



## Article

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1 **Climate change impacts in multispecies systems: drought alters food web**  
2 **size-structure in a field experiment**

3

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*Abstract.*

Experimental data from intergenerational field manipulations of entire food webs are scarce, yet such approaches are essential for gauging impacts of environmental change in natural systems. We imposed two years of intermittent drought on stream channels in a replicated field trial, to measure food web responses to simulated climate change. Drought triggered widespread losses of species and links, with larger, rarer taxa and those that were rare for their size (but not necessarily rare absolutely) being especially vulnerable. This altered many network properties, including size-scaling relationships within and across food chains, whereas other properties, such as connectance, were unaffected. These findings highlight the urgent need for high-resolution, experimental food webs data in future studies. The loss of not only large species, but also those that were rare for their size, provides a newly refined way to gauge likely impacts that may be applied more generally to other systems and/or impacts.

*Keywords:* allometric scaling; ecological networks; experimental mesocosms; stream ecosystems; tritrophic food chains; trivariate food webs.

## 1 *Introduction*

2 Most empirical studies of climate change in multispecies systems have focused on  
3 community structure or ecosystem processes in space-for-time or temporal surveys (e.g.  
4 [1,2]), or laboratory experiments (e.g., [3]). Unfortunately, the former are often confounded  
5 (e.g. long-term change in other stressors; biogeographical effects in space-for-time surveys)  
6 and such correlative approaches are therefore unable to discern causal relationships.  
7 Laboratory experiments inevitably suffer from limited realism, but they can identify  
8 mechanisms [4-6]. A compromise between realism, control, and replication may be reached  
9 in larger-scale mesocosm field experiments, several of which have recently demonstrated  
10 responses to warming [7-10] and simulated precipitation changes [11].

11         One seemingly common effect of climate change is that larger organisms seem to  
12 suffer disproportionately, particularly from warming [9,12]. This non-random loss or  
13 reduced abundance of larger species has important implications for size-structured food webs  
14 [13], especially in aquatic systems [14-19]. Allometric scaling relationships offer a  
15 potentially powerful means of gauging responses to perturbations or environmental stress in  
16 “trivariate food webs”, in which nodes are species populations mapped onto body mass-  
17 abundance (*MN*) axes and connected via their feeding links (e.g., [16, 20]). “Trivariate”  
18 refers to the fact that *MN* data accompany the traditional food web directed-graph data.  
19 Whole-system *MN* scaling can be decomposed to examine size structure across different  
20 levels of resolution [20], from pairwise links to tritrophic chains to the entire food web, with  
21 emergent properties appearing at the higher levels (i.e., the food web is more than the sum of  
22 its parts [21]). Ours is the first study to employ such approaches to assess the impacts of  
23 simulated climate change on replicated, experimental food webs.

1           Field manipulations examining climate change impacts have largely overlooked the  
2 possible food-web consequences of droughts, which are predicted to increase in frequency  
3 and intensity in the near future [22], although a few experiments have been conducted at the  
4 community or ecosystem level (e.g., [23]). Even partial or temporary drying can threaten the  
5 local survival of many species, especially in fresh waters [24-27]. We carried out the first  
6 long-term (i.e., intergenerational) replicated field experiment to assess the impact of drought  
7 on stream food web structure, adding a new dimension to previous studies in the same model  
8 system (*cf* [28-30]).

9           Eight artificial stream channels were exposed to either intermittent drought (6-days of  
10 dewatering per month) or left as permanently flowing controls, to mimic the patchy drying of  
11 natural river beds during extreme low flows [28-30]. The experiment ran for two years,  
12 allowing intergenerational responses to be manifested, and at the end four replicate food webs  
13 were constructed per treatment. Earlier work in this system has focussed on the impacts of  
14 drought on the nodes (species), but not the links, in the food webs. The control channels  
15 contained realistic food webs [31,32] and local extinctions of several large, rare predator  
16 species were observed in the experimental treatments [28-30], so we anticipated significant  
17 drought impacts on network structure. Several additional traits were also associated with  
18 drought vulnerability, some of which were correlated with body mass (e.g., longevity and  
19 voltinism), whereas others were not (e.g., taxa that were primarily aquatic throughout their  
20 life-cycle) [30]. Insects with a terrestrial adult stage and other taxa with drought-resistant  
21 traits were relatively unaffected, and some of the smaller taxa even flourished in the drought  
22 treatments [30].

23           Given these marked changes in community composition, we hypothesised that  
24 drought would alter food web structure, particularly via the loss of large species. We also  
25 hypothesised that taxa that were rare for their body mass (i.e., with large negative residuals

1 from the general community-wide *MN* scaling relationship, as opposed to just being rare *per*  
2 *se*) would be more likely to be lost from the webs. We predicted this would reduce the  
3 community *MN* constraint space (*sensu* [33]) and that many tritrophic food chains would  
4 collapse into simpler pairwise feeding links. Further, the loss of species that deviate from the  
5 general *MN* scaling relationship should homogenize trophic link angles in the drought  
6 treatment, where angles are measured relative to the positive horizontal axis in  $\log(N)$ -versus-  
7  $\log(M)$  space. This represents the first attempt to characterise the impacts of a component of  
8 climate change experimentally across different levels of resolution, from pairwise links to the  
9 entire trophic network, in a realistically complex experimental model.

10

## 11 *Methods*

12 The experiment was conducted over 24 months (March 2000 – February 2002) in outdoor  
13 stream channel mesocosms at the Freshwater Biological Association River Laboratory, UK  
14 ( $50^{\circ}40'48''\text{N}$ ,  $2^{\circ}11'06''\text{W}$ ) [31], which were immediately adjacent to a chalk stream and  
15 received water and suspended particles (including algae, detritus, and invertebrates) through a  
16 feeder pipe. Each channel (width 0.33 m, length 12 m, depth 0.30 m) was controlled by  
17 upstream input valves and drained freely under gravity, via an outlet 10 cm above a  
18 downstream channel. Channels were filled with a 20 cm layer of stony substrate, providing  
19 both benthic and interstitial substrata in which suitably adapted species could find refuge  
20 during drought [28, 29]. Physicochemistry was similar among channels and the source stream  
21 [29, 31], as were the algal and invertebrate assemblages that established prior to the  
22 application of the drought treatment [28-32].

23 Unfiltered stream water was diverted into all channels in the initial two months.

24 Intermittent droughts (six days of flow cessation per month) were then applied to one channel

1 per block, to mimic the repeated dewatering of patches of the river bed that occurs during  
2 severe droughts [30] (which are predicted to increase in the near future [22]). Under the  
3 drought treatment, surface flows ceased and drying of exposed substrata occurred in patches  
4 over the six days, whereas the interstices beneath the bed surface remained wet, and small  
5 pools persisted [28]. Surfaces of exposed substrata dried at natural ambient rates, such that  
6 the stress experienced by organisms stranded in the channels was consistent with those in  
7 adjacent drying stream reaches [30]. Flows were continuous in the control channels  
8 throughout the experiment.

9         At the end of the experiment we collected the entire invertebrate assemblage in each  
10 mesocosm and constructed food webs by direct observation of feeding links (i.e., the contents  
11 of the whole of each channel were used as true replicates, and all individual animals present  
12 were counted). Animals were identified to the lowest practicable taxonomic unit (usually  
13 species or genus), counted and measured (63,092 individuals) to the nearest 0.1 mm, and  
14 individual body mass (mg dry weight) was calculated using length-mass regressions (see [30]  
15 and references therein). Biomass of basal resources (detritus and algae) was estimated as the  
16 ash-free dry mass of material collected from the surfaces of mineral substrata (n=8) in each  
17 mesocosm, and abundance and individual body mass were also derived where possible [28,  
18 30].

19         Feeding links were determined directly by analysis of dissected gut contents (of 4,305  
20 individuals in total), from five fields of view per individual at x 200 magnification. Gut  
21 contents were identified as algae, fungi, invertebrates, plant detrital fragments and amorphous  
22 detritus, and identified to genus or species where possible. Food webs were constructed  
23 independently for each replicate (after [32]), and a range of network properties were  
24 calculated, including: web size ( $S$ , the number of trophic elements), number of feeding links  
25 ( $L$ ) and directed connectance ( $C = L/S^2$ ). We also inferred *per capita* interaction strength for



1 each link, based on consumer-resource body mass allometries, using the following equation,  
2  $(\log_{10}((M_{Consumer}/M_{Resource})^{0.75}))$ , after [34], as the distribution of weak versus strong links can  
3 influence network stability [35].

4 *MN* trivariate webs were produced for each replicate, using base-10 logarithms  
5 throughout; by overlaying links between consumers and resources on the  $\log(N)$ -versus-  
6  $\log(M)$  scatterplot [after 16]. Several community metrics were defined from this plot, many  
7 following Cohen et al [21]. The community-wide *allometric scaling coefficient* or *slope* is  
8 defined as the slope of the ordinary linear regression line of abundance ( $\log(N)$ ) as a function  
9 of body mass ( $\log(M)$ ) for all taxa connected to the web by a trophic link. The *allometric*  
10 *angle* of a given web was defined to fall between  $-90^\circ$  and  $90^\circ$ , and corresponded to the  
11 allometric slope (i.e., the angle from the positive horizontal axis). The *community span* is the  
12 range of  $\log(M)$ , from the smallest to the largest taxa, plus the range of  $\log(N)$ , from the rarest  
13 to the most abundant taxa, over all connected taxa in the web. We also derived the minimum  
14 convex hull area in *MN* space that bounded all the connected species within each web.

15 The *link distance* between a consumer (C) and its resource (R) was defined by Cohen  
16 et al [21] as  $|\log(M_C) - \log(M_R)| + |\log(N_C) - \log(N_R)|$ . This is the  $l_1$ -distance or Manhattan  
17 distance from mathematics. The first term,  $|\log(M_C) - \log(M_R)| = |\log(M_C/M_R)|$ , is the absolute  
18 log body mass ratio, i.e., the number of orders of magnitude of difference in body mass. The  
19 second term,  $|\log(N_C) - \log(N_R)| = |\log(N_C/N_R)|$ , is the absolute log density ratio, i.e., the  
20 number of orders of magnitude of difference in population density.

21 When plotting a link as a vector from R to C, its *length* is the distance from resource  
22 R to consumer C ( $l_1$  distance, as defined above). Its *angle* is the anticlockwise turn (between  
23  $-180^\circ$  and  $180^\circ$ , where  $-180^\circ$  is allowed but  $180^\circ$  is not) to the link from a horizontal arrow  
24 parallel to the  $\log(M)$ -axis starting from R and pointing right. If the link angle equals  $-45^\circ$ ,

1 then its slope equals -1 and resource biomass  $B_R = M_R N_R$  equals consumer biomass  $B_C =$   
2  $M_C N_C$ . Further, if population productivity and consumption scale allometrically with  $M$  as  
3  $NM^b$ ,  $0 < b < 1$ , then in a link with slope  $-b$ , the population productivity and consumption of  
4 R equals that of C. Typically, scaling coefficients of  $b = 2/3$  (angle  $-33.7^\circ$ ) or  $3/4$  (angle -  
5  $36.9^\circ$ ) are assumed [21]. Thus, link angles and slopes show how biomass and population  
6 productivity and consumption change from resource to consumer.

7 We calculated several measures of network sub-structure in addition to the link  
8 lengths and angles described above. Following Cohen et al [21], a *2-chain* depicts a tritrophic  
9 interaction consisting of three taxa (R, intermediate taxon I, and C), and two links (the lower  
10 link between R and I, and the upper link between I and C). On *MN* plots, the upper link will  
11 lie below and to the right of the lower link if body mass increases and abundance declines  
12 moving up the 2-chain, as in many food webs. The *2-span* is the distance from R to C.  
13 Within each chain  $L_{\text{lower}}$  and  $A_{\text{lower}}$  describe the length and angle of the lower link (from R to  
14 I), respectively. Similarly,  $L_{\text{upper}}$  and  $A_{\text{upper}}$  describe the length and angle of the upper link  
15 (from I to C), respectively. Since  $2\text{-span} \leq L_{\text{upper}} + L_{\text{lower}}$  by the triangle inequality for the  
16 Manhattan distance, the mean difference between 2-span and  $L_{\text{upper}} + L_{\text{lower}}$  for all 2-chains  
17 measures how much they depart on average from the general “rules” of  $M_R \leq M_I \leq M_C$  and  $N_C$   
18  $\leq N_I \leq N_R$ .

19 The *between-angle* of a 2-chain is the angle in the interval  $[-180^\circ, 180^\circ]$  from the  
20 vector (R, I) to the vector (I, C). Positive angles are anticlockwise rotations from the lower to  
21 the upper link, negative angles are clockwise rotations (e.g., if the lower link is  $-50^\circ$  and the  
22 upper link  $-35^\circ$ , then the between-angle is  $+15^\circ$ ). The mean and standard deviation of  
23 between-angles over all 2-chains describes how log body mass ratios and log population  
24 density ratios vary between successive links in 2-chains. A positive between-angle value

1 means that biomass, population productivity and population consumption increase faster in  
2 the upper link (I, C) than in the lower link (R, I).

3 Maximal food chains (“chains” henceforth) from a basal to a top taxon were counted  
4 as any chain passing from resource to consumer at each link, but not including the same  
5 taxon twice (cannibalistic links were excluded and cycles were not traversed completely  
6 when present); statistics related to chains were also computed. The community span must  
7 exceed or equal the span of every chain, where the *chain span* is the Manhattan distance  
8 between its top and basal taxa. Community span minus mean chain span describes the extent  
9 to which average chains traverse the web in  $(\log(M), \log(N))$  space. The *count chain length* is  
10 the number of links contained within a chain. The *sum chain length* is the sum of the lengths  
11 of links within the chain. The *wiggling* of a web is the mean sum chain length divided by the  
12 mean chain span, with a minimum possible value of 1: values  $>1$  represent the average  
13 magnitude of changes in direction of links in chains as links progressed from basal to top  
14 taxa, after [21].

15 Between-treatment differences in these various parameters were tested using paired *t*-  
16 tests, with blocks representing pairs. Logistic regressions were used to ascertain whether  
17 body size and rarity-at-size were important determinants of extinctions from the food webs.  
18 Here, two predictors were computed per species in the control replicate of each block: 1)  
19  $\log(M)$  itself, to account for larger species having higher extinction risk; 2) the residual from  
20 the  $\log(N)$ -versus- $\log(M)$  regression. This gave two numbers for each species in each  
21 replicate per block. If the same species was present in the control replicates of two blocks,  
22 separate numbers were derived for it. The response variable was whether or not a species  
23 went extinct (True, False) in the paired drought treatment replicates. Logistic regression was  
24 performed using two models, one with predictor  $\log(M)$  only and one with both  $\log(M)$  and  
25 residuals as predictors, to see whether rarity-at-size provided any additional explanatory

1 power for loss from the food web, in addition to body size alone (already a well known  
2 predictor of extinction risk). Since absolute rarity is correlated with size and rarity-at-size is  
3 independent of size for webs with homoskedastic  $\log(N)$ -versus- $\log(M)$  regressions (i.e., most  
4 webs [36]), the latter measure is a fundamentally new possible determinant of extinction risk.  
5 All computations were done using *R* [37].

6

## 7 *Results*

8 Drought significantly reduced the numbers of species and links, and the *MN* slope across the  
9 web steepened slightly from -0.50 to -0.52, suggesting reduced efficiency of energy transfer  
10 (Tables 1 and S1 and S2). As predicted, body mass influenced vulnerability to drought, with  
11 a second-order effect of rarity (Figure 1), and both had consequences for trophic structure. In  
12 line with our experimental hypotheses, the coefficient (-0.22) for  $\log(M)$  in our logistic  
13 regressions demonstrates that larger species were more likely to be lost from the webs, and  
14 the coefficient (0.7943) for residuals shows that more-positive residuals were more likely to  
15 persist than negative ones, which indicate rarity for size ( $P < 0.0001$ ; Table S1).

16 Some of the higher resolution data revealed marked changes within the food web  
17 (e.g., numbers, angles and lengths of links between species pairs or within tritrophic chains).  
18 Other measures, however, including some commonly used lower-resolution properties (e.g.,  
19 connectance) were unaffected (Table 1). In agreement with our predictions, as species were  
20 lost and/or had their links stripped away, maximal food chains shortened across the web. The  
21 proportion of intermediate nodes declined, basal nodes increased, and top level nodes  
22 remained the same. Intermediate nodes were “lost” either via extinction or by promotion to  
23 the termini of chains (Figure 2; Table 1, S1). As predicted, the total number of tritrophic  
24 food chains therefore declined, with many collapsing into simple pairwise links. Further, due

1 to the loss of rare-at-size species, link angles and 2-chain between-angles were more tightly  
2 constrained in the drought treatments than in the controls (Figures 3 and 4). The proportion  
3 of weaker links in the web ( $\log_{10}((M_C/M_R)^{0.75}) < 5$ ) declined significantly ( $t$  3.85,  $P = 0.031$ ),  
4 whereas the strongest links ( $\log_{10}((M_C/M_R)^{0.75}) > 10$ ) remained the same ( $t$  0.63,  $P = 0.573$ )  
5 (Figure S2). In general, drought tended to simplify and homogenise the structure of the food  
6 web.

7

## 8 *Discussion*

9 This is the first replicated network-level study of the impact of a component of climate  
10 change in a long-term (i.e., intergenerational) field experiment. We found clear evidence that  
11 drought triggered the widespread loss of species and links and the homogenisation of size-  
12 scaling in the remaining food chains. The perturbed webs were bounded within a smaller  
13 constraint space and fitted more tightly to the general  $MN$  scaling relationships than did the  
14 controls, causing changes at the higher levels of resolution (e.g., among the webs' pairwise  
15 links and tritrophic chains). Drought caused a “winnowing of the web” (*cf* [38]), as nodes  
16 (and links) were stripped out to leave a skeleton outline within the same community span and  
17 only slightly steeper overall  $MN$  slope; but the winnowing was not random in  $MN$  constraint  
18 space. The thinning effect explains reductions in community biomass and secondary  
19 production reported in earlier studies [30]. Several other, more commonly-measured web  
20 properties (e.g., connectance) did not respond.

21 Large size and absolute rarity both increased vulnerability to drought and were  
22 associated with each other [28-30], with a second-order but important rarity-at-size effect that  
23 was distinct from overall rarity effects. Species below the general  $MN$ -scaling line were  
24 especially vulnerable, being already rarer in the controls than expected based on their size.

1 The approach used here may be useful for assessing impacts of stressors in ecological  
2 networks in general, and warrants further exploration in other systems where we have data  
3 from trivariate food webs exposed to perturbations (e.g., [39]).

4 The larger consumers that were lost were predominantly aquatic throughout their life-  
5 cycle, whereas the surviving large insect species possessed a terrestrial adult phase, enabling  
6 them to (re)colonise denuded patches. Many of the smaller taxa survived the drought, most  
7 likely in patches of wetted refugia, and some even flourished (e.g. certain midge larvae and  
8 small oligochaete worms) suggestive of release from competition and/or predation from the  
9 larger taxa [30].

10 Overall, the particular combination of different losers and winners in response to  
11 drought had clear consequences for the food web. The taxa that were lost from the webs  
12 were often the termini of tritrophic chains, which subsequently collapsed into 2-species links,  
13 leaving previously intermediate species as the new top-level nodes. The loss of potentially  
14 strong interactors (e.g., large predators and efficient algal grazers) [40, 41] could have had  
15 stabilising effects on the remnant drought webs, although this may have been offset by the  
16 concurrent loss of weak interactions (Figure S4) [35, 41].

17 Intriguingly, we found similar values for several parameters in our webs and those  
18 from Tuesday Lake following a manipulation that caused high levels (50%) of species  
19 turnover (e.g. measures of the wiggling of the web; cf Table 1 and S2 with those from Cohen  
20 et al. [21]). Other measures differed in absolute terms but responded similarly to  
21 perturbations: e.g., mean 2-span values in our webs were about twice those in Tuesday Lake,  
22 yet disturbances led to reduced values in both systems. Identifying which measures are more  
23 sensitive to perturbations is key to assessing the impacts of environmental change in complex  
24 natural systems: focussing on the more commonly used low-resolution properties (e.g.,

1 connectance, for instance), would have missed important structural changes within the food  
2 web. The next move towards understanding climate change impacts will necessitate  
3 modelling the dynamical consequences of structural change, if we are ultimately to predict  
4 impacts on the stability of natural food webs [42,43].

5

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13

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- 16

1 Figure Legends

2

3 Figure 1: Food web nodes from the field experiment, plotted as a function of the body mass  
4 ( $\log_{10}(M)$ ) and abundance ( $\log_{10}(N)$ ) of each species. Each panel shows a comparison  
5 between a replicate control food web and its paired drought treatment: black circles denote  
6 species that were present in both webs, yellow diamonds denote species that were in the  
7 drought treatment but not in the control, and red triangles denote species in the control but  
8 lost from the drought webs. Ordinary linear regression lines were used to assess extinction risk  
9 and so were fitted to black and red species only.

10

11 Figure 2. Food webs from the manipulative field experiment, in which eight replicate stream  
12 channels were exposed to monthly intermittent drought [d] or permanent flow [c]. The webs  
13 are ordered vertically by trophic level, from basal resources to apex predators. Black circles  
14 denote species that were present in both webs, yellow diamonds denotes species in the  
15 drought treatment but not in the control, and red triangles denotes species that were in the  
16 control but were lost from the webs exposed to drought. Numbers correspond to species  
17 identifiers (see Suppl. Mat. for codes and taxonomic identities).

18

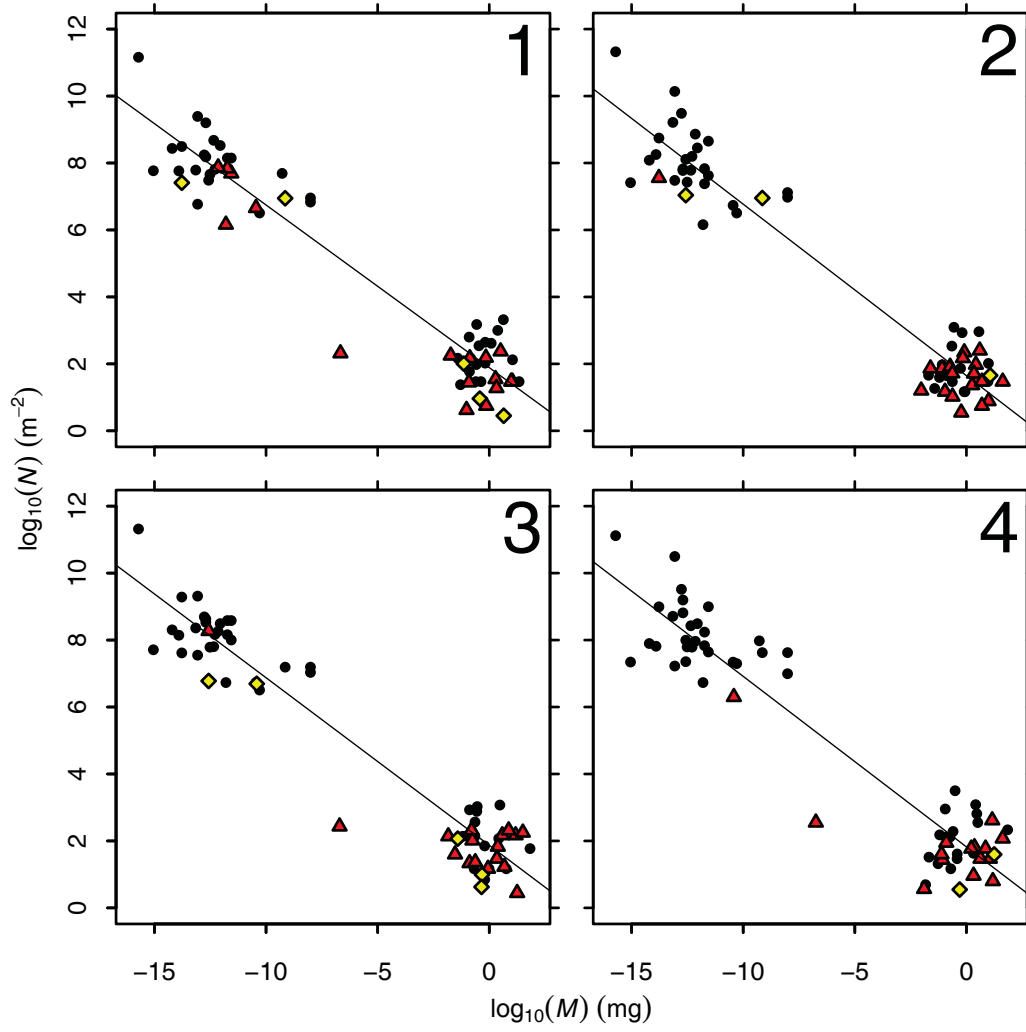
19 Figure 3: Upper angle  $A_{\text{upper}}$  versus lower angle  $A_{\text{lower}}$  of all 2-chains within food webs from  
20 the control and drought treatments. Vertical and horizontal solid lines represent median lower  
21 and upper angles for all 2-chains (see Methods). One representative web (c4, d4) per  
22 treatment is shown here; all eight (c1-c4, d1-d4) are shown in Figure S3.

23

- 1 Figure 4: Network substructure in control and drought treatments: two span as a function of
- 2 between angle ( $A_{\text{between}}$ ) within each food web (see Methods). One representative web (c4,
- 3 d4) per treatment is shown here; all eight (c1-c4, d1-d4) are depicted in Figure S4.

1 Figure 1

2



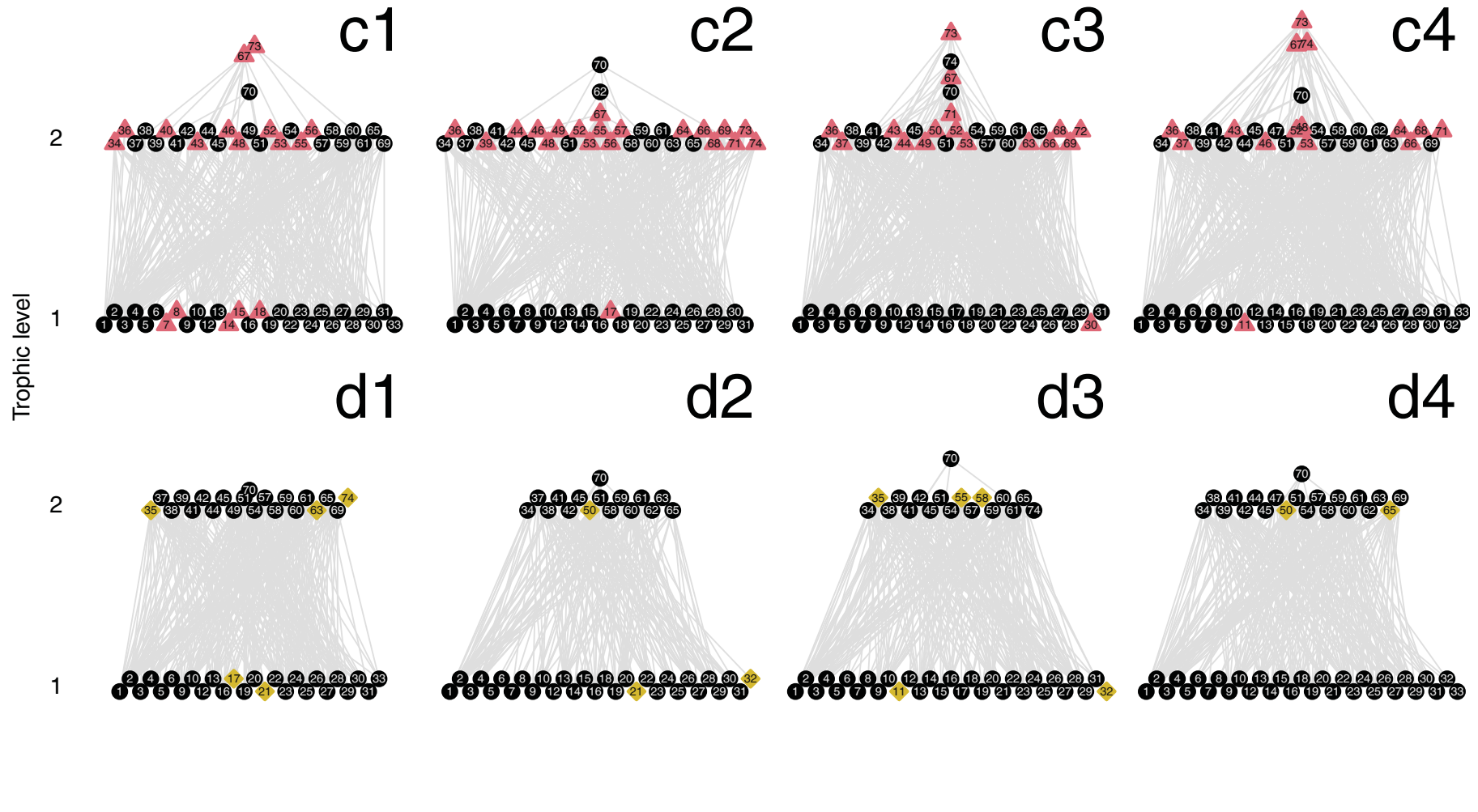
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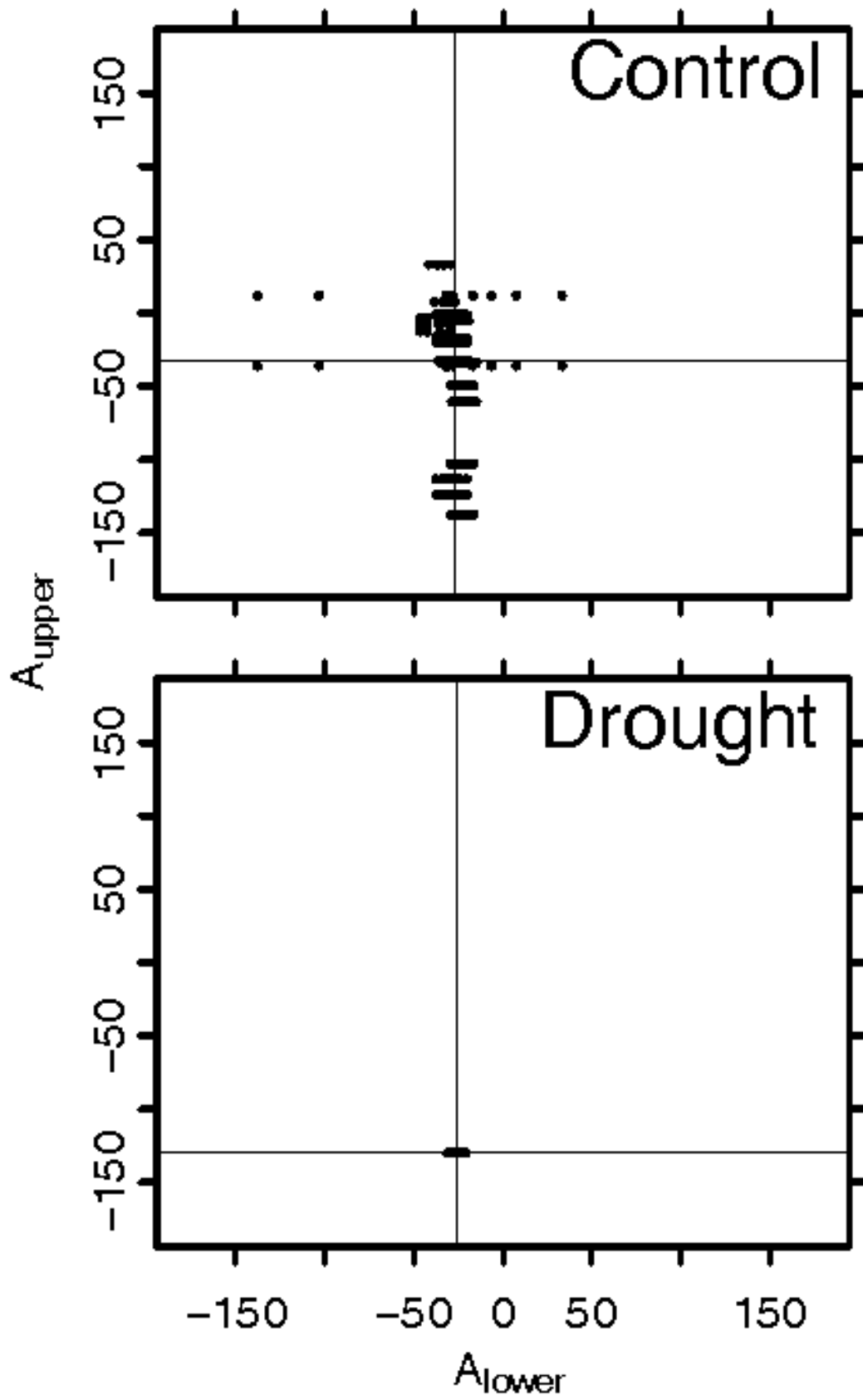
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1 Figure 2





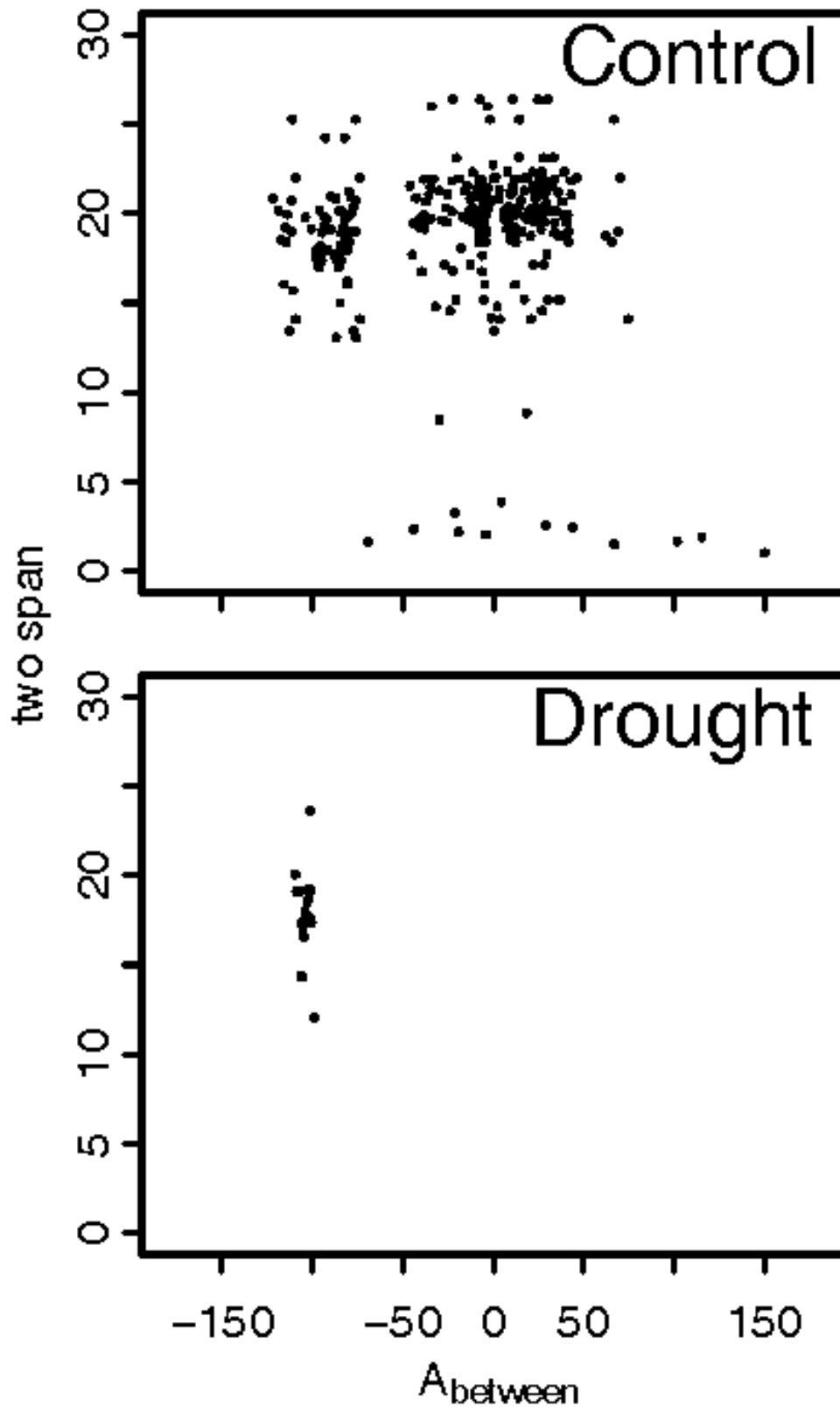
1 Figure 3



2

3

1 Figure 4



2

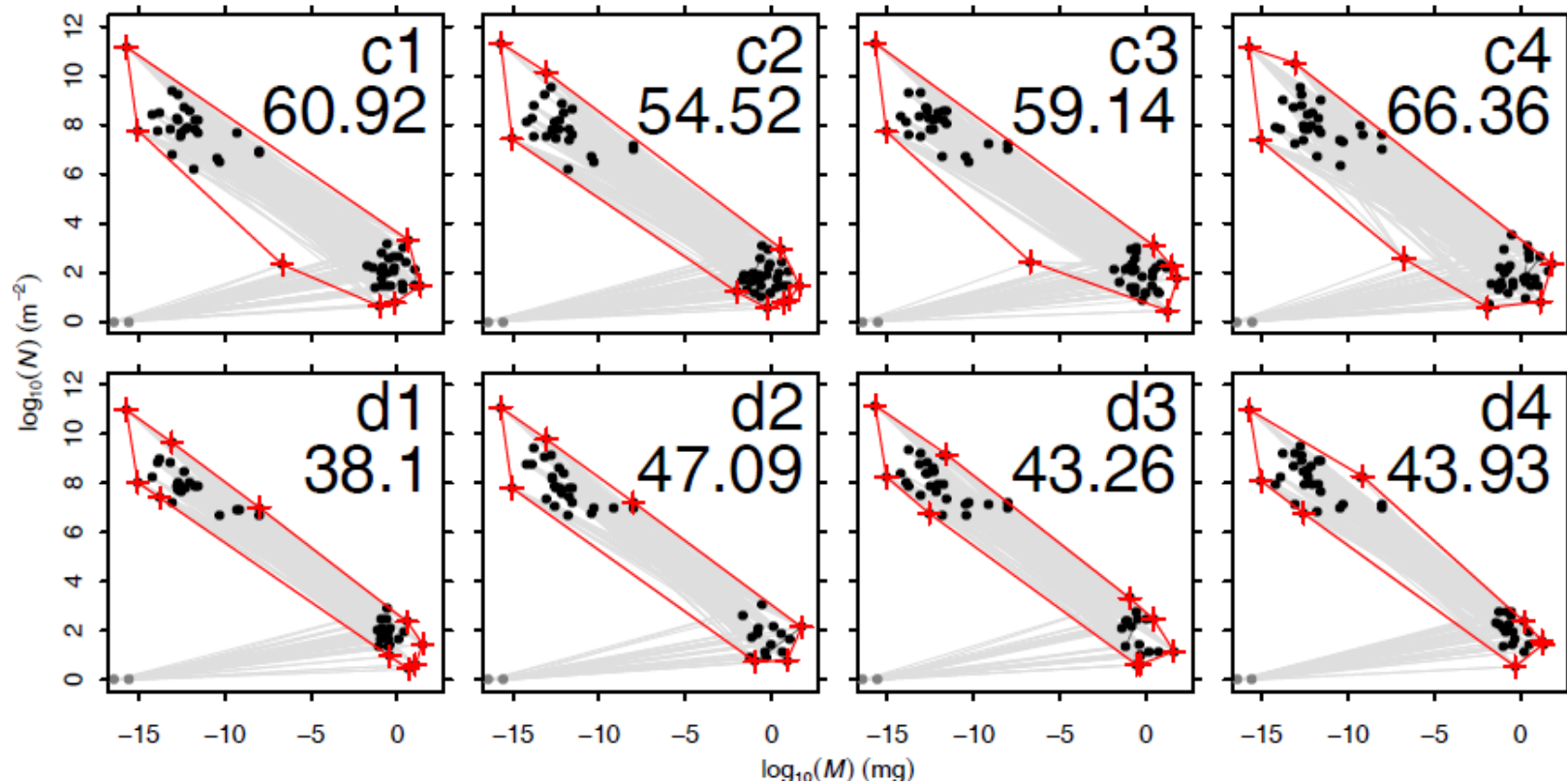
3

Table 1. Mean  $\pm$ SE food web parameters for the control (c1-c4) and drought (d1-d4) treatments. See Methods for details and Table S1 for additional statistics. Paired  $t$ -tests were performed (channels in each block formed a pair) to test for significance of mean differences ( $d$ ) from zero.

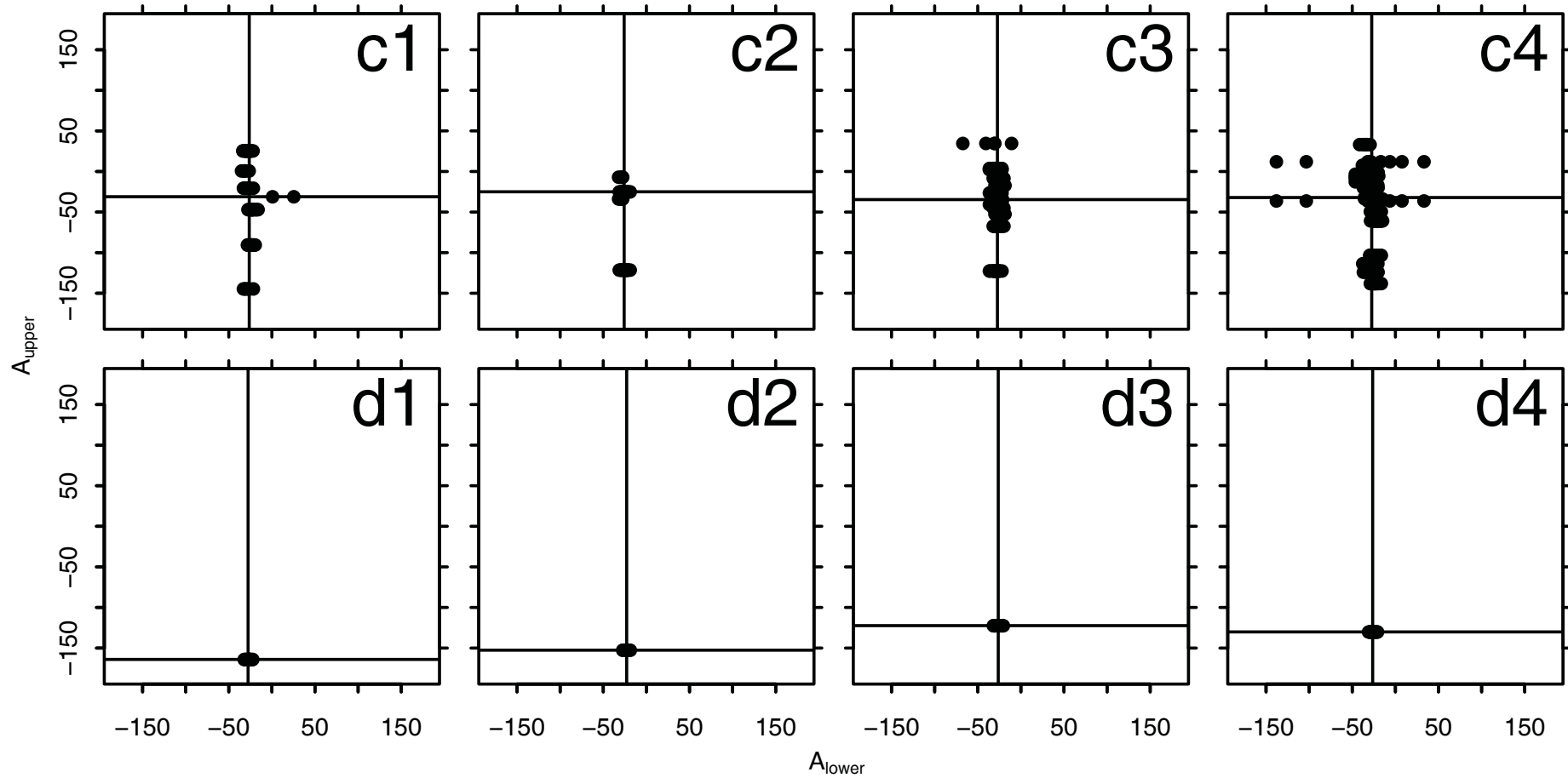
	Control webs	Drought webs	$d$	$t$	$P$
<i>Links and tritrophic interactions</i>					
Log <sub>10</sub> number of tritrophic chains	2.12 $\pm$ 0.20	1.33 $\pm$ 0.01	0.79 $\pm$ 0.19	4.25	0.024
Mean 2-span	19.2 $\pm$ 0.19	18.05 $\pm$ 0.11	1.13 $\pm$ 0.18	6.21	0.008
$L$ / number of 2-chains	3.99 $\pm$ 1.5	12.35 $\pm$ 0.94	-8.36 $\pm$ 2.1	-3.99	0.028
<i>Community scaling</i>					
Community span	28.1 $\pm$ 0.17	27.7 $\pm$ 0.08	0.33 $\pm$ 0.17	1.94	0.148
$MN$ scaling coefficient (web allometric slope)	-0.50(0.006)	-0.52(0.002)	0.017(0.005)	3.71	0.034
Constraint space ( $MN$ convex hull area)	60.23 $\pm$ 2.45	43.09 $\pm$ 1.86	17.14 $\pm$ 3.60	4.76	0.018
<i>Wiggling of chains</i>					
Mean chain span	19.4 $\pm$ 0.17	18.7 $\pm$ 0.10	0.69 $\pm$ 0.11	6.06	0.009

Mean chain span/community span	0.69±0.01	0.67±0.01	0.017±0.005	2.99	0.058
<i>Connectance (full web, including all nodes and links)</i>					
<i>S</i> , the number of food web nodes	62±1.3	48.5±1.3	13.5±1.19	11.34	0.001
<i>L</i> , number of links	366±31.8	241±20.0	125±35.2	3.55	0.038
<i>C</i> , directed connectance	0.95±0.007	0.10±0.008	-0.007±0.011	-0.65	0.56
Maximum trophic level (basal to apex chains)	2.53±0.05	2.16±0.04	0.37±0.05	7.64	0.005
Proportion of top species	0.42±0.03	0.37±0.02	0.045±0.05	0.99	0.396
Proportion of intermediate species	0.10±0.02	0.02±0.001	0.08±0.02	3.59	0.037
Proportion of basal species	0.48±0.008	0.61±0.02	-0.12±0.03	-4.50	0.020

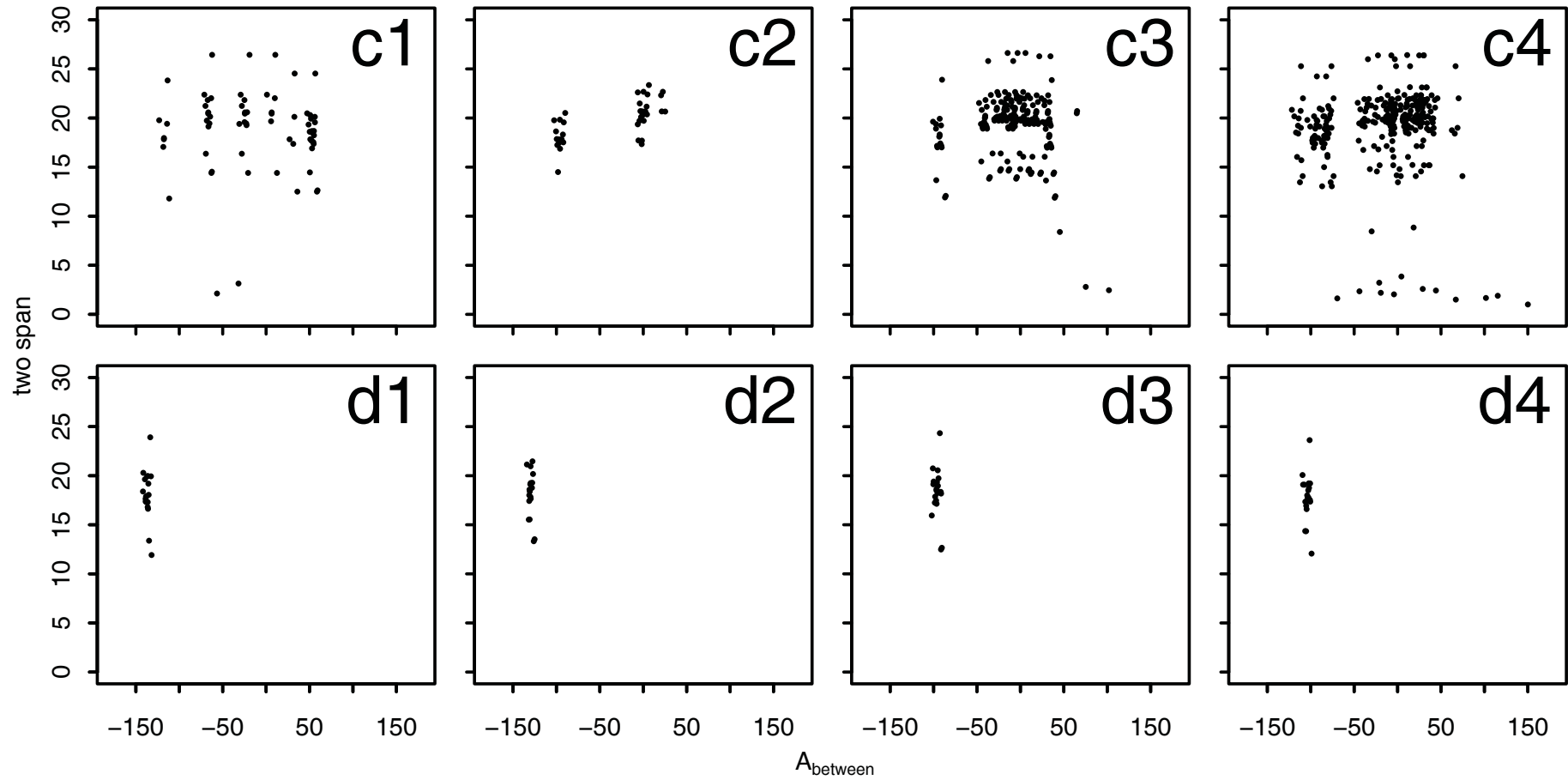
Supplementary Figure S1. Trivariate food webs from a field experiment (monthly drought [d1-d4] versus permanent flow [c1-c4]). Each node is plotted as a function of its body mass ( $\log_{10}(M)$ ) and abundance ( $\log_{10}(N)$ ). The polygonal convex hulls fitted to each web bound all interactions, excluding detritivorous feeding (note: detrital resources do not have a clearly defined individual mass and have therefore been placed in the bottom left hand corner of each web for illustrative purposes).



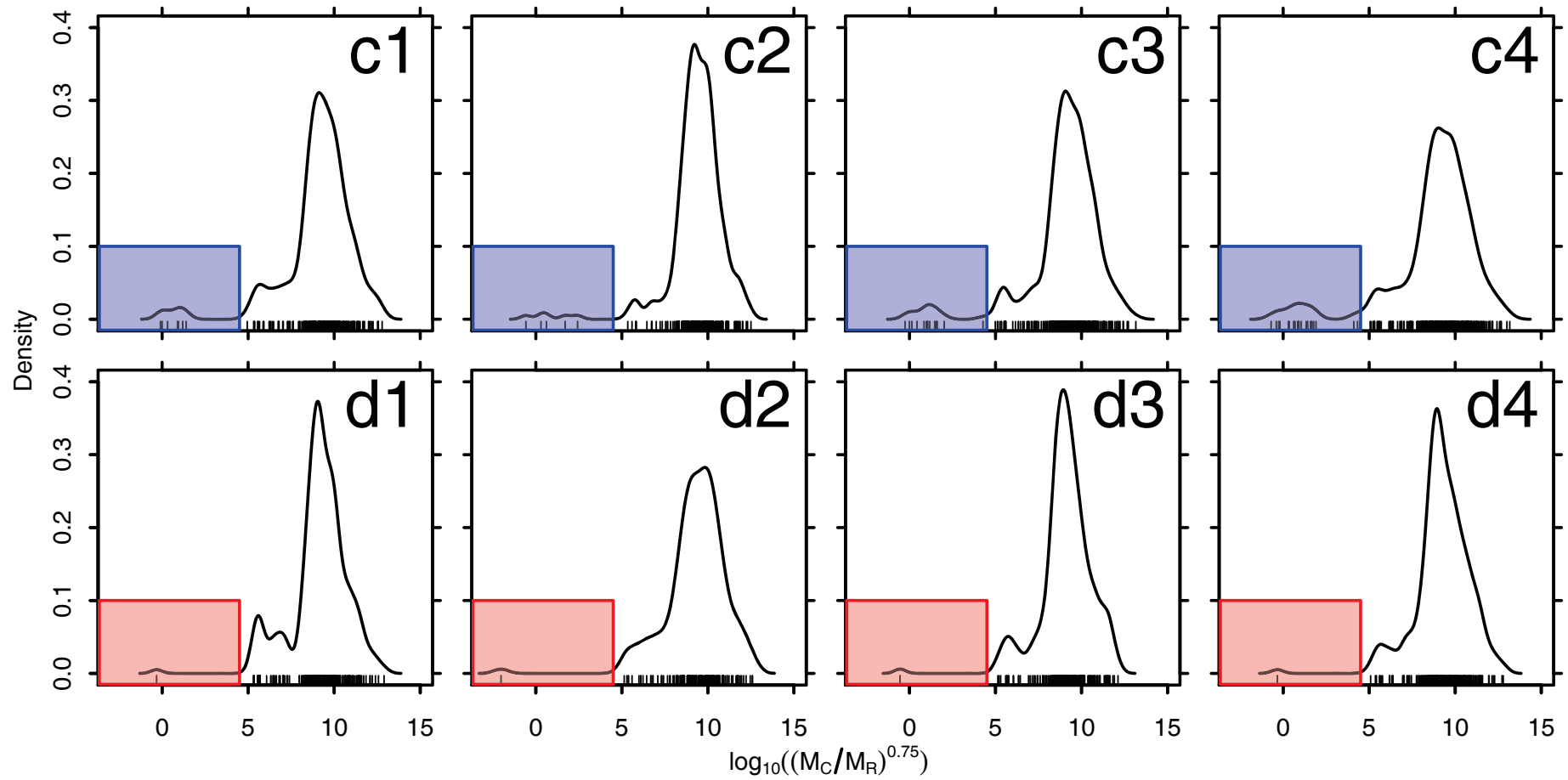
Supplementary Figure S2. : Upper angle  $A_{\text{upper}}$  versus lower angle  $A_{\text{lower}}$  of all 2-chains within each food web. Vertical and horizontal solid lines represent median lower and upper angles for all 2-chains (see Methods for details).



Supplementary Figure S3. Network substructure in control (c1-c4) and drought (d1-d4) treatments: two span as a function of upper angle  $A_{\text{between}}$  within each food web (see Methods).



Supplementary Figure S4. Per capita interaction strengths, inferred from a simple allometric scaling relationship (see main text), plotted as frequency distributions for the control (c1-c4) and drought (d1-d4) treatments. Note the reduction in “weak” links in the drought treatments, as highlighted within the transparent rectangles.





Supplementary Table S1. Parameters and test statistics from logistic regressions performed on the likelihood of species being lost from the food web on the basis of their body size ( $\text{Log}_{10}M$ ) and rarity-at-size (residual term) (See Methods for details). Significance codes: ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05.

	Estimate	S.E.	z-value	$P (> z )$
Intercept	0.083	0.187	0.443	0.658
$\text{Log}_{10}M$	-0.22	0.036	-6.063	1.34e-09 ***
Residual	0.794	0.200	3.978	6.95e-05 ***

Supplementary Table S2. Mean  $\pm$ SE food web statistics for the control (c1-c4) and drought (d1-d4) treatments at the end of a two-year experimental manipulation, and results of paired  $t$ -tests ( $t$ ,  $p$ ) for differences ( $d$ ) from zero. See Methods for details and Table 1 in the main text for additional comparisons.

	Control webs	Drought webs	$d$	$t$	$p$
<i>Links and tritrophic interactions</i>					
Mean link length	18.2 $\pm$ 0.18	18.6 $\pm$ 0.11	-0.4 $\pm$ 0.19	-2.11	0.116
Mean $L_{\text{upper}}$	2.14 $\pm$ 0.26	1.88 $\pm$ 0.79	0.263 $\pm$ 0.628	0.42	0.703
Mean $L_{\text{lower}}$	17.3 $\pm$ 0.17	18.3 $\pm$ 0.39	-1.00 $\pm$ 0.253	-3.95	0.029
Mean $L_{\text{upper}} + L_{\text{lower}}$	19.5 $\pm$ 0.28	20.2 $\pm$ 1.12	-0.74 $\pm$ 0.86	-0.85	0.457
2 $\times$ mean link length/mean 2-span	1.90 $\pm$ 0.01	2.06 $\pm$ 0.02	-0.16 $\pm$ 0.03	-5.25	0.012
Mean $L_{\text{upper}} + L_{\text{lower}}$ /mean 2-span	1.02 $\pm$ 0.00	1.12 $\pm$ 0.06	-0.10 $\pm$ 0.05	-1.88	0.157
<i>Community scaling</i>					
Mean count chain length	1.49 $\pm$ 0.17	1.10 $\pm$ 0.01	0.39 $\pm$ 0.17	2.32	0.103

Mean count chain length × mean link length/community span	1.0±0.10	0.7±0.01	0.23±0.10	2.32	0.103
<i>Wiggling of chains</i>					
Mean sum chain lengths	19.5±0.22	18.9±0.19	0.62±0.27	2.31	0.103
Mean sum chain lengths/mean chain span	1.01±0.003	1.01±0.007	-0.004±0.09	-0.47	0.674
Mean sum chain lengths/community span	0.70±0.01	0.68±0.01	0.01±0.01	1.45	0.243
<i>Connectance (full web, including all nodes and links)</i>					
(No. of taxa) <sup>2</sup>	3849±160.1	2358±129.85	1492±132	11.30	0.001
No. of trophic links/(number of taxa) <sup>2</sup>	0.1±0.01	0.1±0.01	-0.01±0.01	-0.93	0.423
No. of trophic links/taxa	5.89±0.46	4.96±0.38	0.93±0.61	1.52	0.225

Table S3. List of trophic elements in stream channel food webs. Numerical node identifiers (e.g. Fig. 2) are given in brackets.

#### Basal resources

[1] Amorphous detritus (FPOM)

[2] Plant fragments (CPOM)

[3] Fungal spores

[4] Fungal mycelia

#### Primary producers

[5] *Psammothidium lauenburgianum* (Hustedt) Bukhtiyarova & Round

[6] *Planothidium lanceolatum* (Bréb. ex Kützing) Round & Bukhtiyarova

[7] Algal cysts

[8] *Amphora ovalis* (Kützing) Kützing

[9] *Amphora pediculus* (Kützing) Grunow in Schmidt

[10] *Chroococcus minor* (Kützing) Nägeli

[11] *Cymbella lanceolata* (Ehrenberg) Kirchner

[12] *Encyonema minutum* (Hilse in Rabenhorst) Mann

[13] *Cocconeis placentula* Ehrenberg

[14] *Cymatopleura solea* (Brébisson & Godey) W. Smith

[15] *Diatoma vulgare* Bory

[16] *Staurosira elliptica* (Schumann) Williams & Round

[17] *Staurosirella leptostauron* (Ehrenberg) Williams & Round

[18] *Fragilaria vaucheriae* (Kützing) Petersen

[19] *Gongrosira incrustans* Reinsch

[20] *Gomphonema olivaceum* (Hornemann) Brébisson

- [21] *Gyrosigma* sp.
- [22] *Melosira varians* Agardh
- [23] *Nitzschia dissipata* (Kützing) Grunow
- [24] *Navicula gregaria* Donkin
- [25] *Navicula lanceolata* (Agardh) Ehrenberg
- [26] *Navicula menisculus* Schumann
- [27] *Nitzschia perminuta* (Grunow) M. Peragallo
- [28] *Navicula tripunctata* (O.F. Müller) Bory
- [29] *Rhoicosphenia abbreviate* Agardh) Lange-Bertalot
- [30] *Surirella minuta* Brébisson in Kützing
- [31] *Spirulina* sp.
- [32] *Surirella brebissonii* Krammer & Lange-Bertalot
- [33] *Synedra ulna* (Nitzsch) Ehrenberg

#### Consumers

- [34] *Asellus aquaticus* (L.)
- [35] *Eiseniella tetraedra*
- [36] *Elmis aenea* (Müller)
- [37] *Ephemera danica* Müller
- [38] *Gammarus pulex* (L.)
- [39] *Heterotrissocladus* sp.
- [40] *Leuctra geniculata*
- [41] *Limnius volckmari* (Panzer)
- [42] Naididae
- [43] Ostracoda
- [44] *Oulimnius tuberculatus* (Müller)
- [45] *Pisidium* sp.
- [46] *Polypedilum* sp.

- [47] *Prodiamesa olivacea*
- [48] *Sericostoma personatum* (Spence)
- [49] Simuliidae
- [50] *Tipula montium* Egger
- [51] Tubificidae
- [52] *Ancylus fluviatilis* (Müller)
- [53] *Athripsodes* spp.
- [54] Baetidae
- [55] *Brachycentrus subnubilus* Curtis
- [56] *Brychius elevatus* (Panzer)
- [57] *Cricotopus* sp.
- [58] *Cryptochironomus* sp.
- [59] *Radix balthica* (L.)
- [60] *Microtendipes* sp.
- [61] *Potamopyrgus antipodarum* (J.E.Gray)
- [62] *Procladius* sp.
- [63] *Synorthocladius* sp.
- [64] *Theodoxus fluviatilis* (L.)
- [65] *Tinodes waeneri* (L.)
- [66] *Valvata piscinalis* (Müller)
- [67] *Erpobdella octoculata* (L.)
- [68] *Haliplus lineatocollis* (Marsham)
- [69] *Hydropsyche* spp.
- [70] *Macropelopia* sp.
- [71] *Pentaneura* sp.
- [72] *Platambus maculatus* (L.)
- [73] *Polycentropus flavomaculatus* (Pictet)

[74] *Sialis lutaria* (L.)