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Predator and detritivore niche width helps to explain biocomplexity of experimental detritus-based food webs in four aquatic and terrestrial ecosystems

Loreto Rossi, Antonella di Lascio, Pasquale Carlino, Edoardo Calizza, Maria Letizia Costantini *

Department of Environmental Biology, "Sapienza" University of Rome, Via dei Sardi 70, 00185 Rome, Italy

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ABSTRACT

In the study of food webs, the existence and explanation of recurring patterns, such as the scale invariance of linkage density, predator–prey ratios and mean chain length, constitute long-standing issues. Our study focused on litter-associated food webs and explored the influence of detritivore and predator niche width (as $\delta^{13}C$ range) on web topological structure. To compare patterns within and between aquatic and terrestrial ecosystems and take account of intra-habitat variability, we constructed 42 macroinvertebrate patch-scale webs in four different habitats (lake, lagoon, beech forest and cornfield), using an experimental approach with litterbags. The results suggest that although web differences exist between ecosystems, patterns are more similar within than between aquatic and terrestrial web types. In accordance with optimal foraging theory, we found that the niche width of predators and prey increased with the number of predators and prey taxa as a proportion of total taxa in the community. The tendency was more marked in terrestrial ecosystems and can be explained by a lower *per capita* food level than in aquatic ecosystems, particularly evident for predators. In accordance with these results, the number of links increased with the number of species but with a significantly sharper regression slope for terrestrial ecosystems. As a consequence, linkage density, which was found to be directly correlated to niche width, increased with the total number of species in terrestrial webs, whereas it did not change significantly in aquatic ones, where connectance scaled negatively with the total number of species. In both types of ecosystem, web robustness to rare species removal increased with connectance and the niche width of predators. In conclusion, although limited to litter-associated macroinvertebrate assemblages, this study highlights structural differences and similarities between aquatic and terrestrial detrital webs, providing field evidence of the central role of niche width in determining the structure of detritus-based food webs and posing foraging optimisation constraints as a general mechanistic explanation of food web complexity differences within and between ecosystem types.

1. Introduction

The study of similarities between aquatic and terrestrial food webs has contributed significantly to our understanding of network topology (Pimm et al., 1991; Riede et al., 2010; Shurin et al., 2006), with particular emphasis on stability mechanisms and biodiversity management (Ings et al., 2009; McCann, 2000). However, despite the ecological importance of these issues, questions remain regarding the determinants of the number of links per species (i.e. linkage density) and their role in web stability. In addition, the differences and similarities in web topology between aquatic and terrestrial environments have not yet been fully elucidated. Concerning the relationship between the number of links and the number of species in a web, two hypotheses have been proposed: the 'link-species scaling law' predicts an average of two links per species in any given food web ($L/S \sim 2$) whereas the 'constant connectance' hypothesis (where $C \sim L/S^2$ is constant) suggests that the number of links per species is proportional to the number of species (Martinez, 1992).

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* Corresponding author. Tel.: +39 064940800; fax: +39 064940800.
E-mail address: marialetizia.costantini@uniroma1.it (M.L. Costantini).

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The latter hypothesis implies that average niche width increases with the number of species. This is in contrast to the species packing predicted by niche theory (Pianka, 1976; Winemiller et al., 2001), while it is consistent with optimal foraging theory, which predicts an increase in consumer diet breadth as the *per capita* levels of food decrease (Calizza et al., 2012; MacArthur and Pianka, 1966; Pyke et al., 1977).

To date, the role of niche width in web structure has mainly been investigated by network topology models, some of which use foraging theory as a mechanistic explanation (Beckerman et al., 2006; Ings et al., 2009; Petchey et al., 2008; Williams et al., 2010). Although the ecological niche concept has undergone a renaissance in recent years (Jackson et al., 2011), there have been few field studies designed to measure the niche width of invertebrates in food webs (e.g. Calizza et al., 2012; Woodward and Hildrew, 2002), and the mechanisms by which niche width regulates detritus-based web topology remain uncertain.

Differences in carbon flow pathways and detritus accumulations between aquatic and terrestrial webs have been observed. Ultimately, these differences arise from the different chemical composition of autotrophs, which influences consumption by heterotrophs (Cebrian and Lartigue, 2004; Chase, 2000; Costantini et al., 2008; Nowlin et al., 2008; Shurin et al., 2006). The source, quantity and quality of detritus affect the population density, feeding rates and trophic niche of detritivores and thus their interactions with other species in the web. In fact, detritus heterogeneity allows detritivores to specialise on a variety of discrete resources represented by combinations of different substrates and microorganisms, mainly fungi, with acknowledged effects on both competitive interactions and predator foraging behaviour (Calizza et al., 2012, 2013a; Costantini and Rossi, 1995, 2010). These interactions in turn regulate energy flows (Cebrian and Lartigue, 2004; Cyr and Pace, 1993; Shurin et al., 2006) and matter cycling rates in ecosystems (Calizza et al., 2013a; Costantini and Rossi, 2010; Hladyz et al., 2009; Rossi et al., 2007).

Despite their importance and pervasiveness, there are fewer complete topological descriptions of detrital webs than of other web types (Calizza et al., 2012; Hildrew, 2009; Rooney and McCann, 2012; Tavares-Cromar and Williams, 1996), mainly owing to the difficulties inherent in traditional web construction techniques (Scheu, 2002). More recently, food webs have been studied using stable isotope analysis (SIA), which, due to the natural variation of δ^{13}C and δ^{15}N in space and between trophic levels, has been a useful technique across ecosystem types (terrestrial, freshwater, marine) and web compartments (i.e. primary producers vs. organic detritus) (Fry, 2006; Mestre et al., 2013; Rossi et al., 2010). Since the stable isotope ratios in an organism's tissues derive from all the trophic pathways that converge in that individual, they reveal the individual and/or population trophic niche and position in the web (Hoeinghaus and Zeug, 2008; Layman et al., 2007a,b; Post, 2002; Romanuk et al., 2006). Unlike gut contents, stable isotopes integrate feeding over a relatively long time period, and therefore do not reflect material ingested only occasionally by consumers. However, isotopic variation depends not only on diet, but can also result from inherent variation in consumers, associated with individual physiology and variability in diet-tissue fractionation, as well as from measurement errors (Barnes et al., 2008; Bearhop et al., 2002; Vander Zanden et al., 2012 and literature cited therein). Bayesian mixing models can be applied to the isotopic data to determine the probability of a resource being a consumer's food by incorporating these isotopic signature uncertainties, thus providing more robust information (Jackson et al., 2011; Parnell et al., 2010; Phillips, 2012).

In this study, we performed SIA coupled with qualitative gut content analysis and applied Bayesian mixing models to describe detritus-based food webs and explore the influence of detritivore and predator guild niche width on web topology across aquatic and terrestrial habitats. Specifically, in order to elucidate similarities between aquatic and terrestrial food webs, we compared covariation patterns and determined sources of possible differences within and between these two major types of ecosystem. In accordance with optimal foraging theories (Pyke et al., 1977) and both model and experimental food web studies (Beckerman et al., 2006; Calizza et al., 2012; Petchey et al., 2008), we assumed that decreasing per capita food level increases the niche width of predators and prey and thus the number of links in a web. We hypothesised that this would influence the link-species relationship and other link-related web properties such as web compartmentalization and robustness to species loss. Specifically, we expected the link-species relationship to be characterised by a sharper slope at lower food levels, which may explain differences between ecosystem types. Testing this hypothesis entailed combining information on food niche width, web topology and food level (as number of prey per predator and amount of detritus per detritivore) from very different habitats (lake, lagoon, beech forest and cornfield). We used litterbags to collect macroinvertebrates and constructed 42 experimental macroinvertebrate detritus-based food webs at the local scale, which also enabled us to examine intra-habitat web variability (Jana and Bairagi, 2014; Thompson and Townsend, 2005). We measured web structural parameters including linkage density (*L*/*S*), mean chain length and connectance. To compare niche width across habitats and trophic levels, and to avoid potentially spurious relationships with web parameters arising from the use of topological-based niche metrics such as the number of prey species (or number of links) in a predator diet, we measured trophic niche as δ^{13}C variation (Layman et al., 2007a,b; Sanders et al., 2014).

2. Materials and methods

2.1. Habitat description

Lake: Lake Bracciano is an oligo-mesotrophic volcanic lake, located 32 km northwest of Rome at 160 m above sea level (Lazio, Italy, 42°05′N, 12°12′E), included in a Regional park since 1999. The lake has a surface area of 57 km^2, a perimeter of about 31.5 km and a maximum depth of 165 m. Three small towns border the lake: Bracciano, Anguillara Sabazia and Trevignano Romano. Fifteen sampling sites were chosen in the riparian belt along the perimeter, taking into account sources of intra-habitat variability: the geological substratum (chaotic tuff vs. leucitic lavas), depths (0.7 and 3 m), bottom slope, and exposure to sun and wind (i.e. effective fetch). The lake is also characterised by very uneven vegetation and detritus accumulation, which determine isotopically different litter mixtures and variable organic matter percentages in sediments (see also Rossi et al., 2010), both known to be important drivers of invertebrate food web structure (Berg and Bengtsson, 2007; Calizza et al., 2012).

Lagoon: The Lagoon of Santa Gilla, adjacent to the city of Cagliari (Sardinia, Italy, 39°13′N, 9°03′E), is a non-tidal lagoon of about 4000 ha consisting of two main areas: one, extending along a N-S axis, is well-connected to the sea whereas the other, extending along an E-W axis, is more confined and includes salt pans (Saline di Macchiareddu). Salinity, depth and vegetation are the main sources of intra-habitat variability. The study was carried out across the lagoon at eight sampling points (four for each area), two of which were close to salt pans.

Beech forest: The study was carried out in the catchment basin of Lake Vico, a volcanic area located about 50 km north of Rome (Lazio, Italy, 42°19′N, 12°10′E). Since 1982 this area has been part of a Regional Reserve including the lake (510 m above sea level) and Mount Venere (851 m above sea level). The Reserve includes low-elevation ('depressed') mixed beech wood, dominated by *Fagus sylvatica* (CORINE code 41.181), and pure beech stands growing from 550 to 850 m above sea level in deep, fertile volcanic soils. The three sampling sites were located at three different altitudes and slopes and were characterised by different litter accumulations. Another two sampling sites were abandoned since, being located in a more frequented area, litterbags were interfered with by persons unknown.

Cornfield: The study was carried out near Lleida (Catalunya, Spain, 41°38′N, 0°35′E) in harvested experimental cornfields surrounded by abandoned fields. Sampling was conducted in sixteen plots, which had been cultivated in the previous year with three different corn varieties with different growing cycles, and were positioned at the opposite edges and in the centre of the fields.

The number of sampling sites in each ecosystem varied in accordance with habitat size, physical habitat and resource supply (both quality and quantity).

2.2. Macroinvertebrate and detritus sampling

Macroinvertebrate samplings were carried out simultaneously in each ecosystem and replicated in June, July and August 2008 using litterbags (2.0 cm mesh size), each containing 25 grams (dry weight) of the dominant leaf litter in each habitat (*Alnus glutinosa*, *Phragmites communis*, *Zea mays* and *Fagus sylvatica* for the lake, lagoon, cornfield and beech forest respectively).

Each litterbag was incubated for one week with a sporal suspension of one of eight dominant saprophytic fungal species, previously isolated from the respective native plant detritus in accordance with Sabetta et al. (2000) so as to obtain eight different fungal-colonised patches per habitat (Arsuffi and Suberkropp, 1985; Calizza et al., 2013a) with a fungal mass comparable to the natural litter of each ecosystem (Litter quality in supplemental content: Table S1). Five replicate litterbags per fungus were randomly deployed at each sampling site, at least 15 m apart from each other. After seven days' exposure underwater or 14 days' exposure on the soil (sufficient to observe full macroinvertebrate colonisation while limiting litter decomposition and fungal contamination) the litterbags were retrieved and the associated macrofauna were identified to the lowest possible taxonomic level common to all webs and counted. All genera and the majority of families were represented by only one species, with a few exceptions such as the larvae of Chironomidae. Although not all macroinvertebrates were identified to species level, in the text the word 'species' may also refer to higher taxonomic ranks. Specimens of abundant species and those of low-resolved taxa known to include species with different feeding habits (detritivorous or predaceous), such as the larvae of Trichoptera, Diptera and Chironomidae, were fixed in 10% formaldehyde for qualitative gut content analysis; the remaining individuals were left for a few hours in glass bowls to empty their guts for SIA. Isotopic and gut content data were compared in order to ensure unambiguous feeding habit classification, corroborated by the absence of δ^{13}C and δ^{15}N outliers in each group.

Samples of detritus from the upper sediment or soil layer (5 cm thick) were collected at each sampling site, ergosterol concentration as a marker of fungal mass on detritus was determined after reflux in methanol (Sabetta et al., 2000) and the organic content of detritus, bulk sediment and soil was assessed after oven drying (72 h at 60 °C) and muffle furnace combustion (5 h at 500 °C).

2.3. Stable isotope analysis

Animals and detritus from sediments and soil were separately freeze-dried and ground to a fine homogeneous powder in a ball-mill (Fritsch, Pulverisette 23 with a zirconium oxide ball). Samples of 0.18 mg of each single individual when possible (or single taxon after pooling similarly-sized individuals to achieve sufficient mass) and samples of 0.9 mg of detritus from sediments or soil were then analysed in 3.5 mm × 5 mm tin cups using a continuous flow isotope ratio mass spectrometer coupled with an elemental analyzer (IRMS Finnigan Delta Plus and Flash EA 1112 series, Thermo Fisher Scientific, Waltham, MA, U.S.A). The C and N isotopic content was expressed in 'δ' units as the relative difference (in parts per thousand) between the sample and conventional standards (atmospheric N_2 for N; PD-belemnite [PDB] carbonate for C) in accordance with the formula $\delta R(‰) = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}]\,{}^{*}10^3$ (Ponsard and Arditi, 2000), where R is the heavy-to-light isotope ratio of the element ($R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$). The outputs were standardised with atmospheric Nitrogen and $C_{12}H_{14}N_4O_4$ (cyclohexanone-2,4-dinitrophenylhydrazone). All samples were analysed twice and values were averaged.

2.4. Data analysis

2.4.1. δ^{13}C and δ^{15}N distribution in the communities

To compare the isotopic niches of the various communities, community-wide metrics were applied to macroinvertebrate isotopic data in accordance with Jackson et al. (2011) and Layman et al. (2007a), using *stable isotope Bayesian ellipses in R* (SIBER) in the R statistical computing package (R Development Core Team, 2012). Stable isotope values were bootstrapped to 100,000 iterations. The community niche space was calculated as the standard ellipse area (SEAc where "c" stands for "corrected" by degree of freedom; SIBER analysis, Jackson et al., 2011), which provides significant information on the distribution of isotopic values because it is less sensitive to sample size than the total area (TA) used by Layman et al. (2007a), and is equivalent to standard deviation but is valid for bivariate data (Brind'Amour and Dubois, 2013; Jackson et al., 2011; Syväranta et al., 2013).

The δ^{15}N range (NR) in the community niche space represented the vertical structure of the web, providing information on the magnitude of chain length. It was measured separately for detritivores and predators to take account of the magnitude of intra-guild δ^{15}N variation.

Large differences in δ^{15}N values were observed within habitats, which were probably not only associated with diet but also with nutritional, water and salt stresses as well as heterogeneous fungal colonisation of detritus (Adams and Sterner, 2000; Barnes et al., 2007; Costantini et al., 2014). For this reason, only δ^{13}C values were used for determining the niche width of predaceous and detritivorous guilds, which was expressed as δ^{13}C range (CR), i.e. the difference between species with the highest and lowest δ^{13}C values within each guild at each sampling site (Calizza et al., 2013b; Jackson et al., 2012; Layman et al., 2007a). In order to account for potential habitat-driven differences in δ^{13}C we used a relative measure of CR (indicated as CR*), obtained by dividing each CR value by the highest CR value within a given habitat. In addition, the niche width (as δ^{13}C range) of local populations of large-sized species was calculated as the difference between individuals with the highest and lowest values at each sampling site where the number of sampled individuals was >30.

2.4.2. Web construction and metrics

Web construction was based on (i) species' mean abundances on each fungal-colonised patch and (ii) diet, derived from SIA, gut contents (data were only confirmatory and are not reported here) and bibliographical analysis including our own observations and testing (Costantini and Rossi, 2001, 2010; Mulder et al., 2013).

Individuals of all taxa from each patch-scale web, subjected to SIA, were classified into isotope classes marked by intervals of 3.4 ± 1.0‰ for N and 1.2 ± 0.4‰ for C, while foreguts from individuals fixed in formaldehyde were dissected and the contents classified under a microscope into 5 major food sources: amorphous detritus, algae, leaf tissue, fungi and animals (taxonomically identified only when possible). Isotopic and gut data were then matched and checked with existing literature to determine all potential sources of each consumer. Predator diets within each food web were then refined with Bayesian mixing models, which used δ^{13}C and δ^{15}N values and yielded output values in the form of probability distributions (central tendency values and credibility intervals). The SIAR model was fitted using standard MCMC (Markov Chain Monte Carlo) methods with Metropolis–Hastings steps, which produce plausible values for dietary source proportions using a Dirichlet prior distribution (Parnell et al., 2010). Thus, while δ^{13}C range (CR) provided a measure of resource use on a continuous axis common to all species and was used to measure niche width, mixing models took account of the number and relative importance of items in their diet and were used to construct the food webs. In our study, predator–prey links were based on the presence or absence of a species in the diet of another species, by assigning 1 or 0 in a binary matrix and assembling a food web diagram from these trophic linkages. Detritivore-basal resource links were determined on the basis of the occurrence of detritivorous species on the eight fungal-litter patches (Calizza et al., 2012, 2013a) and natural detritus was used as the isotopic baseline at each sampling site.

After constructing the 42 binary matrices, web topology was analysed by calculating: (1) species richness, S; (2) the number of consumer-resource links, L; (3) linkage density, L/S; (4) mean chain length as the average number of links per chain; (5) connectance as $C_{\min} = 2L/([S(S-1)])$; (6) web compartmentalization as $C = 1/(S(S-1))\sum_{i=1}^{S}\sum_{\substack{j=1\\ i\neq j}}^{S} s_{ij}$ (Pimm and Lawton, 1980), where S = the number of taxa, $s_{ij} = S_1/S_2$, with S_1 = the number of taxa linked to taxa i and j, and S_2 = the number of taxa linked to either taxon i or taxon j; (7) species overlap as $\alpha_{ij} = \sum_h p_{ih}p_{jh}/\sqrt{\sum_h p_{ih}^2 p_{jh}^2}$ (Pianka, 1976), where p_{ih} and p_{jh} represent the proportions of species i and j on resource h; (8) web robustness to bottom-up extinctions (*sensu* Dunne, 2009), as the proportion of rare species whose removal induced the loss of 50% (removed species + secondary extinctions) of total species, mathematically determined by sequential species deletion starting from the rarest.

2.4.3. Statistics

Results in the text are reported as mean ± 1 SE. Means were compared by t-test, and Pearson's correlation coefficient was determined to evaluate the relationships between variables where possible. When necessary, data were log-transformed in order to better normalise distributions before analysis. When the assumption of equality of variances was not respected, or log-transformation of data did not allow data normalisation, the unequal variance t-test and Mann–Whitney U-test were used respectively. The paired t-test was used in order to compare detritivore and predator CR values. Due to imbalances in the data associated with the different number of sampling sites between habitats, regression models with a 95% confidence band and regression model interaction with dummy variables (1 = terrestrial, 0 = aquatic) were performed in order to compare patterns of covariation, with significant model interaction terms denoting differences between, and therefore similarity within, the two types of ecosystem. The regressions of pooled samples are reported in the text or in Figures only for cases when the small samples (the lagoon and the beech forest) fell into the 95% prediction confidence band of the regression lines of the more numerous samples (the lake and the cornfield respectively). Log-transformed data were used to compare regression slopes.

Analysis of similarities (ANOSIM) was used to compare the species assemblages of sampling sites within each habitat. The SIMPER test (SIMilarity PERcentage), based on Bray–Curtis distance and species abundance, was used to quantify mean community dissimilarity between sampling sites within each habitat. This test gives a measure, expressed as a percentage, of taxonomical dissimilarity between species assemblages: the higher the value obtained for a given habitat, the more different the communities across sampling sites.

Differences in the isotopic distribution of taxa in the bi-plot space (δ^{13}C and δ^{15}N) between sampling sites within each habitat were tested by PERMANOVA based on Euclidean distances (Anderson, 2001).

3. Results

3.1. δ^{13}C and δ^{15}N distribution and guild niche width

Average organic matter content in sediments and soils (AFDM%) did not differ among ecosystems whereas it varied considerably within ecosystems, particularly the aquatic ones (Table 1). The niche space of aquatic communities was characterised by higher average δ^{13}C values than terrestrial ones, consistent with the higher average δ^{13}C values detected in sediment detritus compared to that of soils (−18.48 ± 1.89‰ and −25.56 ± 2.13‰ respectively; Fig. 1). Overall, the niche space of aquatic communities, measured as SEAc, was narrower (Mann–Whitney test U = 82.5 $p < 0.001$) and more variable in space than terrestrial ones (Table 1). A clear isotopic divergence was observed between the sampling sites of the lagoon, whereas the 3 beech forest communities were isotopically more homogeneous than the others (Fig. 1). The isotopic distributions of taxa in the C and N biplot space differed significantly among sampling sites within all habitats (PERMANOVA, Lake: F = 5.5 $p < 0.0001$; Lagoon: F = 47.9 $p < 0.0001$; Corn field: F = 2.3 $p < 0.001$; Beech forest: F = 3.9 $p < 0.01$). Within ecosystem types, the lake and cornfield communities had wider niche spaces than the lagoon and beech forest communities respectively (lake vs. lagoon: t = 2.8 $p < 0.05$; corn field vs. beech forest: t = 13.5 $p < 0.001$). No relationship was found between the community niche space and the total number of species (r = 0.19 df = 40 p = n.s.).

Terrestrial detritivores and predators displayed higher δ^{15}N enrichment with respect to their resources than their aquatic counterparts (Fig. 2). The isotopic distance from the predator with the highest δ^{15}N value to the basal resource (Δ^{15}N‰) was related to the mean food chain length in the web (r = 0.59 $p < 0.001$ df = 40; Table 1).

Terrestrial communities also exhibited broader predator trophic niche width (as CR) (t-test t = 6.4 $p < 0.0001$) and higher species overlap (as mean α) (t-test t = 4.6 $p < 0.0001$) (Table 1; Fig. 2), which were positively related only in this ecosystem type (r = 0.63 df = 17 $p < 0.01$). The niches of aquatic and terrestrial detritivores were much broader than those of predators (paired t-test t = 5.9 $p < 0.0001$) and broader in aquatic than in terrestrial webs, although the difference was not statistically significant (t-test n.s.). In both types of web an inverse relationship was found between the relative CR values (CR*) of predators and prey (r = −0.53 df = 17 $p < 0.05$ and r = −0.37 df = 21 p = 0.08 for terrestrial and aquatic webs respectively). The differences in niche width between environmental types at each trophic level reflected differences in *per capita* resource availability: the lower the levels of food the broader the average niche of the guild (Fig. 2).

3.2. Food webs and niche width

Web size was comparable across habitats (13–19 taxa per patch-web in the lake, 17–25 in the lagoon, 13–17 in the cornfield and 23–26 in the beech forest), but significant differences were

Table 1

Food web and community descriptors for 42 invertebrate communities from four habitats.

Habitat	#Web	AFDM%	N° ind.	PPR	SEAc (‰)	L/S		Cmin	C	Chain Length		R
						Total	Predator–Prey			MCL	Δ^{15}N max (‰)	
LAKE	1	19.7	557.5 ± 102.2	0.12	9.9	2.0	0.2	0.33	0.23	1.7	5.8	0.19
	2	25.2	732.5 ± 124.8	0.11	9.3	2.1	0.5	0.33	0.26	1.7	6.0	0.50
	3	2.6	650.0 ± 75.0	0.12	11.6	2.8	0.6	0.35	0.29	1.9	5.8	0.40
	4	2.1	418.8 ± 44.3	0.28	11.0	2.9	1.0	0.38	0.41	2.0	7.1	0.45
	5	22.4	332.1 ± 10.7	0.22	9.9	2.0	0.8	0.31	0.44	1.6	5.8	0.50
	6	2.4	260.8 ± 29.3	0.10	12.0	1.9	1.4	0.24	0.22	1.8	7.3	0.34
	7	1.8	394.6 ± 44.5	0.28	18.8	1.9	1.4	0.27	0.21	1.8	7.0	0.46
	8	1.7	206.7 ± 31.6	0.18	19.4	2.1	0.5	0.28	0.42	1.6	6.1	0.27
	9	5.2	456.3 ± 100.8	0.09	9.6	1.6	0.3	0.23	0.24	1.6	5.6	0.45
	10	1.8	376.0 ± 20.1	0.30	9.1	1.2	1.1	0.17	0.15	1.8	4.1	0.37
	11	4.2	601.0 ± 50.3	0.22	6.2	1.8	0.9	0.20	0.15	1.8	4.1	0.36
	12	34.2	190.6 ± 23.8	0.17	3.1	1.7	0.5	0.24	0.23	1.8	4.1	0.29
	13	2.7	1544.8 ± 195.9	0.08	6.5	1.9	0.7	0.25	0.19	1.8	5.1	0.40
	14	2.7	682.3 ± 56.2	0.31	6.7	1.1	0.7	0.16	0.18	1.5	5.2	0.37
	15	10.1	470.8 ± 68.5	0.14	7.6	2.4	0.8	0.29	0.22	1.8	6.3	0.45
	Mean ± S.E.	*9.3 ± 2.8*	*525.0 ± 84.8*	*0.18 ± 0.02*	*10.0 ± 1.1*	*2.0 ± 0.1*	*0.8 ± 0.1*	*0.27 ± 0.02*	*0.26 ± 0.02*	*1.8 ± 0.03*	*5.7 ± 0.3*	*0.39 ± 0.02*
	Δ%	*95.0*	*87.3*	*72.8*	*84.0*	*60.6*	*89.2*	*57.8*	*65.4*	*25.7*	*43.4*	*62.0*
LAGOON	16	17.6	202.8 ± 47.1	0.04	7.0	1.5	1.4	0.15	0.10	1.8	4.6	0.33
	17	5.9	618.0 ± 68.5	0.11	6.7	1.6	0.8	0.20	0.17	1.8	3.7	0.43
	18	5.3	115.0 ± 19.9	0.19	4.0	2.0	0.7	0.17	0.17	1.9	7.1	0.28
	19	5.2	191.0 ± 49.1	0.15	6.8	1.5	0.4	0.15	0.42	2.1	4.6	0.39
	20	2.9	271.0 ± 34.5	0.09	9.7	1.7	0.6	0.19	0.15	1.9	8.3	0.25
	21	2.6	32.8 ± 5.8	0.14	5.3	1.0	0.2	0.10	0.11	2.0	7.0	0.27
	22	2.9	179.3 ± 37.7	0.08	5.7	1.7	0.1	0.19	0.15	2.1	11.7	0.25
	23	2.6	20.0 ± 6.2	0.04	7.1	1.0	0.4	0.10	0.11	1.8	5.1	0.23
	Mean ± S.E.	*5.6 ± 1.8*	*203.7 ± 66.5*	*0.11 ± 0.02*	*6.5 ± 0.6*	*1.5 ± 0.1*	*0.6 ± 0.1*	*0.16 ± 0.01*	*0.17 ± 0.04*	*1.5 ± 0.2*	*6.5 ± 0.9*	*0.30* ± 0.03*
	Δ%	*85.0*	*96.8*	*81.5*	*58.8*	*48.6*	*89.7*	*47.2*	*75.5*	*53.3*	*68.1*	*46.8*
CORN FIELD	24	6.6	84.5 ± 17.5	0.69	13.4	1.4	0.9	0.23	0.12	1.9	5.7	0.32
	25	6.6	104.3 ± 48.8	0.67	15.3	1.8	1.3	0.29	0.18	1.6	5.2	0.39
	26	8.4	56.5 ± 24.6	0.70	20.3	1.5	1.2	0.21	0.19	1.9	6.1	0.40
	27	5.8	90.1 ± 23.3	0.63	14.0	1.9	1.4	0.25	0.15	1.9	7.5	0.34
	28	5.8	67.0 ± 16.4	1.15	20.8	1.9	1.4	0.27	0.17	2.0	8.6	0.42
	29	4.9	103.2 ± 19.5	0.88	15.9	2.0	1.8	0.21	0.22	1.9	8.6	0.31
	30	5.6	155.6 ± 50.9	1.15	18.2	2.1	1.7	0.26	0.16	2.2	9.4	0.33
	31	6.7	64.7 ± 17.4	1.24	25.1	2.1	0.8	0.32	0.21	1.9	6.4	0.50
	32	6.4	120.1 ± 8.5	1.00	18.6	1.8	0.8	0.22	0.24	2.1	7.3	0.19
	33	6.6	78.3 ± 18.1	2.31	14.4	1.2	1.0	0.19	0.23	1.9	5.6	0.31
	34	5.3	67.4 ± 20.3	0.78	23.7	1.6	1.4	0.24	0.18	2.0	9.6	0.32
	35	7.4	94.7 ± 15.5	0.53	15.5	1.7	0.7	0.28	0.19	1.7	7.2	0.26
	36	5.1	54.1 ± 7.7	0.58	18.1	1.5	1.0	0.23	0.11	2.1	7.9	0.43
	37	5.9	85.1 ± 19.8	0.78	13.5	2.1	1.1	0.26	0.17	2.1	8.6	0.32
	38	7.5	183.2 ± 24.0	0.50	15.9	2.1	1.1	0.25	0.16	2.1	9.3	0.40
	39	6.9	113.7 ± 14.9	0.30	18.3	2.1	1.3	0.26	0.14	2.2	9.3	0.36
	Mean ± S.E.	*6.3 ± 0.2*	*95.2 ± 8.8*	*0.87 ± 0.12*	*17.6 ± 0.9*	*1.8 ± 0.1*	*1.2 ± 0.1*	*0.25 ± 0.01*	*0.17 ± 0.01*	*2.0 ± 0.05*	*7.6 ± 0.4*	0.35 ± 0.02
	Δ%	*41.7*	*70.4*	*87.0*	*46.6*	*45.5*	*61.1*	*39.7*	*54.4*	*29.6*	*45.8*	*61.8*
BEECH FOREST	40	7.5	40.3 ± 4.6	0.64	5.0	2.5	1.0	0.20	0.16	2.1	7.5	0.22
	41	9.3	32.3 ± 6.1	0.59	5.7	2.3	1.2	0.21	0.17	2.2	8.8	0.26
	42	6.4	30.9 ± 4.8	0.50	5.1	2.0	0.5	0.21	0.12	1.9	9.5	0.27
	Mean ± S.E.	*7.7 ± 0.8*	*34.5 ± 3*	*0.58 ± 0.04*	*5.3 ± 0.2*	*2.3 ± 0.2*	*0.9 ± 0.2*	*0.21 ± 0.01*	*0.15 ± 0.01*	*2.1 ± 0.1*	*8.6 ± 0.6*	0.25 ± 0.01
	Δ%	*31.2*	*23.3*	*22.4*	*12.3*	*22.0*	*56.9*	*6.1*	*26.9*	*12.5*	*20.4*	*18.5*

AFDM%: organic matter content in sediment as percentage; N° ind.: mean (±S.E.) number of individuals per litterbag; PPR: predator–prey ratio in terms of number of individuals; SEAc: corrected isotopic standard ellipse area; L/S: feeding linkage density; Cmin: connectance; C: compartmentalization; MCL: mean number of links per chain; Δ^{15}N (‰) max: max δ^{15}N–min δ^{15}N within each patch-scale community; R: web robustness (*: R = 0.36 ± 0.02 if two sites close to salt pans are excluded). *Δ%*: intra-habitat variability of each parameter as (max-min)/max × 100.

observed in community abundances and composition within the four ecosystems (Table 1; one-way ANOSIM $p < 0.05$ for each habitat). Specifically, the degree of taxonomical dissimilarity between sampling sites was higher in aquatic communities than in terrestrial ones (SIMPER test, Lake = 55.7% and Lagoon = 75.0% vs. Corn-field = 49.3% and Beech forest = 40.1%). Such values imply substantial turnover of species across sampling sites within all habitats. Furthermore, a higher proportion of predaceous taxa was observed in terrestrial than aquatic communities, as both number of taxa (Predator–detritivore taxa ratio = 1.41 ± 0.11 vs. 0.27 ± 0.03; *t*-test $t = 12.4$ $p < 0.0001$) and number of individuals (Predator–detritivore abundance ratio = 0.82 ± 0.11 vs. 0.16 ± 0.02, *t*-test $t = 10.6$ $p < 0.0001$). The cumulative species lists with feeding habits are shown in Table 2.

Forty-two patch-scale webs (one per sampling site: 15 for the lake, 8 for the lagoon, 16 for the corn-field and 3 for the beech-forest) were analysed; for simplicity the summary-web of each ecosystem (i.e. a meta-web obtained by cumulating all taxa and all patch-scale feeding links identified within each habitat) is shown in the Supplemental content (Fig. S1). The patch-scale webs differed significantly between ecosystem types in terms of compartmentalization, chain length, linkage density and robustness (Table 1). Compartmentalization was highest and directly related to connectance in the lake, and in both aquatic ecosystems it was inversely associated with the CR of predators ($r = -0.61$ df = 13 $p < 0.05$ and $r = -0.77$ df = 6 $p < 0.05$ in the lake and lagoon respectively). In terrestrial webs, chains were longer than in aquatic ones, in terms of

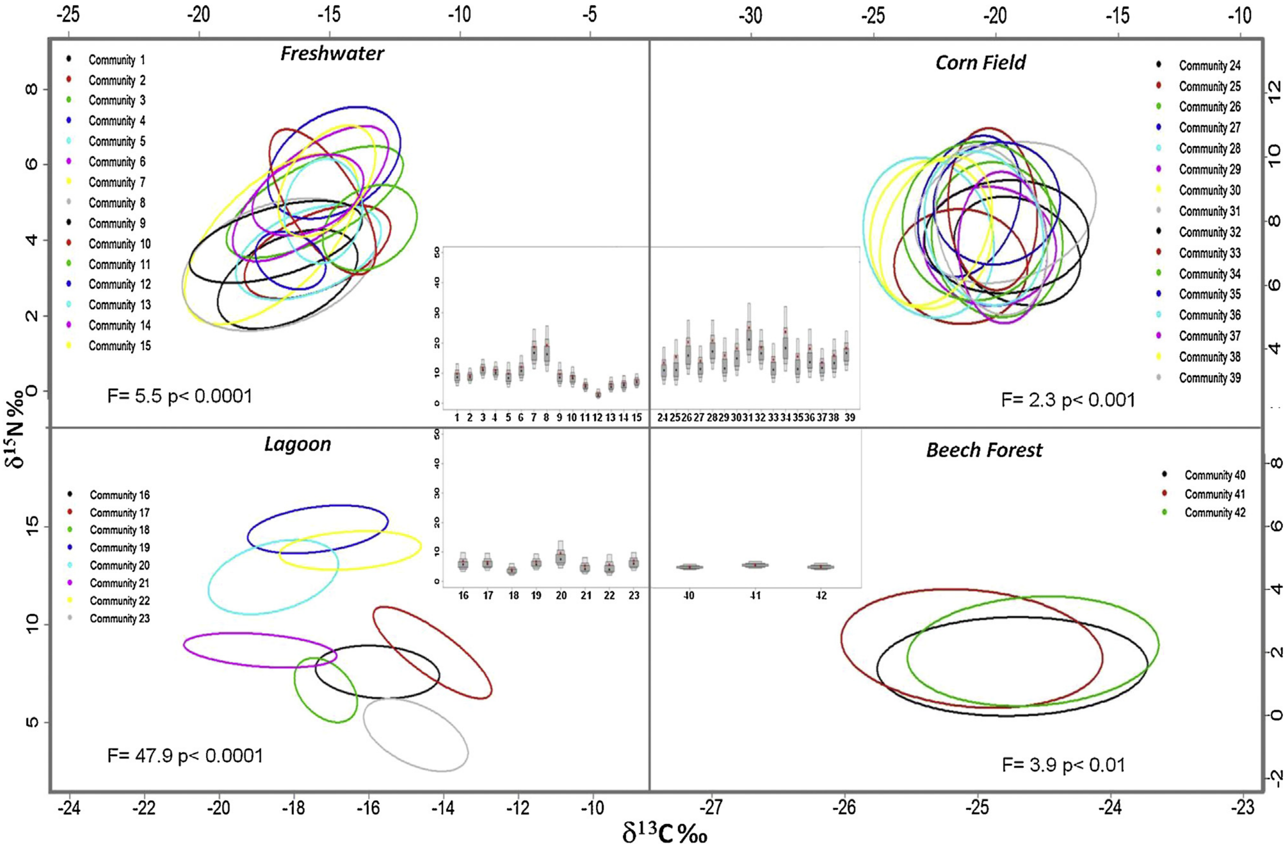

Fig. 1. Standard Ellipse Areas (SEAc) and density plots showing confidence intervals of 42 communities from 4 different habitats. (Note that habitats have different δ^{13}C and δ^{15}N scales). Red point indicates mean SEAc values obtained after 10^5 reiterations using Bootstrap calculation. Grey shades from dark to light represent 50%, 75% and 95% credibility intervals.

average number of links per chain (Mann–Whitney test $U = 88$ $p < 0.001$), and their length increased with the number of species, S ($r = 0.46$ df = 17 $p < 0.05$).

The number of links (L) increased with S in both web types but with significantly different regression slopes (Fig. 3). While the relationships lay between the L = S^2 and L = S-1 limits in both cases, they followed an L-S scaling law in aquatic webs ($t = 0.73$ df = 48 n.s.) but not in terrestrial ones ($t = 9.40$ df = 44 $p < 0.01$). Accordingly, connectance ranged between 0.1 and 0.4 (scaling negatively with S) in the former ($r = -0.65$ df = 21 $p < 0.001$) and between 0.2 and 0.3 (regardless of web size) in the latter. Only in terrestrial webs did linkage density (L/S) increase with S ($r = 0.68$ $p < 0.01$ df = 17).

The L/S of predators (predator–prey links) was on average higher in terrestrial than in aquatic webs (Table 1; *t*-test $t = 4.0$

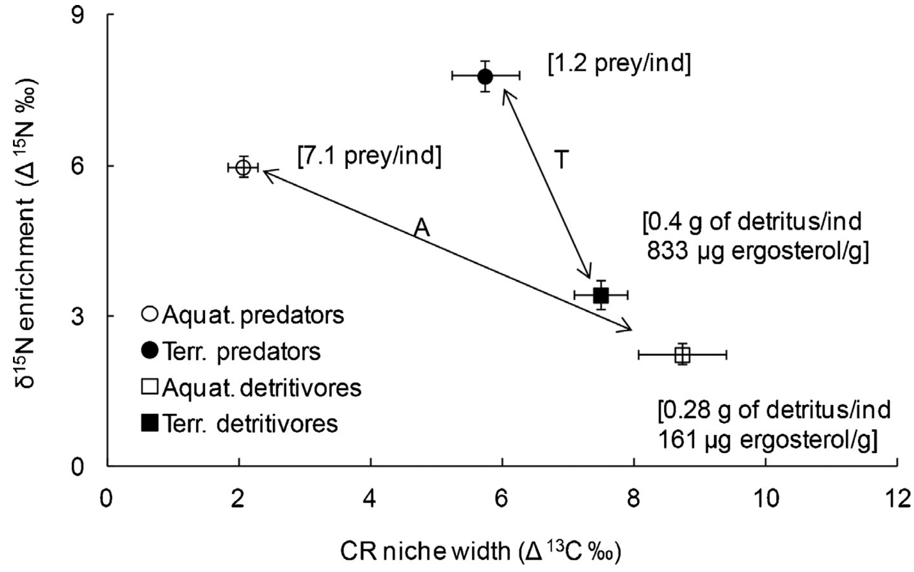

Fig. 2. Bi-plot graph of aquatic (A) and terrestrial (T) species (mean ± S.E.) based on CR and δ^{15}N enrichment, calculated as difference between maximum δ^{15}N of consumers and δ^{15}N of detritus. Brackets near symbols show availability of resources for each category.

Table 2
List of invertebrate taxa collected in four ecosystems and shown in meta-webs in Fig. S1, Supplemental material (code number in column #). p = predators, d = detritivores.

LAKE		#	LAGOON		#	CORNFIELD		#	BEECH FOREST		#
TRICLADIDA			TRICLADIDA			OLIGOCHAETA			GASTROPODA		
Dugesia sp.	p	2	*Dugesia* sp.	p	2	Lumbricidae	d	13	Limacidae	d	26
HYRUDINEA			NEMATODA	d	24	GASTROPODA			ISOPODA		
Erpobdella sp.	p	4	OLIGOCHAETA	d	20	Helicidae	d	14	*Trachelipus arcuatus*	d	23
OLIGOCHAETA	d	18	POLICHAETA	p	3	ISOPODA			*Philoscia muscorum*	d	21
GASTROPODA			*Neanthes succinea*	p	4	*Armadillidium vulgare*	d	15	*Porcellio scaber*	d	24
Bithynia tentaculata	d	7	HYRUDINEA			ARACHNIDA			ARACHNIDA		
Lymnaea auricularia	d	14	*Erpobdella sp.*	p	7	Trombidiformes	p	7	*Nemastoma* sp.	p	7
Musculium sp.	d	20	GASTROPODA			Araneae	p	3	Araneae	p	13
Valvata piscinalis	d	12	*Bittium reticulatum*	d	15	Pseudoscorpiones	p	2	*Dysdera* sp.	p	11
Physa acuta	d	13	*Hydrobia* sp.	d	18	EMBIOPTERA	d	12	Pseudoscorpiones	p	12
Planorbis planorbis	d	10	Hydrobidae	d	16	BLATTOIDEA			Trogulidae	p	14
Theodoxus fluviatilis	d	11	Lymnaeidae	d	17	Blattidae	d	11	*Euscorpius* sp.	p	15
Acroloxus lacustris	d	16	Potamididae	d	14	LEPIDOPTERA (l.)			HYMENOPTERA		
AMPHIPODA			BIVALVIA			Noctuidae	d	19	*Ichneumon* sp.	p	2
Echinogammarus veneris	d	6	*Abra segmentum*	d	29	DIPLURA	d	10	Formicidae	p	5
DECAPODA			AMPHIPODA			COLEOPTERA			COLEOPTERA		
Palaemonetes antennarius	d	19	*Phtisica marina*	d	12	Carabidae (l.)	p	6	*Lampyris noctiluca* (l.)	p	8
ARACHNIDA			*Corophium* sp.	d	13	*Harpalus* sp.	p	9	*Trechus quadristriatus*	p	1
Hydracarina	p	1	*Gammarus insensibilis*	d	19	Staphylinidae	p	8	Staphylinidae sp.1	p	3
DIPTERA (l.)	d	15	*Stenothoe monoculoides*	d	23	DERMAPTERA			Staphylinidae sp.2	p	16
Ortocladiinae (l.)	d	17	*Microdeutopus gryllotalpa*	d	21	Forficulidae	p	5	Curculionidae	d	19
TRICHOPTERA			*Talitrus saltator*	d	28	DIPTERA			DIPTERA (l.)	d	17
Ecnomus tenellus (l.)	p	3	DECAPODA			Cecidomyiidae (l.)	p	1	Nematocera (l.)	d	25
Leptoceridae sp. (l.)	d	8	*Carcinus mediterraneus*	p	1	COLLEMBOLA	d	18	RAPHIDIOPTERA (l.)	p	4
EPHEMEROPTERA (l.)	d	9	ISOPODA			CHILOPODA			COLLEMBOLA	d	18
ODONATA			*Sphaeroma ephippium*	d	27	Geophilidae		4	BLATTOIDEA		
Crocothemis sp. (l.)	p	5	*Sphaeroma hookeri*	d	26	DIPLOPODA			*Ectobius* sp.	d	20
			Sphaeroma monodi	d	25	Julidae	d	16	CHILOPODA		
			Idotea baltica	d	22	Polydesmidae	d	17	*Geophilus* sp.	p	9
			DIPTERA						*Cryptops* sp.	p	6
			Chironomidae (l.)	d	9				*Lithobius* sp.	p	10
			COLEOPTERA						DIPLOPODA		
			Berosus sp.	d	11				*Polyxenus* sp.	d	22
			Coleostoma sp.	d	10						
			Dytiscus sp.	p	6						
			Dytiscus sp. (l.)	p	5						
			CNIDARIA								
			Actinidae	p	8						

$p < 0.001$) and was negatively associated with the L/S of detritivores (detritivore-resource links) in both web types ($r = -0.60$ df = 17 $p < 0.01$ for terrestrial webs and $r = -0.54$ df = 21 $p < 0.01$ for aquatic webs). At each trophic level, L/S was strongly related to the CR* (Fig. 4a and b). With both guilds, CR* increased with the number of taxa belonging to the guild as a proportion of the total taxa in the web, S, and the increase was sharper in terrestrial than aquatic webs (Fig. 4c and d; Homogeneity of slopes; Detritivores: $F = 5.2$ $p < 0.05$; Predators $F = 4.4$ $p < 0.05$). At the single species level, the δ^{13}C range increased with the number of taxa in the guild, as observed particularly for the most abundant and widespread species in the study habitats (i.e. Diplopoda in the cornfield, $r = 0.78$ $n = 9$ $p < 0.05$, *P. muscorum* in the beech forest, $r = 0.99$ $n = 3$ $p < 0.10$; *E. veneris* in the lake, $r = 0.84$ n = 6 $p < 0.05$; n = number of sampling sites with at least 30 large-sized individuals).

Web robustness to rare species loss was on average higher in aquatic than in terrestrial webs (Table 1) and in both web types it increased with connectance (aquatic webs: $r = 0.47$ df = 21 $p < 0.05$; terrestrial webs: $r = 0.55$ df = 17 $p < 0.05$) and predator CR* (aquatic webs: $r = 0.47$ df = 21 $p < 0.05$; terrestrial webs: $r = 0.51$ df = 17 $p < 0.05$).

4. Discussion

Understanding the complexity of biological communities, particularly the patterns and dynamics underlying ecosystem structure and functioning, represents a major challenge in ecology (Allesina and Bodini, 2005; Anand et al., 2010; McCann, 2000). Food webs reflect a key aspect of this ecological complexity, making it possible to investigate ecosystems starting from the description of species interactions and identity. However, the spatial patchiness of local conditions is a recurrent ecosystem feature that has strong influence on local patterns of species interactions (Calizza et al., 2015; Careddu et al., 2015; Jana and Bairagi, 2014) and contributes to overall biocomplexity even in apparently uniform habitats, with important consequences for the interpretation of food web patterns at the habitat scale (Thompson and Townsend, 2005). In our comparative study, observations were based on 42 patch-scale litter-associated macroinvertebrate webs in four different habitats, thoroughly reconstructed using common sampling and data treatment protocols in accordance with an experimental approach. Despite the different size of the study habitats, the use of consistent spatial (i.e. patch-scale) and temporal (i.e. seasonal) resolution excluded the influence of the varying sampling scale on food web size and complexity (Ings et al., 2009). Specifically, larger spatial scales could erroneously lead us to merge feeding interactions between taxa that do not co-occur at the local scale at which macroinvertebrates actually operate. This in turn could generate artefacts and putative food webs that are more complex than those really occurring on the local level (Thompson and Townsend, 2005), and obscure local dynamics and patterns of species interactions (Brose et al., 2004; Holt, 2002). In our study, simultaneous samplings in each habitat during a limited time period reduced biases arising from temporal variability (Ings et al., 2009; Tavares-Cromar and Williams, 1996), while

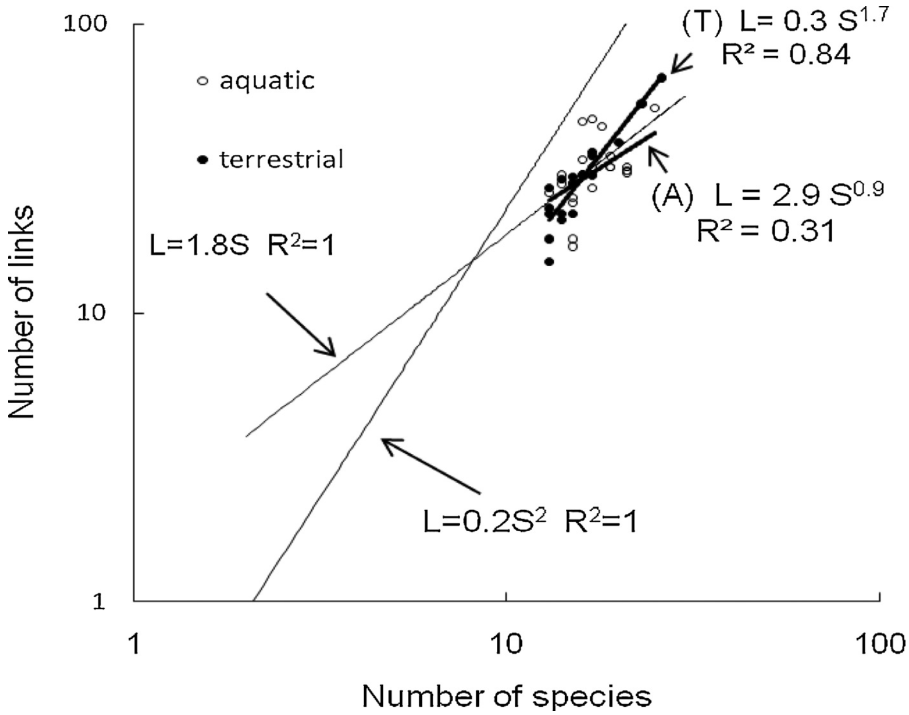

Fig. 3. Relationships between number of links and species in terrestrial (T) and aquatic (A) webs. Closed symbols = terrestrial webs, open symbols = aquatic webs. Upper line is prediction of 'constant connectance' hypothesis (links scaling as S^2) and lower line is prediction of link-species scaling (fixed number of links per species).

environmental differences and the distance between sites, along with the limited vagility of macroinvertebrates, preserved data independence. This is supported both by the high taxonomical dissimilarity between the patch-scale webs (particularly the aquatic ones) and the presence of isotopically different communities within ecosystems, which can be associated with heterogeneous spatial distributions of basal resources, as clearly observed in lake, cornfield and lagoon. Comparisons limited to the dimensional class of macroinvertebrates not only reduced potential biases associated with pseudo-replication but they also reduced biases related to large body-size differences between species (Shurin et al., 2006). Some habitat-related difference in taxonomic resolution remained but, given the similar size ranges of these litter-associated webs, it could not have significantly affected our comparisons across ecosystems. Indeed, although differences in taxonomic resolution have been suggested as a potential bias in web comparison (Ings et al., 2009), key food web parameters have been shown to be mostly unaffected by species aggregation (Dunne et al., 2002; Martinez, 1992; Williams and Martinez, 2000), particularly regarding linkage density and web connectance (Hall and Raffaelli, 1991; Martinez, 1993; Sugihara et al., 1989). In addition, taxonomic resolution did not differ between trophic levels, thereby excluding guild-related asymmetries that potentially could have weakened topological comparisons (Ings et al., 2009). It was also consistent within each habitat, and thus unlikely to significantly affect comparisons of niche-web metrics covariance patterns across ecosystems.

Although our study focused on smaller webs than other recent community-wide studies, the results show differences in the topological properties of these litter-associated webs that can best be explained by variations in the niche width of detritivores and their predators, in accordance with optimal foraging theory, which predicts that niche width increases as *per capita* level of food decreases (Pyke et al., 1977). In detrital food webs, the abundance and food niches of detritivores are also influenced by resource *quality*, which depends on substrate biochemistry and fungi, with important effects on both predator and detritivore foraging behaviour (Calizza et al., 2013a; Reinolds, 2014). However, high predator-to-prey abundance ratios in the two terrestrial ecosystems cannot be ascribed to lower litter quality for detritivores, as fungal mass was higher than in the two aquatic ecosystems and C:N was high only in the cornfield. The lower fungal mass in aquatic environments has been reported elsewhere (Van Ryckegem et al., 2007), as has the lower prevalence of detritivores (prey) in terrestrial webs (Schoener, 1989). The prey-poor conditions, promoting intraguild predation, can explain the longer food chains in terrestrial habitats (Calizza et al., 2012; Kondoh and Ninomiya, 2009; Pimm, 1982).

Although models of real food webs have successfully invoked the niche concept (Williams et al., 2010), and individual diet breadth models based on foraging theory have been proposed to predict connectance in natural food webs and the degree to which it scales with species richness (Beckerman et al., 2006; Petchey et al., 2008), food niche width has rarely been measured in the field to assess its implications for web structure (Layman et al., 2007b; Winemiller et al., 2001). One exception is the work of Quevedo et al. (2009), who showed that intra-population niche partitioning in generalist predators can promote compartmentalization. Our results demonstrate that web compartmentalization was higher in the lake and covaried with connectance in both aquatic webs. Here, compartmentalization increased with decreasing predator niche width, a result of falling predator-to-prey abundance ratios (Bolnick, 2001; Svanbäck and Persson, 2004).

It was proposed over two decades ago that connectance declines with species richness, but more recently, it has been noted that the number of feeding links per species increases with species richness, implying constant connectance. Link-species scaling is still a subject of debate among ecologists (Hildrew, 2009; Riede et al., 2010). Bengtsson (1994) demonstrated that since most web properties are related to species richness, for proper comparative analyses of food webs it is important to control for effects of web size and other confounding variables. In spite of comparable web size ranges and common web construction methods, in our study we observed that linkage density increased with S in terrestrial food webs, while it remained roughly constant

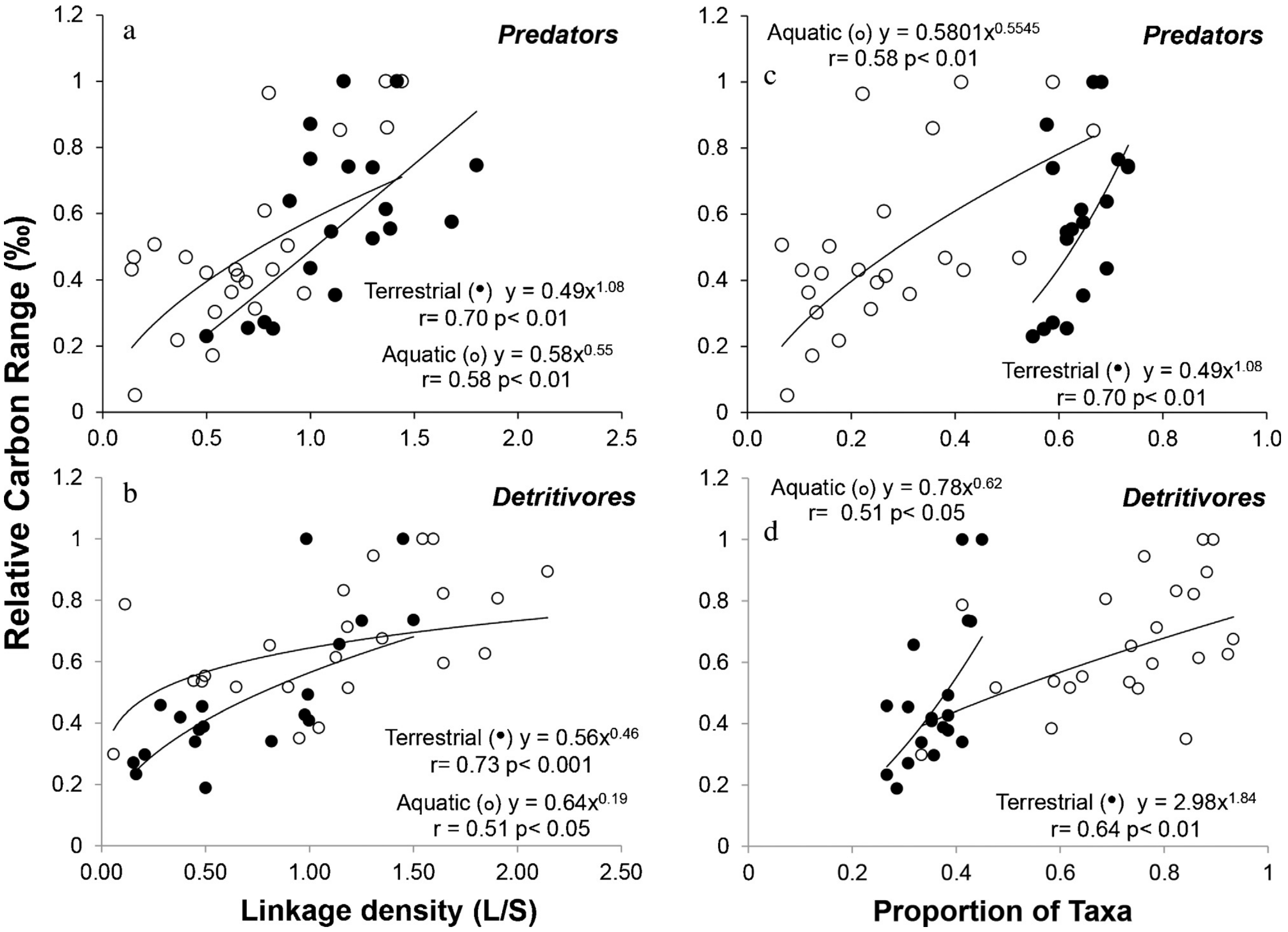

Fig. 4. Relationship of relative CR (CR*) of detritivores and predators to (a and b) linkage density (L/S) and (c and d) number of predators and prey taxa as proportion of total taxa in community. Closed symbols = terrestrial webs, open symbols = aquatic webs.

in aquatic ones, implying declining connectance, as already observed in streams (Hildrew, 2009; Schmid-Araya et al., 2002) and other food web types (Ings et al., 2009). Both alternatives imply that L increases with S: in nature, the exact form of increase and the power function are determined by the mix of species, with diets that either vary or remain the same as other species are added to the web (Havens, 1992). The differential responses of species to resource level could then explain the differences observed in the scaling properties of the studied webs. In our study, the niche width of both predators and prey increased with the number of taxa in the guild as proportion of total taxa in the community, in accordance with optimal foraging theory. However, the rate of increase was higher in terrestrial communities, particularly among predators, which had narrower niches than detritivores. In aquatic webs, the higher *per capita* level of prey, promoting diet specialisation and consequent web compartmentalization, may explain the slower rate of predator niche enlargement. The low assimilation efficiencies of terrestrial detritivores (Shurin et al., 2006) are probably the cause of the somewhat sharper niche enlargement compared to aquatic detritivores with decreasing *per capita* levels of food.

Niche enlargement in terrestrial webs is associated with an increase in species overlap with S, which is in contrast with the predictions of species packing theory (Winemiller et al., 2001). The inverse relationship between predator and prey $\delta^{13}C$ ranges indicated that consumer isotopic variability is not a direct consequence of variation in the isotopic signatures of prey items (Hoeinghaus and Zeug, 2008). On the contrary, it further supports the optimal foraging hypothesis: prey with larger niches, particularly detritivores, being more vagile are easily detected by predators, thus favouring their access to food and specialisation (Pyke et al., 1977; Calizza et al., 2013a).

Niche width also plays a role in web robustness, defined as the proportion of primary species removals that lead to 50% total species loss (Dunne, 2009). Some authors have stated that the removal of highly-connected species results in much higher rates of secondary extinctions and more rapid fragmentation of webs than the removal of random species (Dunne et al., 2002; Dunne, 2009; Solé and Montoya, 2001). However, Allesina et al. (2009) observed that highly connected species are not necessarily the most important as they may hold many redundant links that can be removed without secondary impacts, and they considered only functional links as important. To date, two distinct approaches have therefore been used to test robustness to species loss: the node-oriented approach and the functional connection-oriented approach. However, when a system is perturbed it is the *rarest* species that are usually the first to be lost (Petchey et al., 1999; Raffaelli, 2004). In our study, the bottom-up robustness of webs to rare species loss increased with connectance in both ecosystem types, in accordance with a random species loss model (Dunne, 2009). It also declined with decreasing isotopic niche width of predators, which indicates that with the loss of prey species, communities with specialist predators are structurally more vulnerable.

5. Conclusion

Despite the fundamental importance of the detritus compartment in ecosystems (Rooney and McCann, 2012), classical food web study methods often do not consider the full biological complexity from small organisms to predators at the top of the food chain (Middelburg, 2014). Our experimental approach using litterbags sought to explore also the complex interactions at the base of the detritus-based food webs, by including decomposer fungi-detritus combinations as key elements of the trophic mosaics that mediate trophic links between detritivores and detritus in all natural habitats (Calizza et al., 2013a; Costantini and Rossi, 1995, 2010; Potapov et al., 2013). In addition, the isotopic measurement of niche width enabled comparisons between predator and prey guilds and unbiased assessment of the relationship between niche width and web topological parameters. The results suggest that although web differences exist between brackish and freshwater ecosystems, patterns are more similar within than between aquatic and terrestrial web types. Crucial differences derive from the trophic niche width of predators: narrower trophic niches fragment aquatic networks into weakly interconnected clusters (i.e. higher compartmentalization), while lower prey level in terrestrial networks promotes faster niche broadening as the number of predators proportionally increases. As niche width is related to the number of links per species, this can explain the different types of relationship between the number of links and species richness, and the increasing sensitivity of webs to rare species removal with the decreasing niche width of predators.

Although limited to macroinvertebrate assemblages, our results provide field evidence of the central role of niche width in determining the structure of detritus-based food webs, posing foraging optimisation constraints as a general mechanistic explanation of food web complexity across ecosystems, a thorough understanding of which would benefit from further investigations of species interaction strength and energy flow patterns.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecocom.2015.04.005.

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