength of the scaffold links was variable. In this manner, the compartmentalisation of the food web was promoted, but without resulting in the appearance of isolated subgroups in the community.

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