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

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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 taxa and those that were rare for their size, many of which were predatory, being especially vulnerable. Many network properties, including size-scaling relationships within food chains, changed in response to drought. Other properties, such as connectance, were unaffected. These findings highlight the need for detailed experimental data from different organisational levels, from pairwise links to the entire food web. 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.

Introduction

Most empirical studies of climate change in multispecies systems have focused on community structure or ecosystem processes in space-for-time or temporal surveys (e.g. [1,2]), or laboratory experiments (e.g., [3]). Unfortunately, surveys, which are correlative, are often confounded (e.g., by long-term change in other stressors or biogeographical effects in space-for-time surveys) and unable to discern causal relationships. Laboratory experiments can identify mechanisms, but suffer from limited realism [4]. A compromise between realism and control is reached in larger-scale field experiments, several of which have recently demonstrated responses to simulated climate change [5-8].

There is growing evidence that larger organisms suffer disproportionately from climate change [4,9-11]; their reduced abundance or extinction has important implications for aquatic food webs, many of which are strongly size-structured [12-14]. For instance, changes in the mass and abundance of consumers and resources can trigger trophic cascades and secondary extinctions [4,11]. Quantifying allometric relationships between the abundance and body mass of interacting species therefore offers a potentially powerful means of gauging responses to perturbations and assessing how structural change might be linked to dynamical properties [15]. One way to quantify the size structure of trophic networks is via the construction of “trivariate food webs”, in which nodes are species populations plotted on log-log body mass-abundance (*MN*) axes and are connected via feeding links (e.g., [11, 13,14, 16-18]). Within this log-scale *MN* space, various allometric scaling relationships can be quantified at different organisational levels, from feeding links between species populations, to food chains and coarser-grained attributes of the whole food web [16, 17].

Two basic measures are used here, with other measures based on these; the measures help quantify trophic size structure [16]. The *length* of a trophic link between a consumer, C, and its resource, R, is the number of orders of magnitude of difference in body mass plus the number of orders of magnitude of difference in population density between R and C. The link *angle* relates to the “rate of change” in biomass, population productivity and population consumption from R to C. See Methods for precise definitions and interpretation. Tritrophic chains, which have been the focus of considerable research on indirect effects of consumer-resource interactions in food webs (e.g., trophic cascades), contain an intermediate species, I, between R and C. Derived measures include the *between-angle* in a tritrophic chain, which describes the change of angle in the upper link (I, C) relative to the lower link (R, I) [16, 17]. At the whole-network level, the web’s *allometric slope* is the scaling coefficient of log(N) regressed on log(M) for all the trophically connected species: a steepening of this slope may imply a weakening of top-down effects, as consumers become smaller and/or rarer relative to their resources. Data on links and angles at different levels of organisation within and across the food web can therefore be used to make inferences about the impacts of perturbations, especially where the size spectrum is not affected evenly.

Climate change effects on freshwater ecosystems include predictions that droughts will increase in frequency and intensity in the near future [19-21]. Even partial or temporary drying can threaten the local survival of many species, especially those that are large, rare and/or high in the food web [9,10,22-24]. It is also plausible, though not previously demonstrated, that species that are rare for their size could be especially vulnerable to local extinction, even if these species are not rare absolutely. Rarity-for-size should be evident from residuals from the food web’s general log(N)-versus-log(M) regression, which typically describes the average or expected abundance of a species (given its size) within a web [25]. Taxa could be rare for their size because environmental conditions are sub-optimal for them, and hence they could be particularly vulnerable to the imposition of any additional pressures. Currently, almost nothing is known about food web responses to drought, as the few studies conducted to date have been either correlational surveys or have not measured species-level interactions. There is great potential for drought to alter size-structure at multiple levels of food web organisation. We carried out the first long-term (i.e., intergenerational) replicated field experiment to assess the impact of drought on stream food web size structure.

Eight artificial stream channels were exposed to either intermittent drought (6-days of dewatering per month) or left as permanently flowing controls, to mimic the patchy drying of natural river beds during extreme low flows [22,23]. The experiment ran for two years, allowing intergenerational responses and indirect food web effects to be manifested. At the endpoint, eight replicate food webs were constructed (four per treatment). Earlier work in this system revealed that the control channels contained food webs of realistic complexity [26], and that biomass production of large, long-lived consumers was strongly reduced by drought, with some local extinctions, whereas some smaller short-lived consumers flourished [22,23]. Given that large consumers can impose strong top-down control on their prey, we anticipated significant drought impacts on food web size structure. We tested the following hypotheses: 1) drought causes losses of not only large taxa, but also those that were rare for their body mass; 2) drought steepens the allometric slope of the web, and reduces the area occupied by the community in log-log *MN* space (the “constraint space” *sensu* [27]) due, respectively, to relative increases in the abundances of smaller taxa and loss of rare-for-size species that deviated from the general *MN* scaling relationship; 3) drought causes the collapse of many tritrophic food chains into pairwise feeding links, due to loss of larger predators, with maximum trophic level and mean food chain link count declining accordingly; 4) loss of rare-for-size species homogenizes link angles and between-angles within the web, as link angles deviate most strongly from the angle of the general community log(*N*)-versus-log(*M*) regression slope for trophic links that include these species; 5) indirect effects (i.e., those beyond the direct effects of species loss *per se*), will be manifested.

Methods

The experiment was conducted over 24 months (March 2000 – February 2002) in four blocks of outdoor stream channel mesocosms at the Freshwater Biological Association River Laboratory, UK (50°40’48’’N, 2°11’06’’W) [31], which received water and suspended particles (including algae, detritus, and invertebrates) through a feeder pipe from an adjacent stream. Each channel (width 0.33 m, length 12 m, depth 0.30 m) was controlled by upstream input valves and drained under gravity via an outlet 10 cm above a downstream channel. Channels were filled with a 20 cm layer of stony substrate, providing physical refugia for suitably adapted species during drought [22,23]. Physicochemistry and biotic assemblages were similar among channels and to the source stream prior to drought [22,23,28-29].

Stream water was diverted into all channels in the initial two months. Thereafter, a drought treatment (intermittent flow; 6 d flow cessation per month) was applied to one channel per block, with the second channel in each block acting as a control. The drought treatment mimicked the repeated, patchy dewatering that occurs during severe supra-seasonal droughts [22]. Under drought, surface flows ceased and drying of exposed substrata occurred in patches over the six days, whereas wetted subsurface interstices and small pools persisted [22,23]. Flows were continuous in the control channels throughout the experiment.

At the end of the experiment we collected the entire invertebrate assemblage in each mesocosm and constructed food webs by direct observation of feeding links via analysis of dissected gut contents (of 4,305 individuals in total; five fields of view per individual at x 200 magnification). Gut contents were identified to genus or species where possible. Food webs were constructed independently for each replicate channel (after [26]). The body mass (mg) of each processed animal was calculated from body length (mm), measured to the nearest 0.1 mm, using length-mass regressions (see [22] and references therein),

Macroinvertebrate abundances, N, were determined from Surber samples (0.025m^{-2}) collected from each replicate mesocosm at the end of the experiment. Animals from these samples (n= 3049) were identified to the lowest practicable taxonomic unit (usually species or genus), counted, and measured. Abundance and individual body mass were similarly derived for algal resources [309].

Logistic regressions were used to ascertain whether absolute rarity and rarity-for-size were important determinants of extinction risk of species from the food webs. Here, two predictors were computed per species in the control replicate of each block: 1) log(M) itself, accounting for larger species having higher extinction risk; 2) the residual from the log(N)-versus-log(M) regression of the replicate. Base-10 logarithms were used throughout. The first predictor represents rarity because size and rarity are very strongly correlated in our webs and many others. The second predictor is rarity-for-size: species which are rare for their size will have substantially negative residuals. This gave two numbers for each species in each replicate per block. If the same species was present in the control replicates of two blocks, separate numbers were derived. The response variable was whether or not a species went extinct (True, False) in the paired drought treatment replicates. Logistic regression was performed using two models, one with predictor log(M) only and one with both log(M) and residuals as predictors, to see whether rarity-for-size provided any additional explanatory power for loss from the food web. Logistic regression is a standard technique whereby the transformed risk of an event occurring is written as a linear function of predictor variables. Since absolute rarity is often highly correlated with size and rarity-for-size is independent of size for webs with homoskedastic log(N)-versus-log(M) regressions (i.e., most webs [25], including ours), the latter measure is a new possible determinant of extinction risk.

MN trivariate webs were produced for each replicate channel by overlaying links between consumers and resources on the log(N)-versus-log(M) scatterplot of taxa; several community metrics were defined from this plot [after 16]. The community-wide *allometric slope* is the slope of the log(N)-versus-log(M) ordinary linear regression through all taxa connected to the web by a trophic link. When expressed as an angle between -90° and 90°, measured anticlockwise from the positive horizontal axis, this is the *allometric angle*; for instance, slope -1 corresponds to angle -45°. The *community span* is the range of log(M), from the smallest to the largest taxa, plus the range of log(N), from the rarest to the most abundant taxa, over all connected taxa. We also derived the area of the minimum convex hull (a polygon) in *MN* space that bounded all the connected species within each web [after 27].

The *link length* between a consumer (C) and its resource (R) was defined as $|\log(M_C) - \log(M_R)| + |\log(N_C) - \log(N_R)|$ [16]: *i.e.*, the l_1-distance or Manhattan distance from mathematics. The first term summand is the absolute log body mass ratio, i.e., the number of orders of magnitude of difference in body mass between R and C. The second summand is the absolute log density ratio, i.e., the number of orders of magnitude of difference in population density. When plotting a link as a vector from R to C, its *length* is the distance from R to C (l_1 distance). Its *angle* is the anticlockwise turn to the link from a horizontal arrow parallel to the horizontal (log(M)) axis, starting from R and pointing right (between -180° and 180°, where -180° is allowed but 180° is not). If the link angle equals -45°, then its slope equals -1 and resource biomass $B_R = M_R N_R$ equals consumer biomass $B_C = M_C N_C$ [16].

We also calculated several higher-level measures of network size structure. A *2-chain* is a tritrophic interaction consisting of three taxa (R, intermediate taxon I, and C) and two links [16]. On *MN* plots, the upper link lies below and to the right of the lower link if body mass increases and abundance declines moving up the chain, as in many chains. The *2-span* is the l_1 distance from R to C (Fig. S1). Within each chain L_{lower} and A_{lower} describe the length and angle of the lower link (from R to I); L_{upper} and A_{upper} describe the length and angle of the upper link (from I to C). The *between-angle* of a 2-chain is the angle, between -180° and 180° (including -180° but not 180°), from the vector of the lower link (R, I) to that of the upper link (I, C). Positive angles are anticlockwise rotations (e.g., if the lower link is -50° and the upper link -35°, then the between-angle is +15°). A positive between-angle means that biomass, population productivity and population consumption increase faster in the upper link (from I to C) than in the lower link (from R to I): this may imply increased transfer efficiency moving up the chain, as might arise when comparing a carnivorous upper link with a herbivorous lower link, for instance. It could also imply greater potential for top-down cascades, as the top consumer is larger and/or more abundant than would be expected from simple extrapolation from the lower link. The distribution of between-angles thus describes how log body mass ratios and log population density ratios vary among the tritrophic chains within a food web.

Maximal food chains ("chains" henceforth) from a basal to a top taxon were counted as any chain passing from resource to consumer at each link, but not including the same taxon twice (cannibalistic links were excluded and cycles were not traversed completely). The *chain span* is the l_1 distance between a chain's top and basal taxa. Food chain link count is the average number of links contained within all the chains in the web. Several more familiar whole-network parameters were also calculated, namely: web size (S, the number of nodes), number of feeding links (L) and directed connectance ($C = L/S^2$).

Two additional scenarios were also considered: 1) extinct species in the drought treatment were excluded from controls; and 2) the "core community" alone was considered, i.e., only species that were common to each pair of drought and control webs were considered. This was to gauge potential emergent or indirect effects beyond those due directly to species loss or gain. Between-treatment differences in food web parameters were tested using paired *t*-tests, with blocks providing the pairings. Computations were performed in *R* [31].

Results

As predicted (hypothesis 1), body mass influenced vulnerability to drought, with a second-order effect of rarity-for-size (Figure 1). The coefficient (-0.22) for log(*M*) in our logistic regressions demonstrates that larger species were more likely to be lost. The positive coefficient (0.794) for residuals shows that species that were rare for their size were additionally vulnerable (P <0.0001; Table S1).

Several of the fine-grained measures revealed marked changes within the food web, whereas other measures, including some commonly used ones (e.g., connectance), were unaffected (Table 1). Drought significantly reduced the numbers of species and links. In agreement with predictions (hypothesis 2), allometric slopes steepened slightly but significantly from -0.50 to -0.52, reflecting reductions in large, rare taxa and increases in some of the smaller taxa: these patterns were also evident in the two additional scenarios that accounted for species loss or gain in the drought treatment (Table S1). Convex hull area decreased, but not in either of the additional scenarios. Hypothesis 3 was also supported: as species were lost and/or had their links stripped away, the maximum trophic level of the web decreased as the number of links from the base to the highest predator declined. The proportion of intermediate nodes declined, basal nodes increased, and top level nodes remained the same (Table S2): intermediate nodes were “lost” either via extinction or by promotion to the termini of chains (Figure 2). Consequently, the total number of tritrophic food chains declined, with many collapsing into simple pairwise links, even though mean food chain link count did not decline significantly (Table 1). Hypothesis 4 was supported:

due to the loss of rare-for-size species, link angles and between-angles were more tightly constrained in the drought treatments than in the controls (Figures 3 and 4). Between-angles also became more negative in the drought treatment due to declines in both body mass and abundance of top predators in tritrophic chains.

Although there were some significant differences between treatments in link lengths and angles, allometric slope, and species richness, the other parameters were unaffected by drought in the two additional scenarios for detecting indirect effects (Table S1). Thus indirect effects were generally modest when compared with the direct effects of species change, and the "core community" remained relatively intact: hypothesis 5 was therefore not supported for most measures. Overall, drought tended to simplify and homogenise network size structure, primarily via the direct effects of the loss of larger, rarer (and predominantly, but not always, predatory) species, with only modest indirect effects.

Discussion

This is the first replicated study of the impact of a component of climate change on food web size structure in a long-term field experiment. We found clear evidence that drought triggered the widespread loss of species and links and the homogenisation of aspects of size structure. Because larger species and those that were rare for their size were lost, perturbed webs were bounded within a smaller constraint space and fitted more tightly to *MN* scaling relationships than did controls, causing changes in the finer-grained network properties (e.g., among the webs' pairwise links, tritrophic interactions and food chains). Drought caused a "winnowing of the web" (*cf* [32]), as nodes (and links) were stripped out to leave a skeleton outline within the same community span and only slightly steeper overall *MN* slope (reflecting the relative increase in some of the smaller taxa). The thinning effect explains reductions in community biomass and secondary production reported previously [22]. Other web properties (e.g., connectance) were apparently too coarse-grained to respond to drought. The “core food web” containing species common to both treatments also did not respond strongly to drought for most parameters (Table S1), revealing that drought did not have marked emergent effects beyond the direct impacts of species loss within the two-year time frame of the study. There was no compelling evidence of widespread cascading effects or secondary extinctions, which might be expected if the system were under strong top-down control, although more subtle indirect effects of drought were still evident on the slopes of the core webs and their respective pairwise links.

Large size and absolute rarity are both often associated with increased extinction risk and are usually associated with each other [9,10]. We also found evidence of a second-order but important rarity-for-size effect that was distinct from overall rarity effects. Ecological drift is unlikely to be driving this, as rare species were common in the source stream and recolonised disturbed patches recurrently over the 2-year experiment (Ledger *et al* 2012): *i.e.*, rather than being opportunistic visitors they were permanent residents that were numerically rare, but frequently occurring in the system. Species below the general *MN*-scaling line were especially vulnerable, being already rarer in the controls than expected based on their size. Such species may already be in sub-optimal conditions (hence their relative rarity) and the imposition of additional stress on the system might be sufficient to push them to extinction. Rarity-for-size might therefore help to identify especially vulnerable taxa, without necessarily requiring detailed *a priori* knowledge of trophic position or environmental tolerances.   This could be useful for assessing impacts of stressors in ecological networks in general, and warrants further exploration in systems exposed to perturbations for which *M* and *N* data exist (e.g., [13, 14]).

The larger consumers that were lost were also predominantly aquatic throughout their life-cycle, whereas the surviving large insect species possessed a terrestrial adult phase, enabling them to (re)colonise denuded patches. Many of the smaller taxa survived the drought, most likely in patches of wetted refugia, and some even flourished (e.g. certain midge larvae and small oligochaete worms) suggestive of release from competition and/or predation from the larger taxa [22]. This might also indicate at least some indirect food web effects are modulated by drought, via apparent competition for enemy-free space, as revealed by the modest but significant steepening in the allometric slope of the web, even in the scenarios where we accounted for species loss or gain.

Identifying which food web parameters are most sensitive to perturbations is key to assessing the impacts of environmental change in natural systems: focussing on the more commonly used properties (e.g., connectance), would have missed important and often subtle structural changes. The next move towards understanding climate change impacts will necessitate modelling the dynamical consequences of structural change, if we are ultimately to predict impacts on food web stability [4, 33]. One important pattern emerging from recent research is that large, rare organisms high in the food web suffer disproportionately from environmental warming [9], seemingly due to metabolic constraints [6]. Since drought had similar impacts, these two components of climate change [19-21] could combine to produce lethal synergies in freshwater food webs in the coming decades [4].

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Figure Legends

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

Figure 2. Food webs from the manipulative field experiment, in which eight replicate stream channels were exposed to monthly intermittent drought [d] or permanent flow [c]. The webs are ordered vertically by trophic level, from basal resources to apex predators. Numbers correspond to species identifiers (see Fig. 1 for symbols legend; Suppl. Mat. for codes and taxonomic identities).

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

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

Table 1. Mean ±SE community structure measures for the control (c1-c4) and drought (d1-d4) treatments for connected species within the food web. See Methods for details. Paired *t*-tests were performed to test for significance of mean differences (*d*) from zero. Results for additional scenarios testing for indirect effects (see Methods) are given in Table S1.

	Control webs	Drought webs	*d*	*t*	*P*
Pairwise links, tritrophic interactions and food chains					
Median link *angle*	-27.17±0.24	-27.59±0.24	0.42	3.52	0.039
Mean link length	18.23±0.18	18.62±0.11	-0.40	-2.11	0.125
Median A_{lower}	-26.67±0.40	-25.76±1.02	-0.91	-1.04	0.375
Median A_{upper}	-31.80±1.09	-142.30±9.67	110.5	10.46	0.002
Log_{10} number of tritrophic chains	2.05±0.20	1.29±0.01	0.77	4.05	0.027
Median A_{between}	-8.99±3.93	-116.53±9.78	107.5	13.40	0.001
Mean 2-span	19.2±0.19	18.05±0.11	1.11	6.21	0.008
Mean chain span	19.4±0.17	18.7±0.10	0.69	6.06	0.009
Mean food chain link count	1.49±0.17	1.09±0.01	0.39	2.32	0.103

Trophic level of apex predator (chain length)	2.53±0.05	2.16±0.04	0.37	7.64	0.005
Community scaling and whole-network properties					
Allometric slope	-0.50±0.006	-0.52± 0.002	0.017	3.71	0.034
Community span	28.1±0.17	27.7±0.08	0.33	1.94	0.148
Constraint space area (*MN* convex hull area)	60.23±2.45	43.09±1.86	17.14	4.76	0.018
S, the number of connected food web nodes	60±1.3	46.5±1.3	13.5	11.34	0.001
$\log_{10} L$, number of links	2.48±0.05	2.31±0.04	0.17	3.20	0.050
C, directed connectance	0.08±0.008	0.09±0.008	-0.01	-0.87	0.448