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1 Drought rewires the cores of food webs

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12

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14

15 **Droughts are intensifying across the globe^{1,2}, with potentially devastating implications for**
16 **freshwater ecosystems^{3,4}. We used novel network science approaches to investigate drought impacts**
17 **on stream food webs and explored potential consequences for web robustness to future**
18 **perturbations. The substructure of the webs was characterised by a core of richly-connected species⁵**
19 **surrounded by poorly-connected peripheral species. Although drought caused the partial collapse of**
20 **the food webs⁶, the loss of the most extinction-prone peripheral species triggered a substantial**
21 **rewiring of interactions within the networks' cores. These shifts in species interactions in the core**
22 **conserved the underlying core/periphery substructure and stability of the drought-impacted webs.**
23 **When we subsequently perturbed the webs by simulating species loss *in silico*, the rewired drought**
24 **webs were as robust as the larger, undisturbed webs. Our research unearths previously unknown**
25 **compensatory dynamics arising from within the core that could underpin food web stability in the**
26 **face of environmental perturbations.**

27 Many areas of the world are becoming increasingly prone to drought^{1,2} and declining precipitation
28 coupled with rising demand for water could threaten the integrity of freshwater ecosystems across the
29 globe^{3,4}. In rivers and streams, the elimination of sensitive species could potentially undermine community
30 structure and ecosystem functioning⁷⁻⁹, yet how this affects food web stability - at both substructural and
31 whole-network levels¹⁰ - has yet to be fully elucidated. Responses to climate change are frequently
32 interpreted autecologically, through analysis of individual species traits¹¹, but these ignore the role of
33 species interactions, foraging dynamics and potential compensatory mechanisms such as resource
34 switching, that determine food web stability. Synecological approaches that can address changing species
35 interactions in the context of the whole food web¹²⁻¹⁴, and hence the potential trophic mechanisms behind
36 community-level responses^{15,16}, remain scarce. In addition, there are non-random substructures in food
37 webs which could underpin their responses to perturbations¹⁷. Recent advances in network science have
38 linked the presence of a cohesive “core” of closely interacting nodes and a loosely connected
39 “periphery”^{5,18-20} to the stability of complex (non-ecological) networks^{21,22}. The significance of this for
40 food web responses to an environmental perturbation - drought - is reported here for the first time.

41 The network “core” is a cohesive group of highly connected nodes that governs the functional
42 attributes of a wide range of complex systems¹⁸. It determines system robustness because densely

43 intertwined pathways within the substructure can provide redundancy by buffering external
44 fluctuations^{18,19} without altering overall functioning²³; such structures are absent in less robust, regular
45 small-world networks²⁴. Core size relative to the rest of the web indicates a network's state²⁰⁻²²: large cores
46 provide greater scope for redundancy of links and rewiring in the event of node and link failure, whilst
47 small cores indicate vulnerability and systems being under stress.

48 Here, we quantify experimentally how drought disturbance influences stream food web substructure
49 and model how this then determines robustness to future perturbations. We analysed food webs from a
50 stream mesocosm field experiment in which benthic communities subjected to a drought treatment for two
51 years were compared with undisturbed controls (four replicates; eight food webs in total; see Methods).
52 Food webs were constructed from gut contents analysis of all 3,643 individuals collected at the end of the
53 experiment. These exceptionally well-resolved webs encompassed 783 pairwise trophic interactions
54 among 74 trophic elements, consisting of detrital resources, primary producers and a taxonomically
55 diverse array of invertebrate consumers (Supplementary Table S1). Local extinctions from ecological
56 networks can trigger rippling effects due to the direct and indirect interdependency of consumers and
57 resources; as a result, community fragility to disturbance can be influenced by structural properties, such
58 as how trophic links are distributed among species^{15,16}. We hypothesised that our experimental food webs
59 were governed by a core/periphery structure, as detected recently in a range of non-ecological
60 networks^{5,19,20}. Highly connected core species are functionally important because they provide alternative
61 routes for the flux of matter, and could therefore buffer the effects of perturbations and enhance network
62 stability. Peripheral species are less integral in a topological sense, and changes in the food web
63 composition and configuration are more likely to lead to their isolation (i.e. extinction), as has been
64 observed recently in mutualistic networks²⁵. Specialist consumers from the web periphery are especially
65 vulnerable to extinction because they are more loosely connected and dependent on fewer resource
66 species. Redundancy among the links within the core could, in theory, provide a means of withstanding the
67 effect of species loss and rebalancing the structure of food webs, thereby conserving overall robustness.

68 To test our hypotheses, we applied a novel graph profiling technique⁵ to characterise the cores of our
69 eight highly-resolved replicate food webs^{10,26}. To generate a graph profile for a web, nodes were ranked by
70 their degree (number of links). Starting from the highest degree node, we examined the interconnectedness
71 among the high degree nodes as those of a lower rank were included sequentially. A point is reached

72 whereby the connectivity among the high degree nodes peaks, reflecting the cohesiveness in the core and
73 defining the core boundary, and which is followed by generally decreasing connectedness thereafter. The
74 rest of the nodes form the periphery, which is only loosely connected to the core, and contains few or no
75 links among its constituents. After characterising the core/periphery structure, we then measured the
76 density of interactions within the core and across the web using the “rich-club” coefficient²⁷. To gauge the
77 level of organisation in the core/periphery structure between the drought and control treatments, we
78 employed an ensemble of null networks, whereby links were reshuffled randomly while conserving
79 network properties²⁸. Graph profiles obtained from the null models represent network structures that would
80 simply happen by chance, and they were used to benchmark the link patterns of the empirical webs. The
81 further an empirical web deviates from its null models (i.e. a z -score greater or less than 0), the more
82 significant, in statistical terms, are its link patterns, which also indicates the level of organisation that has
83 taken place to generate the observed pattern. To examine the effectiveness of the compensatory
84 mechanism provided by the core, we studied network robustness by measuring the rate at which the
85 structural integrity of food webs collapsed²⁹ under two commonly simulated species removal scenarios: i)
86 random removal and ii) targeted removal of core species (i.e. high degree species).

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

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

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

127 Our results demonstrate that drought disturbance triggered previously unknown substructural
128 changes within real food webs, beyond the direct and obvious species losses that have been reported
129 elsewhere when based on fixed autecological traits^{6,10}. While the underlying core/periphery structure was

130 robust to perturbations, the composition and configuration of the food web substructures changed
131 markedly, with a steep reduction in interactions among the remaining core species. The ability to predict
132 which networks of species interactions are most vulnerable to anthropogenic pressures, and the
133 identification of a core of species vital to the functioning and persistence of a community within an
134 ecosystem, would greatly enhance our ability to direct conservation efforts more effectively in the face of
135 environmental perturbations^{15,16}. Traditional whole-network metrics, such as connectance, were far less
136 sensitive⁶ than the novel measures applied in this study, and therefore offer less potential for gauging
137 changes in food webs exposed to perturbations. Substructural approaches that capture the plastic
138 synecological traits defined by species interactions could help to unearth compensatory shifts within
139 ecological networks, and provide us with a major new way to detect and understand the effects of
140 environmental change on ecological communities.

141

142 **Additional information**

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

145

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154

155 **Author contributions**

156 M.E.L. and A.M.M. conducted the mesocosm experiments, M.E.L., L.E.B., A.M.M. and G.W. generated
157 the food web dataset, R.J.M. and A.M. designed the network analyses, X.L. implemented the network

158 research, X.L. and C.G. analysed the results, and C.G., M.E.L. and A.M. wrote the manuscript with input
159 from all authors. All authors discussed the results and reviewed the final manuscript.

160

161 **Competing financial interests**

162 The authors declare no competing financial interests.

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249

250 **Figure Legends**

251

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

258

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

263

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

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

277

	Drought			Drought impacted substructures	
	<i>d.f.</i>	<i>p</i>		<i>d.f.</i>	<i>p</i>
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			

278

279 **METHODS**

280 **Experimental design.** Details of the experimental design and methods used to build the food webs are
281 published elsewhere^{10,31}. In brief, the experiment ran for two years (March 2000-February 2002) in
282 outdoor stream mesocosms that consisted of four pairs of channels subjected to either control or drought
283 conditions. All channels were subject to two months of constant flow before a drought treatment (6 days of
284 dewatering per month) was applied to one channel per pair. During the simulated drying periods, surface
285 flows ceased and drying of exposed substrata occurred in patches, whereas the interstices beneath the bed
286 surface remained wet, and small pools persisted at intervals along the length of the dewatered channels³².
287 Surfaces of exposed substrata dried at natural ambient rates such that the stress experienced by organisms
288 stranded in the mesocosms was consistent with those in adjacent drying stream reaches³³. This
289 experimental design simulated periodic drying events occurring during a supra-seasonal drought. Stream
290 drying events have occurred during major droughts in Europe³⁴ and are expected to increase in frequency
291 with climate change³⁵. As with all mesocosm experiments, our design necessitated some trade-off between
292 realism and replication^{26,36}. Nevertheless, the simulated flows were consistent with multiyear droughts in
293 Europe which occur in both summer and winter, and which are characterised by a fragmentary incidence
294 of streamflow deficits through the year³⁴. Our experiment may adequately capture the expected changes in
295 the magnitude and frequency of drying in rivers under climate change but does not necessarily reflect the
296 expected changes in seasonality of these events. At the end of the experiment all invertebrates were
297 collected and identified prior to gut content analysis. All individuals and their gut contents were identified
298 to genus or species level, where possible. The resultant eight food webs are among the most highly
299 resolved to date, comprising 783 pairwise trophic interactions and 74 trophic elements in the aggregate
300 web. Comparison of the control channel food webs to data collected for 82 'natural' river food webs
301 showed the mesocosm channels contained realistic webs, with consistent and similar size structures
302 suggesting that patterns of energy flux between mesocosm consumers and resources were good analogues
303 of those in natural systems³⁷. Species were categorised into three trophic levels: Basal (B), Intermediate (I)
304 and Top (T). A basal species was defined as a species with no prey; a top-level species was referred to as a
305 species with no predators; and the rest were defined as intermediate species.

306

307 **Food web profiling.** The core profiling method identifies a substructure of highly interconnected species

308 by ordering species with respect to the number of connections to other species and the extent to which
 309 those connections link to more highly connected species in the web⁵. Highly interconnected species
 310 constitute the web core, with less-connected nodes forming the periphery. Each food web was represented
 311 as a binary and undirected network with S nodes (species) and E links (the interactions between
 312 species). To obtain a core profile, nodes were ordered in descending order of their degree (i.e. number of
 313 links) and a node with a rank r has degree k_r . The number of links that a node shares with nodes of a
 314 higher rank is k_r^+ and the number of links with nodes of a lower rank is therefore $k_r - k_r^+$. Starting with
 315 the node with the highest rank, the value of k_r^+ fluctuates as nodes from further down the rank are being
 316 included. There will be a point r^* where k_r^+ reaches its maximum and will always be less than $k_{r^*}^+$
 317 thereafter, marking the boundary of the core. To quantify the density of links inside the core, the rich-club
 318 coefficient²⁷ was calculated, which is defined as:

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

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

325
 326 **Null model.** A statistical null model was used to determine the probability of the connectivity observed in
 327 the empirical data. For each empirical food web, we applied a randomisation method²⁸ to generate an
 328 ensemble of 100 networks by randomly reshuffling the links while conserving the properties of the
 329 empirical network, including the number of nodes, the number of links and the degree distribution. This
 330 allows us to assess the statistical significance of the patterns of interactions observed in the empirical webs
 331 with respect to patterns that would simply occur by chance. To quantify how the link density in the core
 332 differs from the random networks, we first referred the rich-club coefficient of the empirical food web and
 333 compared that to its null counterpart by calculating the z -score. A z -score of 0 means that the empirical
 334 data exhibits an organisation of links that is the same as what you would expect from a random case; a

335 value > 0 means that the empirical has a higher than expected density of links, and vice-versa. This
336 effectively describes the degree of organisation of species interactions in the sense that the more
337 improbable a configuration of links is, the more organisation is required to be in place to attain the
338 observed pattern. Again, the rank of species was normalised to compensate for the effect of different web
339 sizes when comparing the control and drought food web pairs.

340

341 **Network robustness.** To assess this, we simulated primary species loss in all the food webs by manually
342 removing species²⁹. Firstly, species were chosen randomly and removed from the food web, together with
343 all their associated links, in an iterative manner. We recorded the total species at each step, which accounts
344 for both primary loss and secondary extinction (as a result of species isolation from resource). Robustness
345 was quantified by the amount of primary extinction required for a total loss of 50% of the species. We
346 repeated this for 100 times for each web and results were averaged. Secondly, species were removed in the
347 descending order of degree which is often considered as the worst case scenario as the most important
348 (connected) nodes are being targeted. Similarly, species were removed in an iterative manner, but the
349 degree order of nodes was re-calculated after each species removal as removing a node and its links may
350 impact on the degree order among the rest of the nodes. Again, robustness was evaluated by the total
351 primary extinction required for a cumulative 50% species loss.

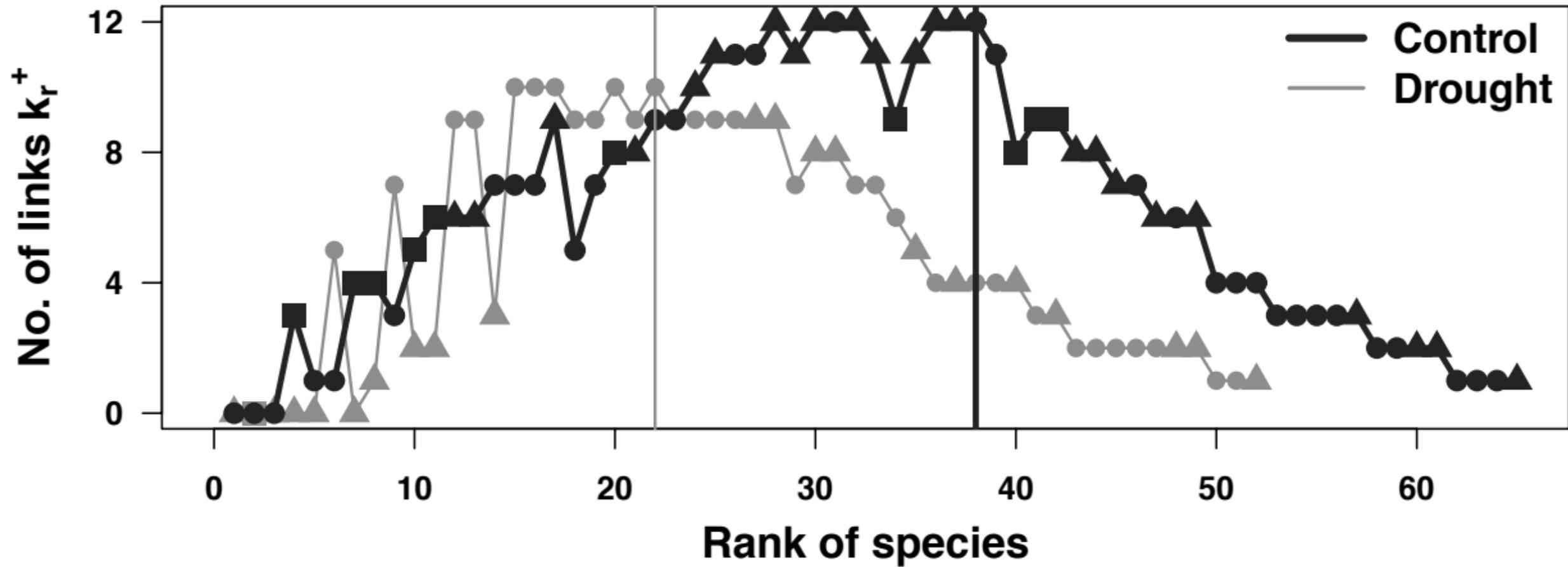
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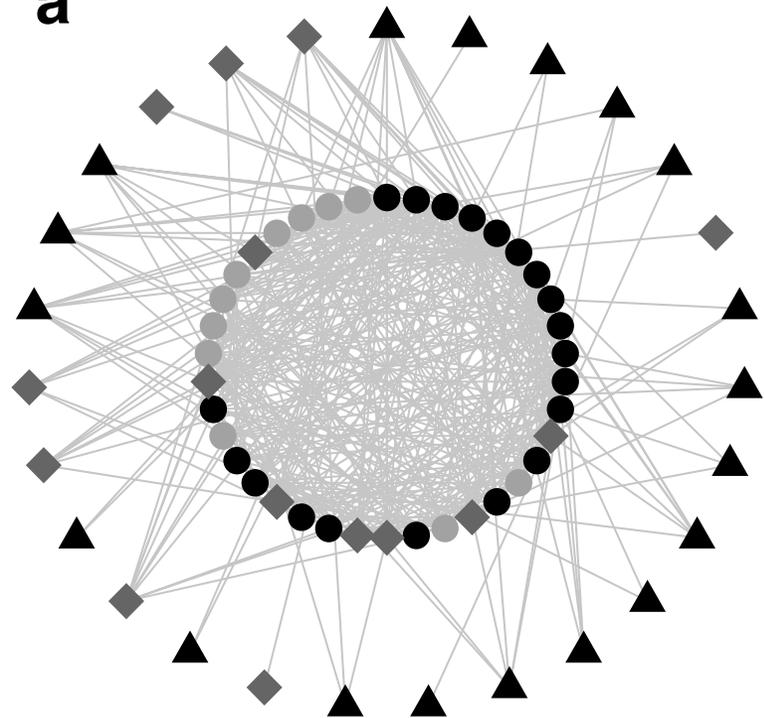
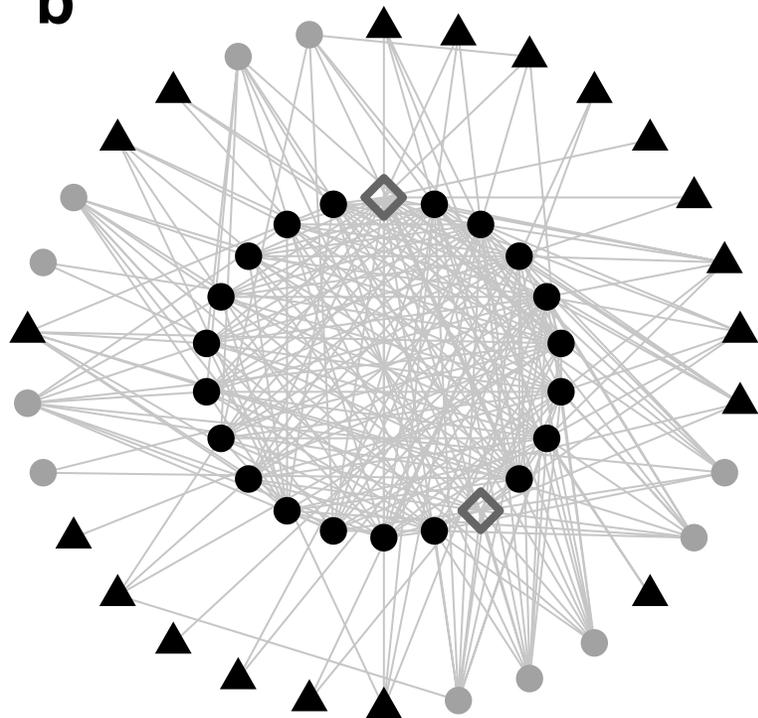
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a**Control****b****Drought**

- Unaffected core species
- ▲ Unaffected periphery species
- Core control to periphery drought
- ▲ Periphery control to core drought
- ◆ Extinction after drought
- ◇ Invasion after drought

