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Drought rewires the cores of food webs

Xueke Lu[1§], Clare Gray[2,3§], Lee E. Brown[4], Mark E. Ledger[5], Alexander M. Milner[5], Raúl J. Mondragón[1], Guy Woodward[3] and Athen Ma[1*]

[1]Queen Mary University of London, School of Electronic Engineering and Computer Science, Mile End Road, London E1 4NS, UK [2]Queen Mary University of London, School of Biological and Chemical Science, Mile End Road, London E1 4NS, UK [3]Department of Life Sciences, Imperial College London, Silwood Park, Buckhurst Road, Ascot, Berkshire, SL5 7PY, UK [4]water@leeds and School of Geography, University of Leeds, Woodhouse Lane, Leeds, LS2 9JT, UK [5]School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK

* email: athen.ma@qmul.ac.uk (Corresponding author)

[§] These authors contributed equally to this work

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Droughts are intensifying across the globe[1,2], with potentially devastating implications for freshwater ecosystems[3,4]. We used novel network science approaches to investigate drought impacts on stream food webs and explored potential consequences for web robustness to future perturbations. The substructure of the webs was characterised by a core of richly-connected species[5] surrounded by poorly-connected peripheral species. Although drought caused the partial collapse of the food webs[6], the loss of the most extinction-prone peripheral species triggered a substantial rewiring of interactions within the networks' cores. These shifts in species interactions in the core conserved the underlying core/periphery substructure and stability of the drought-impacted webs. When we subsequently perturbed the webs by simulating species loss *in silico*, the rewired drought webs were as robust as the larger, undisturbed webs. Our research unearths previously unknown compensatory dynamics arising from within the core that could underpin food web stability in the face of environmental perturbations.

Many areas of the world are becoming increasingly prone to drought[1,2] and declining precipitation coupled with rising demand for water could threaten the integrity of freshwater ecosystems across the globe[3,4]. In rivers and streams, the elimination of sensitive species could potentially undermine community structure and ecosystem functioning[7–9], yet how this affects food web stability - at both substructural and whole-network levels[10] - has yet to be fully elucidated. Responses to climate change are frequently interpreted autecologically, through analysis of individual species traits[11], but these ignore the role of species interactions, foraging dynamics and potential compensatory mechanisms such as resource switching, that determine food web stability. Synecological approaches that can address changing species interactions in the context of the whole food web[12–14], and hence the potential trophic mechanisms behind community-level responses[15,16], remain scarce. In addition, there are non-random substructures in food webs which could underpin their responses to perturbations[17]. Recent advances in network science have linked the presence of a cohesive "core" of closely interacting nodes and a loosely connected "periphery"[5,18–20] to the stability of complex (non-ecological) networks[21,22]. The significance of this for food web responses to an environmental perturbation - drought - is reported here for the first time.

The network "core" is a cohesive group of highly connected nodes that governs the functional attributes of a wide range of complex systems[18]. It determines system robustness because densely intertwined pathways within the substructure can provide redundancy by buffering external fluctuations[18,19] without altering overall functioning[23]; such structures are absent in less robust, regular small-world networks[24]. Core size relative to the rest of the web indicates a network's state[20–22]: large cores provide greater scope for redundancy of links and rewiring in the event of node and link failure, whilst small cores indicate vulnerability and systems being under stress.

Here, we quantify experimentally how drought disturbance influences stream food web substructure and model how this then determines robustness to future perturbations. We analysed food webs from a stream mesocosm field experiment in which benthic communities subjected to a drought treatment for two years were compared with undisturbed controls (four replicates; eight food webs in total; see Methods). Food webs were constructed from gut contents analysis of all 3,643 individuals collected at the end of the experiment. These exceptionally well-resolved webs encompassed 783 pairwise trophic interactions among 74 trophic elements, consisting of detrital resources, primary producers and a taxonomically diverse array of invertebrate consumers (Supplementary Table S1). Local extinctions from ecological networks can trigger rippling effects due to the direct and indirect interdependency of consumers and resources; as a result, community fragility to disturbance can be influenced by structural properties, such as how trophic links are distributed among species[15,16]. We hypothesised that our experimental food webs were governed by a core/periphery structure, as detected recently in a range of non-ecological networks[5,19,20]. Highly connected core species are functionally important because they provide alternative routes for the flux of matter, and could therefore buffer the effects of perturbations and enhance network stability. Peripheral species are less integral in a topological sense, and changes in the food web composition and configuration are more likely to lead to their isolation (i.e. extinction), as has been observed recently in mutualistic networks[25]. Specialist consumers from the web periphery are especially vulnerable to extinction because they are more loosely connected and dependent on fewer resource species. Redundancy among the links within the core could, in theory, provide a means of withstanding the effect of species loss and rebalancing the structure of food webs, thereby conserving overall robustness.

To test our hypotheses, we applied a novel graph profiling technique[5] to characterise the cores of our eight highly-resolved replicate food webs[10,26]. To generate a graph profile for a web, nodes were ranked by their degree (number of links). Starting from the highest degree node, we examined the interconnectedness among the high degree nodes as those of a lower rank were included sequentially. A point is reached whereby the connectivity among the high degree nodes peaks, reflecting the cohesiveness in the core and defining the core boundary, and which is followed by generally decreasing connectedness thereafter. The rest of the nodes form the periphery, which is only loosely connected to the core, and contains few or no links among its constituents. After characterising the core/periphery structure, we then measured the density of interactions within the core and across the web using the "rich-club" coefficient[27]. To gauge the level of organisation in the core/periphery structure between the drought and control treatments, we employed an ensemble of null networks, whereby links were reshuffled randomly while conserving network properties[28]. Graph profiles obtained from the null models represent network structures that would simply happen by chance, and they were used to benchmark the link patterns of the empirical webs. The further an empirical web deviates from its null models (i.e. a z-score greater or less than 0), the more significant, in statistical terms, are its link patterns, which also indicates the level of organisation that has taken place to generate the observed pattern. To examine the effectiveness of the compensatory mechanism provided by the core, we studied network robustness by measuring the rate at which the structural integrity of food webs collapsed[29] under two commonly simulated species removal scenarios: i) random removal and ii) targeted removal of core species (i.e. high degree species).

All eight food webs exhibited a clear core/periphery structure (Fig. 1), as revealed by a distinct peak in their core profiles and a step-change in interconnectedness from high to low-degree species (indicated by a vertical line in Fig. 1, at which the number of links k_r^+ is at its maximum, and after which it decreases steadily). The food web cores contained species from all trophic levels (Fig. 1; Supplementary Table S1) and accounted for (on average) 50% of the species. The proportion of core species was unchanged by drought (t-test, *d.f.=3, p=0.16*; Table 1), despite absolute species losses of 25%. Core size was large relative to non-ecological networks (5-30% of total network size[5,19]), suggesting that natural systems may possess far greater linkage redundancy. Species extinctions were greatest in the periphery (t-test, *d.f.=3, p=0.01;* Table 1), and as expected, species that fell into this category were mainly invertebrate consumers high in the food chain (Supplementary Table S3) which lost all their resources. Drought caused more species in the core to migrate into the periphery of the web via a reshuffling of interactions, than *vice versa* (t-test, *d.f.=3, p=0.01*, Table 1 and Fig. 2). Despite this drought-induced realignment of species, the preservation of the core/periphery structure (Fig. 2) and its relative size is suggestive of underlying inertia within the webs' substructure.

Drought reduced the density of connections within the core (Fig. 3a), as shown by lower rich-club coefficients, ϕ_r. This phenomenon in non-ecological networks is a common response to stress[21,22], and in our case was a result of compensatory re-wiring as core species moved into the periphery: the density of connections in the latter was unaffected by drought, despite peripheral species loss. These changes in network structure reflect consumer-specific shifts in diet potentially resulting from physiological stress, changes in the abundance and distribution of resources and/or modified foraging in the drought-disturbed habitat (see Supplementary Fig. S4 for an example). All webs showed a marked deviation in connectivity from their respective null models within their cores, revealing a systematic, non-random substructure - the first time such a phenomenon has been detected in a manipulative field experiment (Fig. 3b). Drought resulted in a greater decrease in the z-score within the core: link density inside was significantly lower than what would be expected by chance, suggesting even more intense (re)organisation had taken place in response to the drought. This pronounced change in the core supports our hypothesis about its governing role in the re-structuring of food webs under this stressor.

Food webs were robust to simulated random species removal, and this was unaffected by drought (Supplementary Fig. S5): the amount of primary extinction required for 50% species loss was comparable in both treatments (t-test, *d.f.=3, p=0.89;* Table 1). This can be explained by the conservation of the overall core/periphery structure and relative core size. Peripheral species loss would have affected the stability of the drought webs, but the observed movement of species from the core to the periphery rebalanced network structure, thereby conserving robustness to perturbations *in silico*. When the highly connected species were removed first, drought webs were just as robust to species removal as were the control webs (t-test, *d.f.=3, p=0.17;* Table 1). This suggests that although the density of connections within the core was altered by drought, overall network integrity and ability to withstand further perturbations was conserved by species re-alignment. It is conceivable that a threshold core connectance may exist, beyond which this redundancy is lost and the associated food web collapses, echoing ideas suggested by Dunne *et al.*[29] and Krause *et al.*[30]. Identifying this threshold would allow us to better predict which communities are most at risk from environmental change.

Our results demonstrate that drought disturbance triggered previously unknown substructural changes within real food webs, beyond the direct and obvious species losses that have been reported elsewhere when based on fixed autecological traits[6,10]. While the underlying core/periphery structure was robust to perturbations, the composition and configuration of the food web substructures changed markedly, with a steep reduction in interactions among the remaining core species. The ability to predict which networks of species interactions are most vulnerable to anthropogenic pressures, and the identification of a core of species vital to the functioning and persistence of a community within an ecosystem, would greatly enhance our ability to direct conservation efforts more effectively in the face of environmental perturbations[15,16]. Traditional whole-network metrics, such as connectance, were far less sensitive[6] than the novel measures applied in this study, and therefore offer less potential for gauging changes in food webs exposed to perturbations. Substructural approaches that capture the plastic synecological traits defined by species interactions could help to unearth compensatory shifts within ecological networks, and provide us with a major new way to detect and understand the effects of environmental change on ecological communities.

Additional information

Correspondence and requests for materials should be addressed to A.M. Requests for data should be addressed to M.E.L.

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Author contributions

M.E.L. and A.M.M. conducted the mesocosm experiments, M.E.L., L.E.B., A.M.M. and G.W. generated the food web dataset, R.J.M. and A.M. designed the network analyses, X.L. implemented the network research, X.L. and C.G. analysed the results, and C.G., M.E.L. and A.M. wrote the manuscript with input from all authors. All authors discussed the results and reviewed the final manuscript.

Competing financial interests

The authors declare no competing financial interests.

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Figure Legends

Figure 1 Core/periphery structure of control and drought food webs. Comparisons of one pair of control and drought core profiles (all webs shown in Supplementary Fig. S1). Nodes are ranked by their decreasing order of degree and plotted by the number of links with nodes of a higher rank, k_r^+. The control web is plotted alongside its respective drought web. Species were classified as *Basal* (circles), *Intermediate* (squares) or *Top* (triangles). The maximum of the curve k_{r*}^+, defines the boundary of the core for the control and drought webs.

Figure 2 Drought caused species re-alignment in substructures. Comparisons of one pair of control (**a**) and drought (**b**) food web structures (all web pairs shown in Supplementary Fig. S2). Core species in the inner ring are surrounded by peripheral species in the outer ring. In this web pair, drought caused 15 species to go extinct (filled diamonds) and 11 core species to shift to the periphery (light circles).

Figure 3 Drought reduced link density and caused further restructuring in the core. (**a**) The density of connections across the network measured by the rich-club coefficient, ϕ_r, is shown for one pair of control and drought-disturbed mesocosms (all web pairs shown in Supplementary Fig. S3). Nodes were ordered by their degree which were then *normalised* by the size of the network. Boundaries of the cores are marked by vertical lines as in Fig. 1. (**b**) Comparisons of the web pair's deviance in connection density from their respective null models and more negative *z*-scores indicate greater deviance from the null model.

Table 1 Statistics from two independent samples t-tests. The effects of drought on the relative core (Supplementary Table S2) and robustness (Supplementary Table S4) were tested using one-tailed t-test on arcsine transformed data. Two-tailed t-test on arcsine transformed data was applied to examine if peripheral species are more susceptible to extinction and if more core species realigned after drought (Supplementary Table S2). Significant effect/difference are indicated in bold (Further details described in Supplementary Table S5).

	Drought			**Drought impacted substructures**	
	d.f.	*p*		*d.f.*	*p*
Relative core size	3	0.16	More extinction from periphery	3	**0.01**
Robustness (random)	3	0.89	More species realigned from core	3	**0.01**
Robustness (targeted)	3	0.17			

METHODS

Experimental design. Details of the experimental design and methods used to build the food webs are published elsewhere[10,31]. In brief, the experiment ran for two years (March 2000-February 2002) in outdoor stream mesocosms that consisted of four pairs of channels subjected to either control or drought conditions. All channels were subject to two months of constant flow before a drought treatment (6 days of dewatering per month) was applied to one channel per pair. During the simulated drying periods, surface flows ceased and drying of exposed substrata occurred in patches, whereas the interstices beneath the bed surface remained wet, and small pools persisted at intervals along the length of the dewatered channels[32]. 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[33]. This experimental design simulated periodic drying events occurring during a supra-seasonal drought. Stream drying events have occurred during major droughts in Europe[34] and are expected to increase in frequency with climate change[35]. As with all mesocosm experiments, our design necessitated some trade-off between realism and replication[26,36]. Nevertheless, the simulated flows were consistent with multiyear droughts in Europe which occur in both summer and winter, and which are characterised by a fragmentary incidence of streamflow deficits through the year[34]. Our experiment may adequately capture the expected changes in the magnitude and frequency of drying in rivers under climate change but does not necessarily reflect the expected changes in seasonality of these events. At the end of the experiment all invertebrates were collected and identified prior to gut content analysis. All individuals and their gut contents were identified to genus or species level, where possible. The resultant eight food webs are among the most highly resolved to date, comprising 783 pairwise trophic interactions and 74 trophic elements in the aggregate web. Comparison of the control channel food webs to data collected for 82 ‘natural’ river food webs showed the mesocosm channels contained realistic webs, with consistent and similar size structures suggesting that patterns of energy flux between mesocosm consumers and resources were good analogues of those in natural systems[37]. Species were categorised into three trophic levels: Basal (B), Intermediate (I) and Top (T). A basal species was defined as a species with no prey; a top-level species was referred to as a species with no predators; and the rest were defined as intermediate species.

Food web profiling. The core profiling method identifies a substructure of highly interconnected species by ordering species with respect to the number of connections to other species and the extent to which those connections link to more highly connected species in the web[5]. Highly interconnected species constitute the web core, with less-connected nodes forming the periphery. Each food web was represented as a binary and undirected network with S nodes (species) and E links (the interactions between species). To obtain a core profile, nodes were ordered in descending order of their degree (i.e. number of links) and a node with a rank r has degree k_r. The number of links that a node shares with nodes of a higher rank is k_r^+ and the number of links with nodes of a lower rank is therefore $k_r - k_r^+$. Starting with the node with the highest rank, the value of k_r^+ fluctuates as nodes from further down the rank are being included. There will be a point r^* where k_r^+ reaches its maximum and will always be less than k_{r*}^+ thereafter, marking the boundary of the core. To quantify the density of links inside the core, the rich-club coefficient[27] was calculated, which is defined as:

$$\phi_r = \frac{2}{r(r-1)} \sum_{i=1}^{r} k_i^+ = \frac{2E_r}{r(r-1)}$$

where E_r is the number of links shared by the highest ranked r nodes and $r(r-1)/2$ is the maximum number of possible links among these nodes. The connectivity of a core is given by ϕ_{r*} whereby a fully connected core has a value of ϕ_{r*}= 1 and a fully disconnected core gives ϕ_{r*}= 0. Given that drought webs contain fewer species than their control counterparts, results could have been skewed by their reduced web size if their absolute values were used: to overcome this the species rank was normalised by the overall web size.

Null model. A statistical null model was used to determine the probability of the connectivity observed in the empirical data. For each empirical food web, we applied a randomisation method[28] to generate an ensemble of 100 networks by randomly reshuffling the links while conserving the properties of the empirical network, including the number of nodes, the number of links and the degree distribution. This allows us to assess the statistical significance of the patterns of interactions observed in the empirical webs with respect to patterns that would simply occur by chance. To quantify how the link density in the core differs from the random networks, we first referred the rich-club coefficient of the empirical food web and compared that to its null counterpart by calculating the *z*-score. A *z*-score of 0 means that the empirical data exhibits an organisation of links that is the same as what you would expect from a random case; a value > 0 means that the empirical has a higher than expected density of links, and vice-versa. This effectively describes the degree of organisation of species interactions in the sense that the more improbable a configuration of links is, the more organisation is required to be in place to attain the observed pattern. Again, the rank of species was normalised to compensate for the effect of different web sizes when comparing the control and drought food web pairs.

Network robustness. To assess this, we simulated primary species loss in all the food webs by manually removing species[29]. Firstly, species were chosen randomly and removed from the food web, together with all their associated links, in an iterative manner. We recorded the total species at each step, which accounts for both primary loss and secondary extinction (as a result of species isolation from resource). Robustness was quantified by the amount of primary extinction required for a total loss of 50% of the species. We repeated this for 100 times for each web and results were averaged. Secondly, species were removed in the descending order of degree which is often considered as the worst case scenario as the most important (connected) nodes are being targeted. Similarly, species were removed in an iterative manner, but the degree order of nodes was re-calculated after each species removal as removing a node and its links may impact on the degree order among the rest of the nodes. Again, robustness was evaluated by the total primary extinction required for a cumulative 50% species loss.

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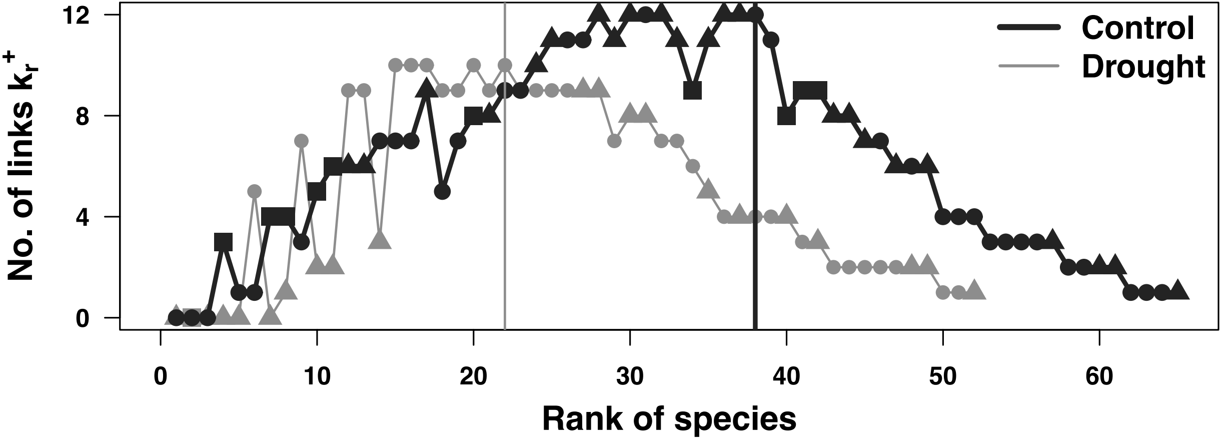
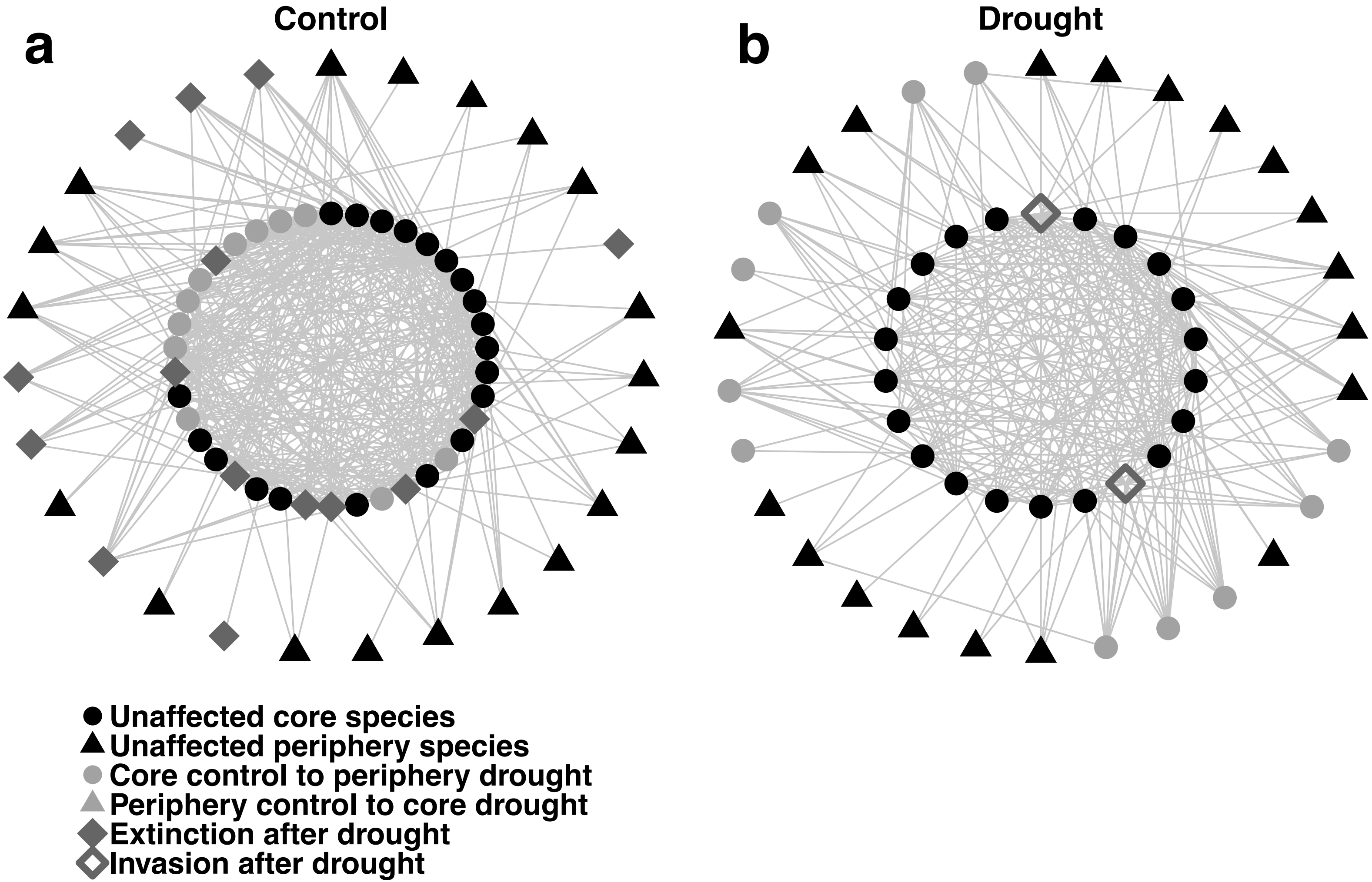
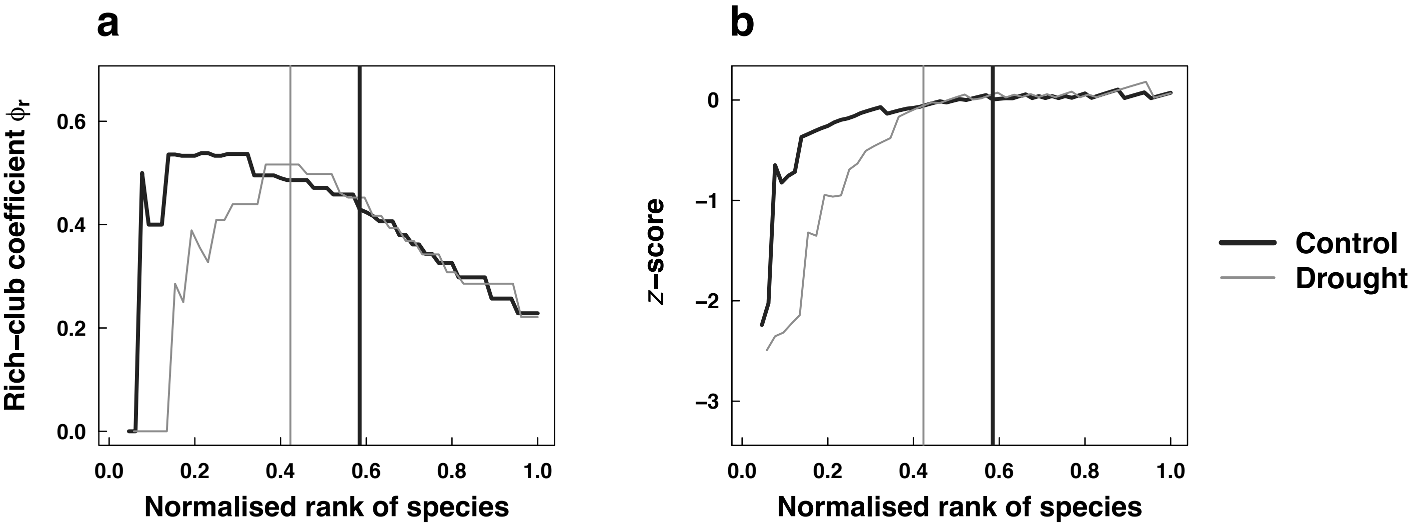

No. of links k_r^+
12
8
4
0
0
10
20
30
40
50
60
Rank of species
Control
Drought


Control
a
Drought
b
● Unaffected core species
▲ Unaffected periphery species
● Core control to periphery drought
▲ Periphery control to core drought
◆ Extinction after drought
◇ Invasion after drought


a
b
Rich–club coefficient ϕ_r
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
Normalised rank of species
z–score
0
−1
−2
−3
0.0
0.2
0.4
0.6
0.8
1.0
Normalised rank of species
Control
Drought