Published article:

Ledger, M.E., , Brown, LE, , Edwards, F, , Milner, A.M., and Woodward, G., (2013) *Drought alters the structure and functioning of complex food webs.* Nature Climate Change, 3 (3). 223 - 227. ISSN 1758-678X

http://dx.doi.org/10.1038/nclimate1684

Drought alters the structure and functioning of complex food webs

Mark E. Ledger[1], Lee E. Brown[2], François K. Edwards[1,3], Alexander M. Milner[1,4], Guy Woodward[5]

[1]School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK.

[2]School of Geography/water@leeds, University of Leeds, Woodhouse Lane, Leeds, LS2 9JT, UK.

[3]Centre for Ecology and Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, OX10 8BB, UK.

[4]Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775, USA.

[5]School of Biological and Chemical Sciences, Queen Mary, University of London, London, E1 4NS, UK.

Correspondence: Dr Mark Ledger, School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK. email: m.e.ledger@bham.ac.uk, phone 0121 414 5540, fax 0121 414 5528.

Climate change is expected to make many regions of the world much drier over coming decades[1,2]. Rivers will be transformed as drought becomes more frequent[3] with potentially severe but largely unknown consequences at the higher (multispecies) levels of organisation[4]. Food webs are complex networks of species and their interactions[5], and here we show experimentally how the intensification of drought may alter their underlying structure and functioning (biomass flux dynamics) profoundly in fresh waters. Drought triggered substantial losses of species and interactions, especially among rare predators, leading to the partial collapse of the webs. Total resource-consumer biomass flux was also strongly suppressed by disturbance, yet several network-level properties (e.g. connectance, interaction diversity) were conserved, driven by consumer resource fidelity, and a substantial reconfiguration of fluxes within the webs as production shifted down the size spectrum from large to small species. Our research demonstrates that drier climates could have far-reaching impacts on the functioning of freshwater ecosystems.

Climate change is altering the global water cycle[1-3], with extensive impacts on local ecosystems[4,6]. In fresh waters, future shifts in the distribution of water will alter river flows and create new hydrologic regimes[3]. Declining rainfall and overuse of water are predicted to increase the intensity and frequency of droughts in river systems[3], threatening the structure and functioning of food webs, and their provision of valuable ecosystem goods and services[4], such as biomass production[6]. Many species adapted to life in permanently flowing waters are vulnerable to drought[7-9], and declining, intermittent flows could modify habitats, stripping away sensitive species and size classes[9-10], with unknown but potentially powerful impacts on food web architecture and dynamics. Biomass fluxes among species are key to understanding such changes because they determine ecosystem production, nutrient cycling, and resilience of food webs[6]. In theory, disturbances may concentrate fluxes into a smaller number of species and feeding paths, eroding resilience to future change by removing alternative trophic pathways[5]. This could be mitigated, however, where compensatory mechanisms (*e.g.* increased production of small taxa as large individuals are lost) reconfigure the food web sufficiently to maintain ecosystem functioning in the face of disturbance[11].

Despite the potential for drought disturbance to alter food web dynamics, previous research has focused on structural attributes of communities[12-14] and little empirical evidence exists for predicting future change on functioning at these higher levels of organisation[6]. Most studies of stream drought have focused on predictable seasonal events and have not addressed how the novel intensified droughts forecast by regional climate models may reshape stream ecosystems[15]. Here, we report the results of an experimental manipulation of highly taxonomically resolved quantified stream food webs conducted to measure the impacts of supraseasonal drought on trophic structure and dynamics. We tested two hypotheses: first, that drought disturbance would generate turnover in biomass production, with small *r*-selected species replacing larger, longer-lived taxa with more *K*-selected traits[16], and second, that dietary generalists would benefit over specialists[17], modifying network properties and biomass flux.

Eight replicate mesocosms (stream channels 0.3 m x 12 m) fed by a river in southern England were subjected to intermittent flow (6-days of dewatering per month), mimicking supraseasonal droughts[8,9] that cause repeated stream drying (see Methods), or left as unmanipulated controls (under perennial flow), for two years. At the end of the experiment we examined treatment effects on taxon richness and biomass of benthic assemblages and quantified network properties and biomass flux through the food webs. Food web nodes and links were identified by direct observation from benthic counts and gut contents analysis (3,643 individuals dissected), respectively. Biomass fluxes were quantified (g AFDM m^{-2} yr^{-1})[18] using ingestion data and published estimates of secondary production[19]. Qualitative and quantitative food web metrics (e.g. connectance, linkage density) were used to characterise drought impacts on network architecture and fluxes[20]. The webs, which are among the most highly-resolved published to date, collectively encompassed 783 pairwise trophic interactions among 84 trophic elements, which consisted of detrital resources (leaf litter and amorphous detritus [*i.e.*, organic matter produced by biofilms]), fungi, benthic algae (green algae, diatoms and cyanobacteria; Supplementary Table 1) and a taxonomically diverse array of macroinvertebrate consumers (*e.g.*, amphipod shrimps, beetles, leeches, snails, worms and larval alderflies, caddisflies, mayflies, stoneflies and midges; Supplementary Table 2).

Drought significantly reduced the number of species (by 21%, from mean 61.0 ± SE 1.6 to 48.0 ± 1.5, ANOVA $F_{1,3} = 28.5$, $P < 0.05$) and links (by 34%, from 376.3 ± 36.2 to 248.0 ± 23.1, ANOVA $F_{1,3} = 21.77$, $P = 0.019$), although resilience to drought varied markedly among trophic groups (Fig. 1, 2). The taxon richness and biomass of basal resources was maintained (Fig. 1), despite a marked shift in dominance from encrusting green algae to diatoms[21]. In contrast, 37% of invertebrate primary consumer taxa were eliminated by drought and their biomass was suppressed by 64%. Extinction was most profound among the predators (78% loss of taxa, Fig. 1a), whose biomass collapsed by 88% under drought (Fig. 1b). For primary and secondary consumers, local extinctions were associated strongly with rarity (logistic regression, $\chi^2 = 9.398$, $P = 0.002$). A particularly striking result was that drought eroded food webs from the top-down, reducing proportions of predators and primary consumers relative to basal species. The loss of predators reduced mean (from 1.49 ± 0.17 to 1.09 ± 0.01, ANOVA $F_{1,3} = 25.36$, $P = 0.015$) and maximum (from 2.53 ± 0.05 to 2.16 ± 0.04, ANOVA, $F_{1,3} = 11.73$, $P = 0.042$) food chain length, consistent with theoretical predictions and field surveys along disturbance gradients[13,14]. Drought caused high mortality among predators stranded in unfavourable habitat[19]. Potential food limitation was, however, partially offset by increased production of many small prey, notably chironomids, supporting our first hypothesis that *r*-selected species would exploit disturbance. This reflected a general shift away from larger taxa that had greater access to 'size refugia' from predation towards a more *r*-selected assemblage better able to access physical refugia from drought[19].

Food webs were largely detritus-based in both treatments, with biomass fluxes from detritus accounting for 96% of all flux (including to predators), and 90 % of biomass flux was channelled through just 5% of links (Fig. 3). The largest fluxes were from amorphous detritus (*i.e.* autochthonous organic matter produced by biofilms) to snails (*Radix balthica* L., *Potamopyrgus antipodarum* L., mean 46% of flux to primary consumers). Only a small proportion of fluxes to primary consumers were transferred to predators (2.2%), because in both treatments many of the primary consumers (e.g. snails, caddis, shrimps) were too large (max. body mass 42 mg) for the gape-limited predators (max. body mass 32 mg) to handle. These size disparities between invertebrate predators and prey may effectively decouple their production in the webs[22].

Drought strongly suppressed the total amount of biomass flux through the food webs by 59.8% (from 98.9 to 39.8 g m^{-2} yr^{-1}; Fig. 3a), despite extensive reconfiguration of fluxes among surviving species: *i.e.* network restructuring did not fully maintain ecosystem functioning. Biomass flux increased through 43% of links, whereas drought caused steep reductions in the remaining pathways, including major fluxes to the highly productive snail populations (maximum 95 % reduction of 43.6 g m^{-2} yr^{-1} to *Potamopyrgus antipodarum* L.). Shifts in biomass flux (*i.e.* faster vs. slower) to consumers were related to their body mass (logistic regression, $\chi^2 = 9.808$, $P = 0.002$), with increasing fluxes confined to small taxa such as midge larvae, and profound reductions for larger species, including snails, amphipod shrimps, caddis and mayfly larvae (Fig. 3b). This pronounced shift of production downwards through the size spectrum conserved the approximately log-normal relative distribution of fluxes within the webs (Fig. 3; equivalent interaction evenness among treatments, Table 1), precluding the potentially destabilising concentration of biomass within fewer species[5].

Surprisingly, several structural network properties (linkage density, connectance and interaction diversity) were unaffected by drought (ANOVA $P > 0.05$, Table 1, Supplementary Table 3) as were absolute and weighted measures of generality (numbers of resources per consumer) and vulnerability (numbers of consumers per resource). These five metrics are a manifestation of foraging behaviour and resource availability[23], and their constancy suggests consumer diets were consistent in the face of disturbance. Contrary to our second hypothesis, we found no evidence that disturbance promoted trophic generalists over specialists through indirect effects on food supply[17], which would increase web connectance and linkage density. Rather, our data show drought acted directly by increasing consumer mortality through physiological stress[19], with large species being most strongly affected, likely reflecting their relatively high metabolic demands[24].

Fresh waters are particularly vulnerable to climate change[25] and our results demonstrate that the present and future intensification of drought may have major effects on both biodiversity and ecosystem processes. The food webs underwent considerable restructuring in trophic height and the magnitude and distribution of biomass fluxes, driven by a reduction in consumer body-size, consistent with the emerging view that global change tends to have disproportionately strong negative effects on larger species[10]. However, the shift in biomass production from large to small species could not compensate fully for losses among the former, resulting in reduced overall biomass flux. Similar functional impairments of food webs can be expected in regions where future climate change exacerbates drought[19]. Such changes have implications for the future stability of food webs in an era of rapidly changing climate, as they could temper the effects of perturbations[11,26].

METHODS

Experimental design and application

A drought experiment was conducted over 24 months (March 2000 – February 2002) in four blocks of two linear stream mesocosms (width 0.33 m, length 12 m, depth 0.30 m) sited outdoors adjacent to, and fed by, a chalk stream at the Freshwater Biological Association River Laboratory, UK (50°40’48’’N, 2°11’06’’W)[19,21] (see Supplementary Method 1). The mesocosms replicate reaches of small headwater streams with stony beds and shallow subsurface sediments (20 cm depth)[19]. Following a two-month colonization period, an intermittent flow regime (6 days of flow cessation per month) was applied to one mesocosm in each block, mimicking supraseasonal hydrologic drought[8,9]. This simulated hydrograph approach allowed us to gauge how the biota responded to repeated stream drying caused by low rainfall[29] and/or overabstraction[30] as two predicted consequences of future climate change under Intergovernmental Panel on Climate Change (IPCC) scenarios[1,2]. As with all mesocosm experiments, our flow manipulations necessitated some trade-off between realism and replication[19,21]. Specifically, the simulated hydrograph may adequately capture the expected changes in the magnitude and frequency of river drying under climate change but does not necessarily mimic the expected changes in seasonality of these events. During 6-d dewatering, surface flows ceased and exposed substrata dried in patches, although water remained in the interstices beneath the bed surface, and small pools persisted at intervals along the length of the dewatered channels[19,21]. Surfaces of exposed substrata dried at natural ambient rates such that the stress experienced by organisms stranded in the mesocosms was consistent with those in adjacent drying stream reaches[19]. In the control mesocosms, flows were continuous throughout the experiment.

Sampling and processing

Estimates of invertebrate biomass were made from samples (Surber sampler 0.025m^2, 300 µm mesh, n=3 per channel) collected monthly from each mesocosm. Invertebrate secondary production was calculated from biomass, determined from 63,092 individual body length measurements, using the size-frequency method (see Supplementary Methods 2), as part of a related study[19]. At the end of the experiment (after two years), we collected the entire macroinvertebrate assemblage in each mesocosm, using samples to construct food webs by direct observation of feeding links in 3,643 individuals in total, and determined biomass of basal resources (detritus and algae) as the ash-free dry mass of material collected from the surfaces of mineral substrata (n=8) in each mesocosm[21].

Food web construction

Binary food webs were constructed based on the presence/absence of resources in the diet of consumers. These webs were then quantified, with links expressed as flows of biomass from resources to consumers for each mesocosm community, using estimates of secondary production[19]. The trophic basis of production method was used to quantify directly-observed feeding links as biomass flux (F_{ij}, g m^{-2} yr^{-1}) from resource i to consumer j (see Supplementary Method 3).

Qualitative and quantitative food web metrics

Metrics derived from binary webs based on the presence-absence of feeding links were: web size (S, the number of trophic elements in each web), number of pairwise feeding links (L), linkage density (L/S), directed connectance, the proportion of all possible links realised (L/S^2), generality (number of resources per consumer, L/S_{consumer}), vulnerability (number of consumers per resource, L/S_{resource}), and mean and maximum food chain length[27]. Quantified food webs were compared using metrics derived from information theory[5,20], specifically quantified weighted measures of linkage density (*LDq*), interaction diversity (*IDq*), interaction evenness (*IEq*), generality (*Gq*) and vulnerability (*Vq*) (see Supplementary Method 4).

Data Analysis

Three-way analysis of variance (ANOVA) was used to test the effect of drought treatment, trophic group and experimental block on taxon richness and biomass (in SPSS 16.0, Chicago, IL, USA). The analysis revealed a significant ($P < 0.05$) interaction between treatment and trophic position and two-way ANOVAs were performed subsequently to test for treatment and block effects on each trophic group. Treatment and experimental block were fixed factors in the analyses and data were log-transformed to homogenise variances. ANOVA also determined effects of treatment and block on food web metrics. Significance levels were adjusted for multiple tests using sequential Bonferroni correction. Logistic regressions tested for relationships between consumer extinctions (binary variable) and ln (abundance), ln (body mass), ln (body length) and voltinism (>1, 1, <1 cycles per year), and between directional shifts in energy flux (increase or decrease under drought, binary variable) and ln (body mass), ln (body length) and voltinism. The presence-absence of consumer species in each web was determined from the collection of the whole community at the end of the experiment.

References

1. Beniston, M. *et al.* Future extreme events in European climate: an exploration of regional climate model projections. *Climate Change* **81**, 71-95 (2007).

2. IPCC, *Climate Change 2007: Impacts, Adaptation and Vulnerability*. Contribution of Working Group II to the Fourth Assessment, Report of the Intergovernmental Panel on Climate Change, eds Parry, M. L., Canziani, O. F., Palutikof, J. P., van der Linden, P. J. & Hanson, C. E. (Cambridge University Press, Cambridge, UK, 2007).

3. Milly, P. C. D., Dunne, K. A. & Vecchia, A. V. Global pattern of trends in stream flow and water availability in a changing climate. *Nature* **438**, 347-350 (2005).

4. Vörösmarty, C. J. *et al*. Global threats to human water security and river biodiversity. *Nature* **467**, 555-561 (2010).

5. Tylianakis, J. M., Tscharntke, T. & Lewis, O. T. Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* **445**, 202-205 (2007).

6. Woodward, G. *et al*. Ecological networks in a changing climate. *Adv. Ecol. Res.* **42**, 72-138 (2010).

7. Boulton, A. J. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshw. Biol.* **48**, 1173-1185 (2003).

8. Lake, P. S. Ecological effects of perturbation by drought in flowing water. *Freshw. Biol.* **48**, 1161-1172 (2003).

9. Lytle, D. A. & Poff, N. L. Adaptation to natural flow regimes. *Trends. Ecol. Evol.* **19**, 94-100 (1994).

10. Daufresne, M., Lengfellner, K., & Sommer, U. Global warming benefits the small in aquatic ecosystems. *Proc. Natl. Acad. Sci. USA.* **106**, 12788-12793 (2009).

11. Ives, A. R. & Cardinale, B. J. Food-web interactions govern the resistance of communities after non-random extinctions. *Nature* **429**, 174-177 (2004).

12. Closs, G. P. & Lake, P. S. Spatial and temporal variation in the structure of an intermittent-stream food-web. *Ecol. Monogr*. **64**, 1-21 (1994).

13. Walters, A.W. & Post, D. M. An experimental disturbance alters fish size structure but not food chain length in streams. *Ecology* **89**, 3261-3267 (2008).

14. Sabo, J. L., Finlay, J. C., Kennedy, T. & Post, D. M. The role of discharge variation in scaling of drainage area and food chain length in rivers. *Science* **330**, 965-967 (2010).

15. Bogan, M. T. & Lytle, D. A. Severe drought drives novel community trajectories in desert stream pools. *Freshwat. Biol*. **56**, 2070-2081 (2012).

16. Pianka, E. R. On *r* and *K* selection. *American Naturalist* **104**, 592-597 (1970).

17. Vázquez, D. P. & Simberloff, D. Ecological specialization and susceptibility to disturbance: conjectures and refutations. *American Naturalist* **159**, 606-623 (2002).

18. Benke, A. C. & Wallace, J. B. Trophic basis of production among riverine caddisflies: implications for food web analysis. *Ecology* **78,** 1132-1145 (1997).

19. Ledger M. E., Edwards F. K., Brown L. E. & Milner A. M. Woodward G. Impact of simulated drought on ecosystem biomass production: an experimental test in stream mesocosms. *Global Change Biol.* **17**, 2288-2297 (2011).

20. Bersier, L. -F., Banašek-Richter, C. & Cattin, M. -F. Quantitative descriptors of food web matrices. *Ecology* **83**, 2394-2407 (2002).

21. Ledger, M. E., Harris, R. M. L., Armitage, P. D. & Milner, A. M. Disturbance frequency influences patch dynamics in stream benthic algal communities. *Oecologia* **155**, 809-819 (2008).

22. Davis, J. M., Rosemond, A. D., Eggert, S. L., Cross, W. F. & Wallace, J. B. Long-term nutrient enrichment decouples predator and prey production. *Proc. Natl. Acad. Sci. USA*. **107**, 121-126.

23. Beckerman, A. P., Petchey O. L. & Warren, P. H. Foraging biology predicts food web complexity. *Proc. Natl. Acad. Sci. U.S.A.* **103**, 13745-13749 (2006).

24. Brown, J. H., Gilooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. Toward a metabolic theory of ecology. *Ecol. Lett.* **85**, 1173-1185 (2004).

25. Heino, J., Virkkala, R. & Toivonen, H. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biol. Rev.* **84**, 39-54 (2009).

26. de Ruiter, P. C., Wolters, V., Moore, J. C. & Winemiller, K. O. Food web ecology: playing Jenga and beyond. *Science* **309**, 68-69.

27. Brown, L. E., Edwards, F., Milner, A. M., Woodward, G. & Ledger, M. E. Food web complexity and allometric scaling relationships in stream mesocosms: implications for experimentation. *J. Anim. Ecol.* **80**, 884-895 (2011).

28. Hynes, H. B. N. & Coleman M. J. A simple method of assessing the annual production of stream benthos. *Limnol. Oceanogr.* **13**, 569-573 (1968).

29. Davey, A. D. & Kelly D. J. Fish community responses to drying disturbances in an intermittent stream: a landscape perspective. *Freshwat. Biol.* **52**, 1719-1733 (2007).

30. Finn, M.A., Boulton, A.J., Chessman, B.C. Ecological responses to artificial drought in two Australian rivers with differing water extraction. *Fundam. Appl. Limnol.* **175**, 231-248 (2009).

Acknowledgements

The Freshwater Biological Association (FBA) and the Centre for Ecology and Hydrology generously supported this research. We would like to thank Rebecca Harris and Patrick Armitage for their significant contribution to the project. Russell Death, Jose Montoya and three anonymous referees provided helpful comments that improved the manuscript. The project was supported by a FBA/Natural Environmental Research Council (NERC) postdoctoral fellowship to MEL and NERC grants NER/B/S/2002/00215 and NE/J02256X/1.

Author Contributions

MEL was responsible for funding application, research design and planning, data collection and analysis, LEB prepared and analysed food webs, FKE collected and analysed data, AMM applied for funds and planned the experiment, GW applied for funds and planned food web research. All authors discussed the results and wrote the manuscript.

Figure legends.

Figure 1. Drought impacts on taxon richness and biomass varied among trophic groups. Mean (± 1 SE) taxon richness (a) and biomass (b) of basal resources, primary consumers and predators in drought and control food webs. Trophic group, drought treatment and their interaction significantly affect taxon richness and biomass (ANOVA, n=24, $P< 0.0001$ in all cases). Asterisks above individual trophic groups denote significant differences between treatments (ANOVA, n=8, $P<0.05$).

Figure 2. Drought reconfigured stream food webs. Quantitative food webs in one block of control (a) and drought disturbed (b) mesocosms (all webs shown in Supplementary Fig. 1). For each web, lower bars are basal resources, middle bars are primary consumers and top bars are predators. For each consumer, the height and width of the bars is proportional to mean annual secondary production and biomass flux from resources (total inflows to consumers), respectively. For basal species, the relative width of bars on the x-axis is proportional to total consumption by invertebrates (total outflows from each resource to consumers), and for this trophic level production (y-axis) was not quantified. The black triangles that link trophic levels illustrate the relative contribution of resource flows to the production of each consumer, summing to the total inflows. Numbers refer to consumer identity and letters distinguish categories of basal resource, omitting rare species (<1% total production). Flows from individual green algae and diatom taxa are grouped for display only. See Supplementary Tables 1 and 2 for full lists of taxa.

Figure 3. Drought reduced and reconfigured biomass flux from resources to consumers. (a) magnitude of biomass fluxes in one block of disturbed and control assemblages (all webs shown in Supplementary Fig. 2). For each treatment, fluxes were ranked from left to right in order of decreasing magnitude. (b) shifts in biomass flux were related to body mass, as revealed by the relationship between mean body mass and mean change in biomass flux to consumers for strongest pathways (> 1 g m^{-2} yr^{-1}). Symbols above and below the dashed line in (b) denote taxa with increasing or decreasing fluxes in response to drought, respectively.

Table 1. Quantitative weighted network properties were conserved under drought. The effect of the treatment was non-significant (ANOVA, $P>0.05$).

Figure 1. Drought impacts on taxon richness and biomass varies among trophic groups. Mean (± 1 SE) taxon richness (a) and biomass (b) of basal resources, primary consumers and predators in drought and control food webs. Trophic group, drought treatment and their interaction significantly affect taxon richness and biomass (ANOVA, n=24, *P*< 0.0001 in all cases). Asterisks above individual trophic groups denote significant differences between treatments (ANOVA, n=8, *P*<0.05).

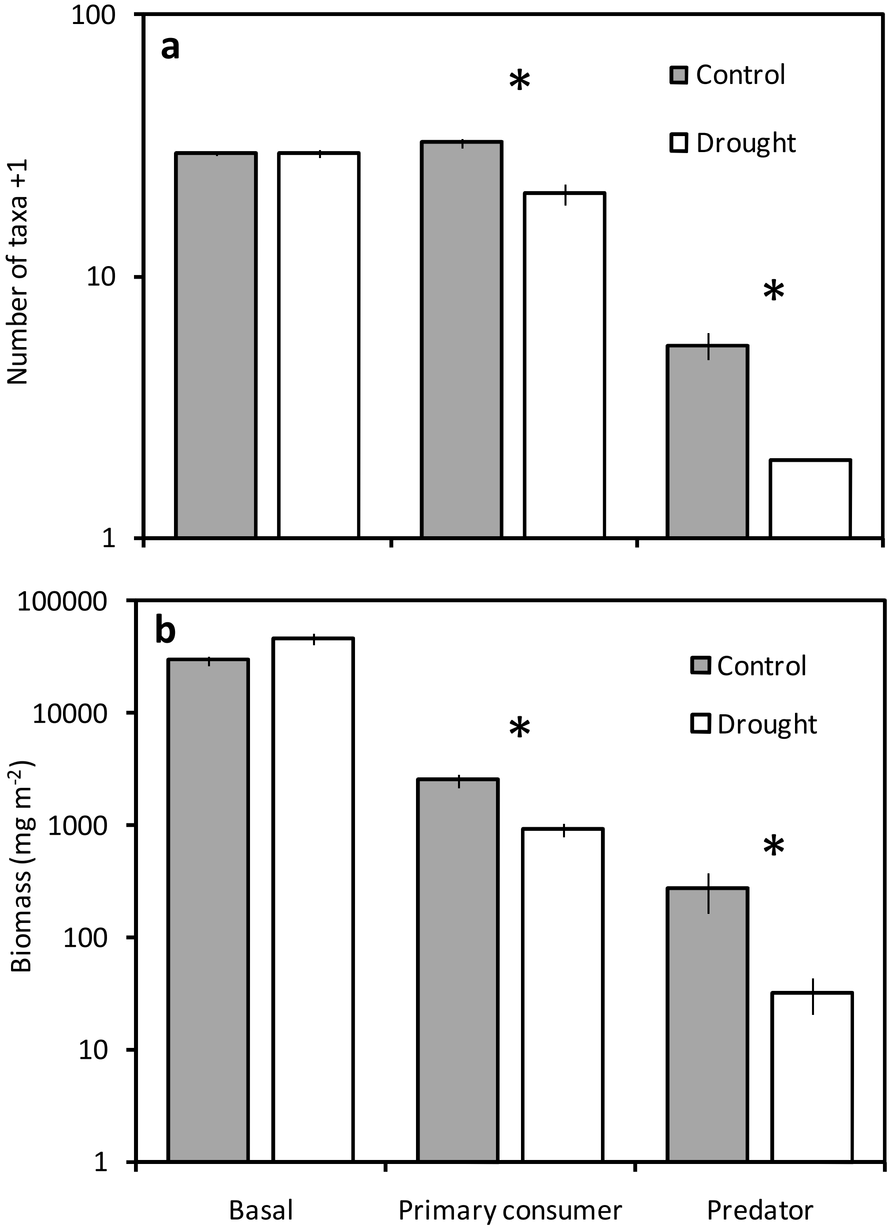


Figure 2. Drought reconfigures stream food webs. Quantitative food webs in one block of control (a) and drought disturbed (b) mesocosms (all webs shown in Supplementary Fig. 1). For each web, lower bars are basal resources, middle bars are primary consumers and top bars are predators. For each consumer, the height and width of the bars is proportional to mean annual secondary production and biomass flux from resources (total inflows to consumers), respectively. For basal species, the relative width of bars on the x-axis is proportional to total consumption by invertebrates (total outflows from each resource to consumers), and for this trophic level production (y-axis) was not quantified. The black triangles that link trophic levels illustrate the relative contribution of resource flows to the production of each consumer, summing to the total inflows. Numbers refer to consumer identity and letters distinguish categories of basal resource, omitting rare species (<1% total production). Flows from individual green algae and diatom taxa are grouped for display only. See Supplementary Tables 1 and 2 for full lists of taxa.

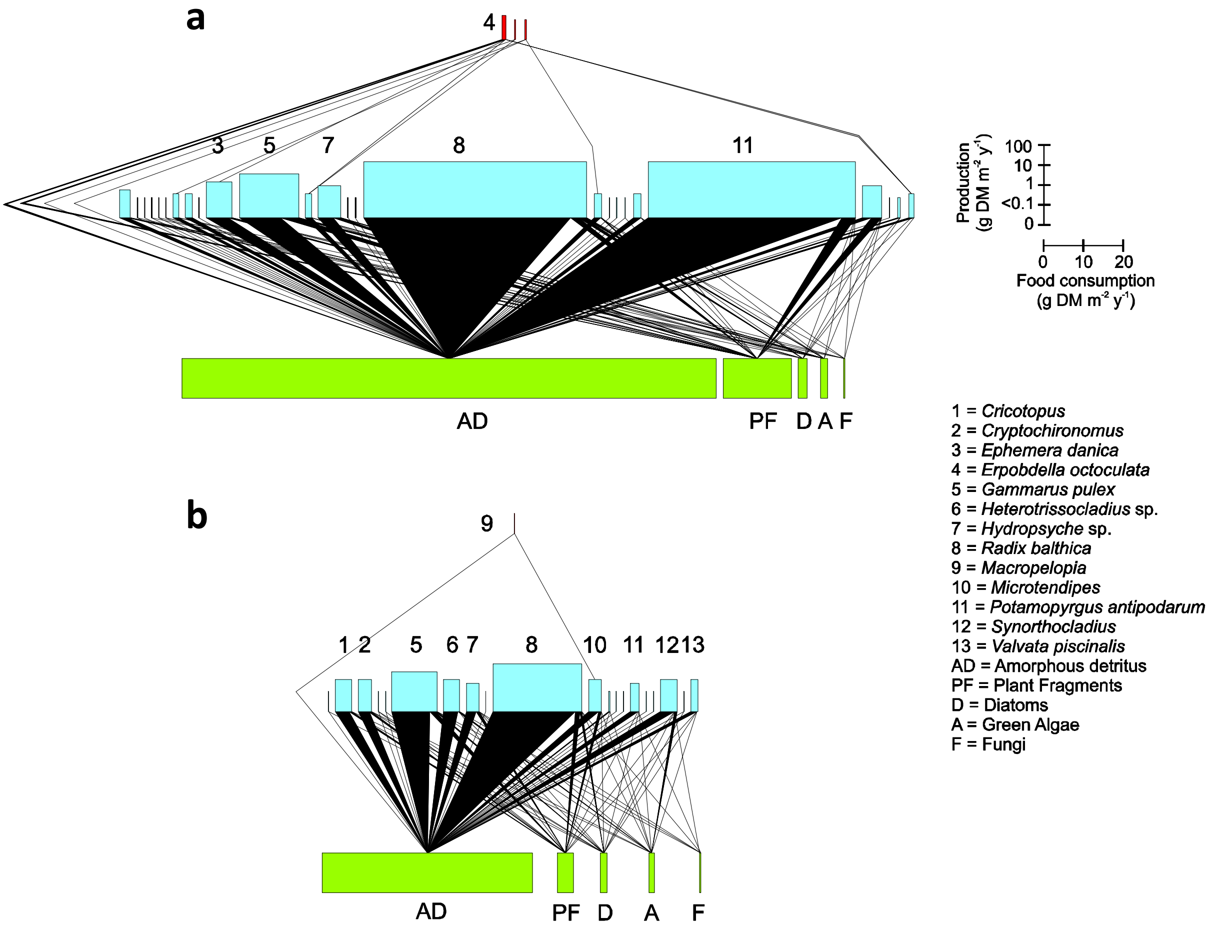


Figure 3. Drought reduces and reconfigures biomass flux from resources to consumers. (a) magnitude of biomass fluxes in one block of disturbed and control assemblages (all webs shown in Supplementary Fig. 2). For each treatment, fluxes were ranked from left to right in order of decreasing magnitude. (b) shifts in biomass flux were related to body mass, as revealed by the relationship between mean body mass and mean change in biomass flux to consumers for strongest pathways (> 1 mg m^{-2} yr^{-1}). Symbols above and below the dashed line in (b) denote taxa with increasing or decreasing fluxes in response to drought, respectively.

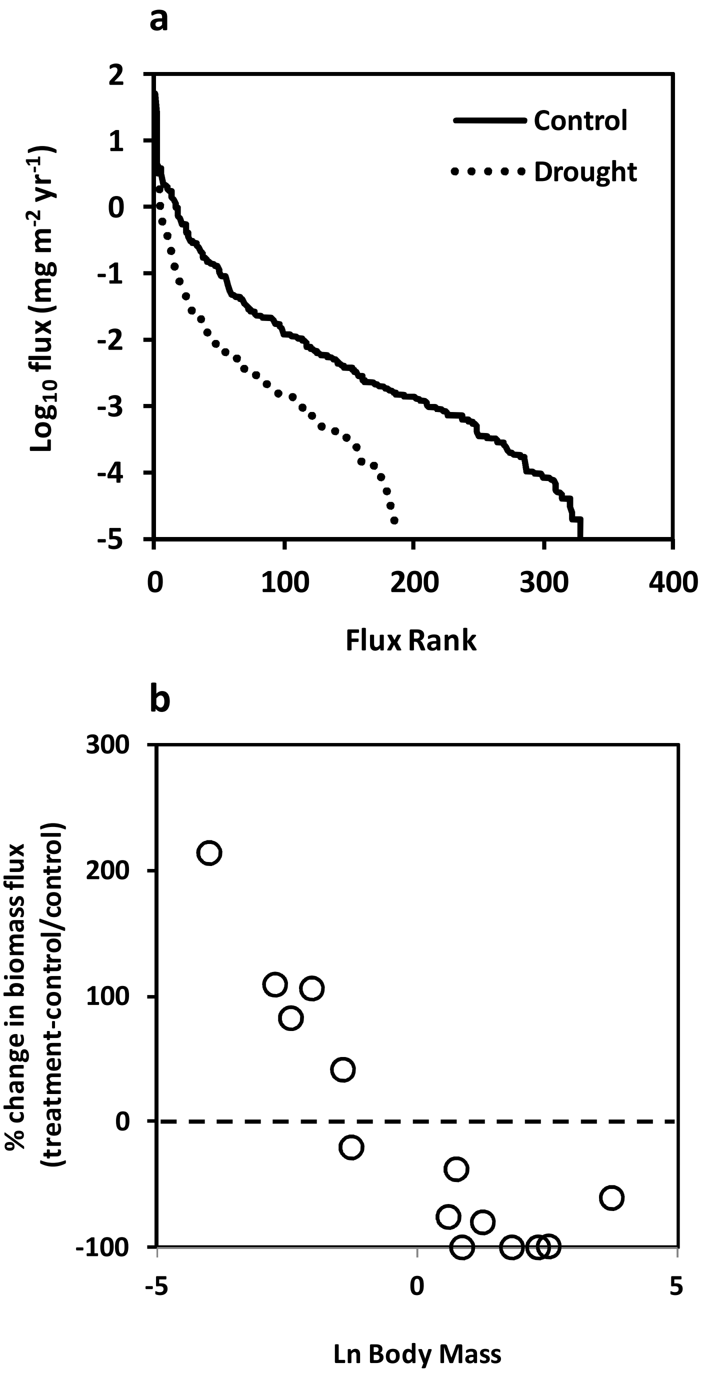


Table 1. Quantitative weighted network properties are conserved under drought. The effect of the treatment was non-significant (ANOVA, $P>0.05$).

	Control		Drought		ANOVA	
Metric	Mean	SE	Mean	SE	$F_{1,3}$	P
Linkage density (LD_q)	5.94	1.16	4.20	0.64	3.33	0.165
Connectance (LD_q/S)	0.09	0.02	0.08	0.01	0.39	0.575
Generality (G_q)	1.82	0.11	1.59	0.08	3.89	0.143
Vulnerability (V_q)	10.06	2.23	6.81	1.21	3.29	0.167
Interaction diversity (ID_q)	3.98	0.35	3.41	0.32	3.36	0.173
Interaction evenness (IE)	0.47	0.03	0.43	0.03	1.90	0.262

SUPPLEMENTARY MATERIALS

Supplementary Method 1

Stream mesocosms. Each mesocosm was a linear channel (width 0.33 m, length 12 m, depth 0.30 m) receiving water and suspended particles (including algae, detritus, and invertebrates) through a 110 mm diameter feeder pipe (6 m length). Water flow was controlled by a valve at the closed upper end of each channel. Water drained freely from mesocosms under gravity, via an open outlet positioned 10 cm above a downstream channel to prevent any potential cross-contamination among the mesocosms. Channels were filled with a 20 cm layer of stony substrate of the same substratum particle size distribution (85 % of particle volume 11-25 mm) and geological parent material (chert) to that of the source stream[19,21], providing both benthic and interstitial substrata in which suitably-adapted species may find refuge during drought[31-32]. Although there is currently no consensus as to the importance of the hyporheic zone as a refugium for biota during drought[33,34], the depth of mesocosm sediments was consistent with that of oxygenated hyporheic sediments (<20 cm) in neighbouring streams[35] and within the range of published estimates of the depth of hyporheic zones[34-38]. Physicochemistry was highly congruent among mesocosms and closely paralleled those of the source stream[31]. Biota (algae and macroinvertebrates) in the mesocosms were taxonomically diverse and similar in composition to nearby streams[32].

Supplementary Method 2

Macroinvertebrates: sample processing and secondary production estimation. Animals in samples were sorted from debris, identified to the lowest practicable taxonomic unit (usually species or genus) and counted. For secondary production estimation, macroinvertebrate body lengths (all sampled individuals, n=63,092) were measured to the nearest 0.1 mm using an ocular graticule and dissecting microscope. Individual biomass (mg dry weight) was calculated for all macroinvertebrate specimens using published length-mass regressions[39]. Secondary production of all macroinvertebrates was calculated from biomass using the size-frequency method[28] (excepting rare taxa < 1 % total abundance where production was estimated by multiplying mean annual biomass by an annual P/B value of the most closely related taxon[19]). Production for the first year and the second year of the experiment was averaged and incorporated in to biomass flux estimates as mean annual secondary production (mg m^{-2} yr^{-1}).

Supplementary Methods 3

Food web construction. Binary food webs were constructed based on the presence/absence of resources in the diet of consumers sampled at the end of the experiment. These webs were then quantified, with links expressed as flows of biomass from resources to consumers for each mesocosm community. The trophic basis of production method[19] was used to quantify directly observed feeding links, with biomass flux ($F_{ij,}$ mg m^{-2} yr^{-1}) from resource i to consumer j estimated as follows:

Determine the proportion of production derived from food type i (B_i):

$B_i = (G_i \times \mathrm{AE}_i) / \Sigma_{\mathrm{G}i=1,\dots,n}$.

Calculate the flow of biomass via food type i to consumer j (F_{ij}).

$F_{ij} = (\mathrm{B}_i \times \mathrm{P}_j) / (\mathrm{AE}_i \times \mathrm{NPE})$

where G_i is the percentage cover of food type i, AE_i is the assimilation efficiency of food type i, P_j is the secondary production[19] of consumer j, and NPE is assumed net production efficiency.

Feeding linkages were determined directly by gut contents analysis (x 1000) of macroinvertebrates. The food webs were dominated by herbivore-detritivores that feed on ubiquitous detritus and microalgae, and our instantaneous sample of diet was characteristic of feeding throughout the year[40]. In total 4,305 dissected guts were examined, with consumed items identified to the lowest practicable taxonomic unit. The guts of invertebrates were dissected at x20 magnification, and the gut contents were mounted on glass slides with an aqueous agent (Aquamount®). Five fields of view were examined on each slide at x 200 magnification using an ocular grid (1 cm^2 divided into 100 cells of 1 mm^2). Gut contents were identified as algae, fungi, invertebrates, large plant detritus and amorphous detritus. Amorphous detritus is organic matter derived from biofilms on the stream bed. It consists of polysaccharide matrix, microorganisms and their by-products[18]. Invertebrate, diatom and other algal components of diet were identified to genus or species whenever possible. The relative amount of each food type in a field of view was derived by counting the squares on the ocular grid dominated by that food type. The percentage of each food type for an individual was then calculated from the five fields of view and expressed as a percentage of the total particle area. Yield effort curves (number of food types versus number of guts examined) were drawn for each taxon to determine when a sufficient number of individuals had been examined to describe its diet accurately[27].

Supplementary Method 4

Quantitative food web metrics. Food webs with links quantified as flux of biomass (mg m^{-2} yr^{-1}) from resources to consumers were compared using metrics derived from information theory[5,20]. For each food web, we determined the quantified, weighted measures of linkage density (*LDq*), interaction diversity (*IDq*), interaction evenness (*IEq*), generality (*Gq*, mean number of resources per comsumer) and vulnerability (*Vq*, mean number of consumers per resource). The metrics incorporate the inflow and outflow of biomass to each species in the food web, and the diversity of biomass flows derived from the resource (H_N, the diversity of inflows) and going to the consumers (H_P) of each taxon k was calculated as:

$$H_{N,k} = -\sum_{i=1}^{s} \frac{b_{ik}}{b_{\bullet k}} \log_2 \frac{b_{ik}}{b_{\bullet k}}$$

$$H_{P,k} = -\sum_{j=1}^{s} \frac{b_{kj}}{b_{\bullet k}} \log_2 \frac{b_{kj}}{b_{\bullet k}}$$

In each food web matrix, column sum $b_{\bullet k}$ and row sum $b_{k\bullet}$ are the sum total biomass flux from resources, and to consumers, of taxon *k*, respectively. The reciprocals of $H_{N\bullet k}$ and $H_{P\bullet k}$ are:

$$n_{N,k} = \begin{cases} 2^{H_{N,k}} \\ 0 \quad \text{if } b_{\bullet k} = 0 \end{cases}$$

$$n_{P,k} = \begin{cases} 2^{H_{P,k}} \\ 0 \quad \text{if } b_{k\bullet} = 0 \end{cases}$$

Weighted quantitative linkage density (LD_q) was calculated as the average of the equivalent numbers of resources ($n_{N,k}$) and consumers ($n_{P,k}$), weighted by their inflows and outflows:

$$LD_q = \frac{1}{2}\left(\sum_{k=1}^{s} \frac{b_{k\bullet}}{b_{\bullet\bullet}} n_{P,k} + \sum_{k=1}^{s} \frac{b_{\bullet k}}{b_{\bullet\bullet}} n_{N,k} \right)$$

where $b_{\bullet\bullet}$ is the total biomass flux in the web matrix[20]. Quantified connectance was calculated as LD_q/S. Weighted generality (G_q) and vulnerability (V_q) were calculated as:

$$G_q = \sum_{k=1}^{s} \frac{b_{\bullet k}}{b_{\bullet\bullet}} n_{N,k}$$

$$V_q = \sum_{k=1}^{s} \frac{b_{k\bullet}}{b_{\bullet\bullet}} n_{P,k}$$

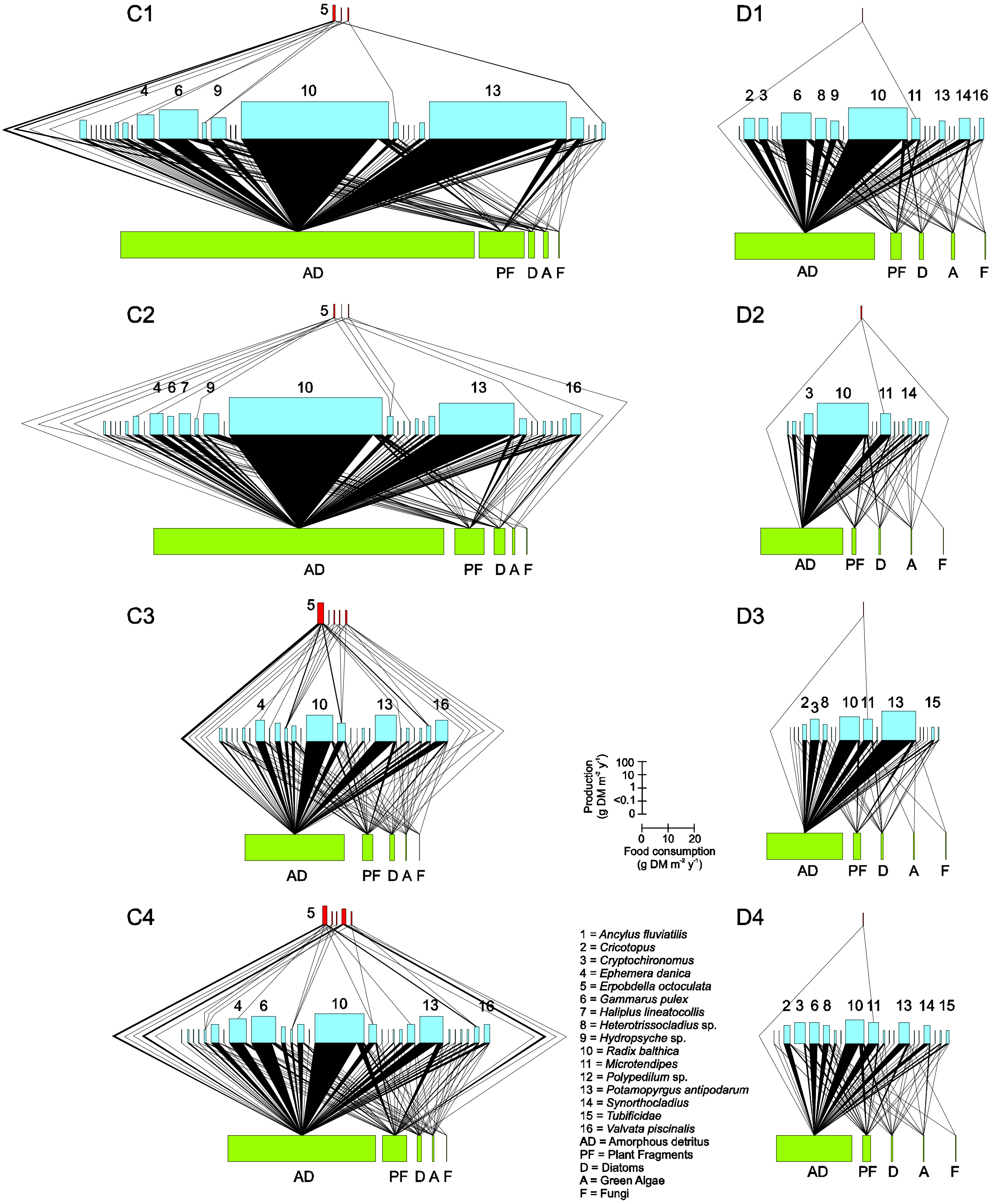
The diversity and evenness of quantified links in each food web was calculated using the Shannon index of entropy:

$$ID_q = \sum p_i \log_2(p_i)$$

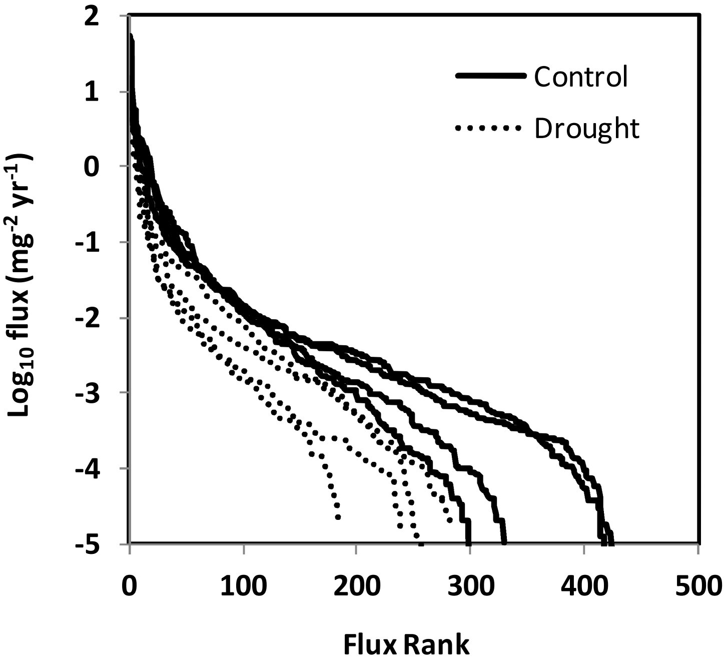
$$IE_q = \frac{\sum p_i \log_2(p_i)}{\log_2 N}$$

Where p_i is the proportional contribution of interaction i to the total number of interactions in the web (N).

Supplementary Figure 1. Quantitative food webs in replicate control (C1-C4) and drought (D1-D4) treatments (webs C1 and D1 shown in Fig. 1). For each web, lower bars are basal resources, middle bars are primary consumers and top bars are predators. For each consumer, the height and width of the bars is proportional to mean annual secondary production and biomass flux from resources (total inflows), respectively. For basal species, the relative width of bars on the x-axis is proportional to total consumption by invertebrates (total outflows from each resource to consumers), and for this trophic level production (y-axis) was not quantified. The black triangles that link trophic levels illustrate the relative contribution of resource flows to the production of each consumer, summing to the total inflows. Numbers refer to consumer identity and letters distinguish categories of basal resource, omitting rare species (<1% total production). Flows from individual algal taxa are grouped for display only. See Supplementary Tables 1 and 2 for full lists of resource and consumer taxa, respectively.



Supplementary Figure 2. Magnitude of biomass fluxes from resources to consumers for all control and drought-disturbed webs. For each treatment, fluxes were ranked from left to right in order of decreasing magnitude.



Supplementary Table 1. List of benthic algae in mesocosm food webs.

Group	Taxon
Bacillariophyceae	*Amphora inariensis* Krammer
	Amphora libyca Ehrenberg
	Amphora ovalis (Kützing) Kützing
	Amphora pediculus (Kützing) Grunow in Schmidt
	Cocconeis placentula Ehrenberg
	Cymatopleura solea (Brébisson & Godey) W. Smith
	Diatoma vulgare Bory
	Encyonema minutum (Hilse in Rabenhorst) Mann
	Fragilaria vaucheriae (Kützing) Petersen
	Gomphonema olivaceum (Hornemann) Brébisson
	Gyrosigma sp.
	Melosira varians Agardh
	Navicula capitata Ehrenberg
	Navicula gregaria Donkin
	Navicula lanceolata (Agardh) Ehrenberg
	Navicula menisculus Schumann
	Navicula tripunctata (O.F. Müller) Bory
	Nitzschia dissipata (Kützing) Grunow
	Nitzschia perminuta (Grunow) M. Peragallo
	Nitzschia sp. 1
	Placoneis clementis (Grunow) E.J. Cox
	Planothidium lanceolatum (Bréb. ex Kützing) Round & Bukhtiyarova
	Psammothidium lauenburgianum (Hustedt) Bukhtiyarova & Round
	Rhoicosphenia abbreviata (Agardh) Lange-Bertalot
	Staurosira elliptica (Schumann) Williams & Round
	Staurosirella leptostauron (Ehrenberg) Williams & Round
	Surirella brebissonii Krammer & Lange-Bertalot
	Surirella minuta Brébisson in Kützing
	Synedra ulna (Nitzsch) Ehrenberg
Chlorophyceae	*Gongrosira incrustans* Reinsch
Cyanophyceae	*Phormidium* sp. 1
	Phormidium sp. 2

Supplementary Table 2. List of macroinvertebrate taxa found in mesocosm food webs. Predatory taxa are highlighted in bold.

Group	Taxon
Oligochaeta	Naididae
	Tubificidae
Gastropoda	*Ancylus fluviatilis* (Müller)
	Potamopyrgus antipodarum (J.E. Gray)
	Radix balthica (L.)
	Theodoxus fluviatilis (L.)
	Valvata piscinalis (Müller)
Bivalvia	*Pisidium* sp.
Hirudinea	***Erpobdella octoculata (L.)***
Isopoda	*Asellus aquaticus* (L.)
Amphipoda	*Gammarus pulex* (L.)
Ephemeroptera	Baetidae
	Ephemera danica Müller
Plecoptera	*Leuctra geniculata* Stephens
Coleoptera	*Brychius elevatus* (Panzer)
	Elmis aenea (Müller)
	Haliplus lineatocollis (Marsham)
	Limnius volckmari (Panzer)
	Oulimnius tuberculatus (Müller)
	Platambus maculatus (L.)
Megaloptera	***Sialis lutaria*** **(L.)**
Trichoptera	*Athripsodes* spp.
	Brachycentrus subnubilus Curtis
	Hydropsyche spp.
	Limnephilus lunatus Curtis
	Polycentropus flavomaculatus **(Pictet)**
	Sericostoma personatum (Spence)
	Tinodes waeneri (L.)
Diptera	*Cricotopus* sp.
	Cryptochironomus sp.
	Heterotrissocladius sp.
	Macropelopia **sp.**
	Microtendipes sp.
	Pentaneura **sp.**
	Polypedilum sp.
	Procladius **sp.**
	Prodiamesa olivacea (Meigen)
	Synorthocladius sp.
	Simuliidae
	Tipula montium Egger

Supplementary Table 3. Qualitative (binary) food web metrics for drought and control stream food webs. Metrics were linkage density (L/S) where L is number of consumer-resource links and S is the number of species in the web, directed connectance (L/S^2), generality ($L/S_{\text{consumers}}$), vulnerability ($L/S_{\text{resources}}$). ANOVA tested for the effect of drought (below) and block (P >0.05, not shown).

	Control		Drought		ANOVA	
Metric	Mean	SE	Mean	SE	$F_{1,3}$	P
Linkage density	5.96	0.53	4.94	0.38	2.20	0.212
Directed connectance	0.09	0.01	0.10	0.01	0.17	0.706
Generality	11.68	1.11	12.84	0.55	1.42	0.390
Vulnerability	6.63	0.63	5.26	0.40	3.37	0.164

Supplementary references

31. Harris, R. M. L., Milner, A. M., Armitage, P. D. & Ledger, M. E. Replicability of physicochemistry and macroinvertebrate assemblages in stream mesocosms: implications for experimental research. *Freshwat. Biol.* **52**, 2434-2443 (2007).

32. Ledger, M. E., Harris, R. M. L., Armitage, P. D. & Milner, A. M. Realism of model ecosystems: an evaluation of physicochemistry and macroinvertebrate assemblages in artificial streams. *Hydrobiologia* **617**, 91-99 (2009).

33. Wood, P J., Bolton, A. J., Little, S. & Stubbington, R. Is the hyporheic zone a refugium for aquatic macroinvertebrates during severe low flow conditions? *Fundam. App. Limnol.* **176**, 377-390 (2012).

34. Dole-Olivier, M.-J. The hyporheic refuge hypothesis reconsidered: a review of hydrological aspects. *Mar. Freshwat. Res*. **62**, 1281-1302 (2011).

35. Trimmer, M., Maanoja, S., Hildrew, A. G., Pretty, J. L. & Grey, J. Potential carbon fixation by methane oxidation in well-oxygenated riverbed gravels. *Limnol. Oceanogr.* **55**, 560-568 (2010).

36. Hill A. R. & Lymburner D. J. Hyporheic zone chemistry an stream-subsurface exchange in two groundwater-fed streams. *Can. J. Fish. Aqu. Sci*. **55**, 495-506 (1998).

37. Lansdown, K., Trimmer, M., Heppell, C. M., Sgouridis, F., Ullah, S., Heathwaite, A. L., Binley A. & Zhang, H. Characteristic of the key pathways of dissimilatory nitrate reduction and their response to complex organic substrates in hyporheic sediments. *Limnol. Oceanogr*. **57**, 387-400 (2012).

38. Mullholland, P. J., Marzolf, E. R., Webster, J. R., Hart, D. R. & Hendricks, S. P. Evidence that hyporheic zones increase heterotrophic metabolism and phosphorus uptake in forest streams. *Limnol. Oceanogr.* **42**, 443-451 (1997).

39. Edwards, F. K., Lauridsen, R. B., Armand, L., Vincent, H. M. & Jones, J. I. The relationship between length, mass and preservation time for three species of freshwater leeches (Hirudinea). *Fundam. Appl. Limnol.* **173**, 321-327 (2009).

40. Harris, R. M. L. Ph.D. Thesis, University of Birmingham (2006).