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Food web's backbones and energy delivery in ecosystems

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1 **Food web's backbones and energy delivery in ecosystems**

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3 Running title:

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5 Ecosystem backbones and energy delivery

6

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Abstract

Food webs can be seen as collections of pathways for energy distribution in ecological communities. Because of thermodynamic as well as ecological constraints such as efficiency in energy transfer, prey preference, and resource availability, all pathways in a food web do not share the same importance in distributing energy to the species. Links responsible for the greatest share of the total energetic throughput form a backbone that is hidden in the structural complexity of the food web network. Thermodynamic efficiency hypothesis would impose energy to reach species at a minimum cost, i.e. with high efficiency in energy transfer; accordingly, the bulk of energy would travel along these trees of minimum length. In other terms, following the thermodynamic efficiency constrain, the backbone formed by strongest energy chains would coincide with the Minimum Length Spanning Tree (MLST), a tree formed by the shortest pathways that keep the food web connected. To test this hypothesis we analyzed 30 well resolved weighted empirical food webs. From each food web we extracted the MLST and a tree composed by the connections of maximum strength, the Maximum Weight Spanning Tree (MWST). To make the comparison robust we computed also the minimum weight spanning tree (MinWST), composed by the links of minimal strength, and extracted 1000 Random Weighted Spanning Trees (RWSTs) to serve as a null model. We contrasted the different tree structures. We found that MWST are significantly shorter than random trees and MinWST, but always longer than MLST. Our results show that the bulk of energy travels throughout the ecosystems along pathways that tend to be short, although they never coincide with the MLST.

46

47 **Key Words:** ecosystem, energy delivery, food web, interaction strength, ecological network,

48 spanning tree.

49

50 **1. Introduction**

51
52 Food webs have long been at the core of ecological research (Hutchinson 1959, May 1973,
53 Cohen and Newman 1985). A food web describes the vast array of feeding interactions between
54 species in a community. Functional properties of ecological communities such as robustness
55 (Dunne et al. 2002, Bellingeri and Bodini 2013, Bellingeri et al. 2013), stability (Rooney et al.
56 2006, Allesina and Tang 2012), and ecosystem response to perturbations (Bodini 2000, Montoya
57 et al. 2009) have been investigated by exploiting the complex architecture of food webs.

58 Nonetheless, disentangling such complexity has proven useful to clarify the origin of observed
59 patterns: simpler topologies that are hidden in the complexity of networks have been identified
60 as relevant for stability (Neutel et al. 2002, Neutel et al. 2007), robustness (Allesina and Bodini
61 2004, Bodini et al. 2009) and ecosystem dynamics (Bascompte et al. 2005, Pascual and Dunne
62 2006). To grasp them, the structural intricacy of food webs had to be unfolded through some
63 network reduction.

64 Energy travels in the ecological community through the whole food web, but it is unlikely that
65 all trophic pathways that compose it share the same importance for energy delivery (Allesina et
66 al. 2006, Serrano et al. 2009). Thermodynamic as well as ecological constraints such as
67 efficiency, prey preference, resource availability, affect the way energy is distributed.

68 Accordingly, preferential pathways may emerge as key players in this respect.

69 Garlaschelli et al. (2003) analysed food webs as transportation networks (Banavar et al. 2009)
70 and proposed that a subgraph called Minimum Length Spanning Tree (MLST) governs energy
71 distribution in ecosystems. These trees are topological architectures made of the minimum
72 number of links necessary to keep a graph connected. That is, MLST is the shortest-length tree

73 subgraph that contains all nodes of the web. In ecological terms, thus, a minimum spanning tree
74 can be seen as the collection of pathways that allows energy (food) to reach all species at a
75 minimum cost. When the magnitude associated with links is not specified, and there is no
76 dissipation, this minimum cost exactly corresponds to the minimum distance from every node to
77 the root of the web, origin node of the web that is used to represent the external environment as
78 the ultimate energy provider for the entire ecosystem (Allesina and Bodini 2005). The low
79 efficiency in resource transfer between trophic levels () indicate that main routes for energy
80 delivery in food webs would be short. According to this Garlaschelli et al (2003) state that
81 minimizing chain length would select food webs as energetic backbones.
82 The structure of these minimum length spanning trees would be the product of the trade-off
83 between maximizing resource input and minimizing competition. Maximizing resource input
84 would require the web to be star-like shaped whereas minimizing competition is possible only in
85 a linear chain. Minimum length spanning trees are something in between the two configurations
86 (Garlaschelli 2004). Van Veen and Murrel (2005) challenged the idea that MLSTs represent the
87 main energetic backbones in food webs. According to these authors, in fact, chain length
88 minimization may remove many of the strongest links in favor of the weakest ones to lower
89 trophic levels (i.e. when predators feed at different life stages). The distributions of interaction
90 strengths, that are highly skewed, with many weak and few strong interactions (De Ruiter and
91 Neutel 1995, Raffaelli and Hall 1996, Sala and Graham 2002, Bersier et al. 2002), would favor
92 the removal of strong links while searching for MLST (Van Veen and Murrel 2005).
93 A major drawback with MLSTs is that they do not consider interaction strength. Measuring the
94 shortest paths to every node does not require link strength to be taken into account. However,

95 insights into how food webs are shaped around the energy flow can be obtained only if
96 interaction strength is incorporated as a fundamental issue (Van Veen and Murrel 2005).
97 In this paper we present the result of a study conducted using 30 well resolved weighted
98 empirical food webs. Its major aim was to shed light on whether MLST is associated to the main
99 energy flow in food webs or, rather, other, longer structures can be responsible for distributing
100 the bulk of energy to the species. To this end we extracted from each of our 30 food webs four
101 different types of spanning trees: i) the Minimum Length Spanning Tree (MLST); ii) the
102 Maximum Weighted Spanning Tree (MWST), a tree composed by the links of maximum
103 energetic magnitude (links of maximum strength) and because of this it represents the true
104 energetic backbone of the ecosystem; iii) the Minimum Weight Spanning Tree (MinWST), i.e. a
105 tree composed by the links that delivery the lowest amount of the energy to any node (links of
106 minimum strength); iv) 1000 Random Weighted Spanning Tree (RWST), that are built by
107 randomly selecting one incoming link to every node. We contrasted for each food web the length
108 of the four different tree structures to unveil whether the MWST, which deliver the greatest
109 amount of energy,, is also the shortest route in the network (i.e. if it coincides with MLST).

110

111 **2. Methods**

112

113 *Empirical food web data set*

114 As many as 30 empirical food webs were derived from systems that were previously investigated
115 as ecological flow networks. Data about their structure and link magnitude were obtained from
116 published papers and reports. In two cases (Lake Scuro and Lake Santo, Province of Parma,
117 Italy) data were gathered from on site research (Bondavalli et al. 2006). Table 1 provides a list of

118 the selected ecosystems and their key references. This table also includes a minimal set of
119 structural parameters, such as number of components (i.e. species and trophospecies), linkage
120 density and connectance.

121
122 [Table 1 goes here]

123
124 Because we framed our study in an energy, bottom-up perspective, we measured interaction
125 strength as the amount of biomass that any consumer population gathers from all of its resource
126 item (no dynamic per-capita effect) and it is quantified as $\text{grC}/\text{m}^2/\text{year}$ (biomass flux, Berlow et
127 al. (2004)).

128 *Spanning trees*

129
130 Rooted spanning trees (the notion of tree comes from Cayley (1891)) are collections of N nodes,
131 which are connected to an origin node called root. N-1 edges (directed links, in our case) make
132 these structures connected. In particular, in these topologies any pair of nodes is connected by
133 one single link and a single path connects each node to the root. Spanning trees can be identified
134 in any connected graph. In food web spanning trees, nodes represent species and links represent
135 trophic interactions among them. In the root we collapse all the environmental supporting
136 functions of the food web (i.e. the external environment, the ultimate provider of energy to the
137 whole web). From every food web we extracted a Minimum Length Spanning Tree (MLST), the
138 Maximum Weight Spanning Tree (MWST), the Minimum Weight Spanning Tree (MinWST), and
139 1000 Random Weighted Spanning Trees (RWSTs) created by randomly selecting one ingoing
140 link to every node.

141 The MLST defines the subset of edges that minimizes the length of the paths (distance) from
142 each node to the root and yet maintains the graph connected. Figure 1 depicts the various forms
143 of trees that we gathered from the Benguela ecosystem, one of the case study selected for our
144 investigation. Figure 1a shows the binary food web of that ecosystem. Figure 1b introduces
145 interaction strength in the food web: arrow thickness is proportional to link strength. The
146 MWST, the MLST, the MinWST and the RWST extracted from the Benguela food web are
147 depicted in Figures 1c, 1d, 1e and 1f, respectively.

148

149 [Figure 1 goes here]

150

151 MLSTs can be computed in binary (qualitative) food web since the minimum distance is the only
152 requirement for selecting the pathways that connect the species to the root. In our MWST
153 pathways that keep the species connected to the root are formed by the strongest links to every
154 node and can be computed only in weighted food webs. The links that form such tree are, *de*
155 *facto*, the energetic backbone for the web. To search for the MWSTs first link strength was
156 normalized. This was done by dividing the magnitude of every link pointing to a given node by
157 the total energy intake to that node (sum of all links pointing to it). This was done for all node in
158 all the webs.. According with this procedure one link is said to be strong when it carries a great
159 fraction of the total energy intake to any given speices. Similarly a link is weak when its share of
160 a node's overall incoming energy is low. After the standardization was accomplished, for each
161 node (in all the food webs) we selected the strongest among its incoming links. This allowed us
162 to obtain the tree of maximum weight (MWST). We computed the MWST using the Chu-Liu-
163 Edmonds algorithm which ensures that the resulting tree structure is connected and composed by

164 the strongest links to each species (Edmonds 1967). The search for MWST links considers for
165 each node the entire set of its incoming links; among these only the one that carries the highest
166 fraction of energy is retained. In the case of cycles, the Chu-Liu-Edmonds algorithm changes the
167 links to eliminate the cycles minimizing the magnitude decrease. Similarly, when selecting the
168 links of minimal weight , i.e. the weakest incoming link to each species, the Chu-Liu-Edmonds
169 algorithm produces the MinWST. Thus the MinWST represents the weak counterpart of the
170 MWST. The procedure of the Chu-Liu-Edmonds algorithm is explained step by step with a
171 simple example in the Appendix.

172 Finally, 1000 RWST were computed for each food web. They were constructed by randomly
173 selecting, for any given node, only one among its incoming links. That is in each run we selected
174 randomly a single resource taken from within each node's alimentary spectrum. RWSTs
175 represent the null models in this analysis. They inform about the expectation of tree composition.
176 The procedure for computing the RWST is as follows: for each node one single resource is
177 maintained by selecting it randomly among all the resources that provide energy to it; if at the
178 end of the selection process cycles are present, the links that form the cycle are discarded and the
179 nodes visited again for a new random search. This procedure is repeated until no cycles remain
180 and the overall structure is a tree.

181 After we extracted MLST, MWST, and RWSTs we computed their length by averaging the
182 number of steps connecting each node to the root. Because trees are structure in which every
183 species has one and only one resource and predator, the computation can be carried out simply
184 by considering that primary producers are one step away from the root (TS=1), grazers are two
185 steps away (TS=2) and so forth.

186

187 **3. Results**

188 Table 2 summarises the main results of the analysis.

189

190 [Table 2 goes here]

191

192 The outcomes of the comparison showed that MLST were always shorter than the MWST and

193 MinWST. We did not test for the statistical difference between these groups because by

194 definition MLST is always less or equal to MWST and MinWST. As many as 26 out of the 30

195 food webs showed MWST shorter than the MinWST. Also 26 of the 30 food webs showed

196 MWST shorter than the average of the RWSTs. Finally 24 of the 30 food webs showed MinWST

197 longer than the average of the RWSTs. We applied the paired Wilcoxon test to compare the

198 length of the MWST, MinWST and RWST. We found: i) the MWST to be significantly

199 shorter than the MinWST (Wilcoxon test, $p < 0.001$), ii) the MWST to be significantly shorter

200 than the RWST ($p < 0.001$); iii) the MinWST to be significantly longer than the RWST

201 ($p < 0.001$).

202

203 **4. Discussion**

204 Ecologists look at general patterns in communities to understand common principles of

205 ecological organization that lies behind the many apparently diverse and idiosyncratic

206 communities. One approach to unveil these principles is to analyse motifs or modules, sub

207 structures that would be responsible for patterns that emerge at the whole ecosystem scale (Milo

208 et al. 2002, Bascompte and Melian 2005). For example, chains of three interacting species locked

209 in omnivory are the minimal configuration from which principles for system stability can be

210 grasped (Neutel, et al. 2002). A view on how food webs work holds that there would be main
211 routes through which energy travels in the ecosystem. Identifying such main routes holds
212 ecological importance. They may show which species are more critical and act as bottleneck for
213 energy delivery to the various speices. Also they could reveal main routes for impèact to spread
214 in the ecosystem following the energy flow and which species are likely to absorb most of these
215 impacts.

216 These routes are substructueres that retain truly relevant connections for energy delivery
217 (Serrano et al.2009), those that possess the greatest share of the total energy flow. Garlaschelli et
218 al. (2003) proposed that such substructures correspond to MLST We show here that these main
219 routes may correspond to spaning trees made of links of maximum magnitude (MWST). A
220 potential problem with spanning trees is that each node draws the bulk of its energy from a single
221 resource. To examine the appropriateness of this assumption we computed for the 30 food webs
222 the distributions of the strength of the links that carried the maximum fraction of energy to the
223 consumers. Results are reported as box plots in Figure 2.

224

225 [Figure 2 goes here]

226

227 On average, from 30% up to 67% of each node's total energy intake can be delivered by one
228 single link (that of maximum magnitude). It seems thus that MWSTs are acceptable proxies for
229 the energetic backbones of food webs. Our analysis showed that MWST do not coincide with the
230 minimum length spaning tree although they tend to be short. They are shorter than expected by
231 chance. In addition the MinWSTs are significantly longer than the RWSTs, i.e. the weakest trees
232 are longer than the random trees. . ì

233 The observed discrepancy between MWSTs and MLSTs may be due to an excess of
234 simplification that MLST imposes to food webs. The food chain length minimization criterion
235 that is applied to obtain MLST is based on the assumption that the shortest pathway to each
236 species is the most important in terms of resource flow (Garlaschelli et al. 2003). This criterion
237 however sacrifices ecology in favor of geometry. Several ecological features may in fact
238 contribute to shape the real energetic backbone. For example, if a species feeds both as a primary
239 carnivore and a secondary carnivore it will be assigned to primary carnivores in the MLST. This
240 ensures that in the MLST this species is connected to the base of the food web through the
241 shortest path. However prey preference (Chesson 1983) may lead this predator to feed
242 disproportionately as a secondary carnivore, elongating the route through which the bulk of
243 energy reaches that species.

244 Thus, delivering at a minimum cost seems rather an asymptotic tendency and its geometric
245 representation, the MLST, is a theoretical configuration that does not represent the main energy
246 flows in real ecosystems. The short structure of the effective backbone for energy flows we
247 discovered in our analysis should be an optimized configuration that emerges from a trade off
248 between maximizing resource input at a minimum cost (minimum trophic level) and a suite of
249 constraints that may include, feeding preference (Chesson 1983), size effect in predator-prey
250 interactions (Hastings and Conrad 1979), dynamical features (Sterner et al. 1997), and efficiency
251 in energy transfer between trophic levels (Hairston and Hairston 1993). The difference between
252 MWST, MinWST and RWSTs that we detected in our 30 empirical food webs may be the
253 outcome of this evolutive trade off.

254 The level of departure of MWST from random expectation seems to correlate with connectance.
255 In Figure 3a we plot the difference in length between RWST and MWST for every food web

256 versus the web connectance (C). The linear relation in Figure 3a is significant although it does
257 not explain well the variability in the data ($p=0.006$, $R^2= 0.22$).

258

259 [Figure 3 goes here]

260

261 The statistical significance would indicate us that the difference in length between MWST and
262 random trees becomes more pronounced as connectance augments. To clarify this outcome we
263 analysed MWST and RWST for their relation with connectance but we did not observe any
264 significant outcome, i.e. the length of the trees is not a function of the web connectance (see the
265 linear regressions in the Appendix, Figure 2). Nevertheless, when the two types of trees are
266 plotted against one another a significant linear trend emerges (Figure 3b). It is interesting to
267 observe that the slope of the regression line is less than 1. This means that for any increment in
268 length shown by RWSTs, also MWSTs increases, but at a lower pace. So the combination of the
269 two results suggests a possible interpretation: higher connectance would allow for a larger set of
270 possibilities for link selection in the construction of random trees (which may include both weak
271 and strong links). Such set of possibility is more restricted for MWST. This may depend on the
272 distribution of link strengths which is highly skewed towards many weak links and few strong
273 links (see O'Gorman et al. 2010 and references there in).

274 However the selection of the strongest incoming link for each node depends on the criteria used
275 for resolving the food webs, that is lumping taxonomic species into trophic species (Van veen and
276 Nurrel 2005). If these procedures could be standardized somehow a better representation of the
277 MWST could be obtained making this analysis more robust.

278

279 [Figure 3 goes here]

280

281 Another drawback of spanning trees is that they are overly structural simplifications that
282 eliminate cycles and hierarchies typical of the food webs (Allesina and Bodini 2005). In the face
283 of these problems the disparity filter technique (Serrano et al. 2009) would be more appropriate
284 than spanning trees to determine how many connections for every node can be included in the
285 structure that carries a statistically disproportionate weight, and for this reason, can be
286 considered as the energetic backbone for the food web. This structure would not only contain the
287 links carrying the largest weight in the network, but also all the other links that can be considered
288 relevant as for their energy content, according to a predefined significance level (Serrano et al.
289 2009).

290 However searching for such disparity backbones can decompose the food web in a collection of
291 subsystems that are dominated by significant fluxes but that may be also disconnected from one
292 another (Serrano et al. 2009). In these cases it is impossible to identify main routes for energy
293 transfer from producers to consumers because disparity backbones may not keep the whole web
294 connected. It follows that any hypothesis about optimal length for energy pathways cannot be
295 tested. A further difficulty arises because of the "non-tree" structure of disparity backbones,
296 which allows nodes to be connected to the root by multiple pathways. For these reasons we
297 considered reducing food webs to spanning trees more appropriate for the objectives of this study.
298 Although it has been said that the number of links in a MLST gives the trophic level of each
299 node (Garlaschelli et al. 2003) we reiterate that this number (even in MWST and random trees)
300 should not be confused with the trophic level. In fact many links that contribute to define
301 species' trophic level are excluded when trees are constructed.

302 In conclusion, we considered spanning trees useful to understand how energy can travel in food
303 webs. In doing so we looked at food webs only in their role of transportation networks. Although
304 our results tend to confirm the hypothesis that main channels for energy delivery tend to be short,
305 we would not fuel the debate around the relationship between food chain length, energetic
306 transfer efficiency and stability (Pimm and Lawton 1977, Lawton 1989, Rooney et al. 2006).
307 Simplifying food web networks to trees, as we said above, removes much of the interesting
308 information that resides in the multiple links between species and that is central in the debate
309 over stability and food chain length (Rooney et al. 2006). Also the trees that we extracted from
310 the food webs do not necessarily identify with food chains as classically measured (Hall and
311 Raffaelli 1993, Post 2002).

312 An additional difficulty that suggests not inferring about food chain stability using our results
313 relates to the way we measured interaction strength. Much of the work on stability, in fact,
314 calculates interaction strengths as the values of the elements of the community matrix and
315 represents the size of the effects of species on each other's dynamics near equilibrium (Neutel et
316 al. 2002). On the other hand measuring link strength simply as energy flow from a resource to its
317 consumer species fits with the idea of food webs as transportation networks.

318

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320

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323

324

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443 **Tables**

444

445 **Table 1.** The 30 empirical food webs and their features. S number of species; L number of links,
 446 L/S Linkage density; C Connectance. The keys DRY and WET identify food webs of the same
 447 ecosystem referring to dry and wet season respectively.

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Food web	S	L	L/S	C	References
Northern Benguela ecosystem, Namibia	16	64	4.00	0.267	Heymans et al. 2004
Caete´ Mangrove Estuary, Brazil	18	62	3.44	0.203	Wolff et al. 2000
Caribbean marine ecosystem, Philippines	248	3253	13.12	0.053	Optiz 1996
Maspaloma Lagoon, Canary Islands	18	24	1.33	0.078	Almunia et al. 1999
Lower Chesapeake Bay in Summer	31	57	1.84	0.061	Hagy 2002
Middle Chesapeake Bay in Summer	31	77	2.48	0.083	Hagy 2002
Upper Chesapeake Bay in Summer	31	83	2.68	0.089	Hagy 2002
Crystal River Creek (Delta Temp)	21	60	2.86	0.143	http://www.cbl.cees.edu/~ulan/ntwk/network.html .
Cypress wetland Dry Season - Florida	64	448	7.00	0.111	Heymans et al. 2002
Cypress wetland Wet Season - Florida	64	439	6.86	0.109	Heymans et al. 2002
Everglades Graminoids Dry Season ó Florida	63	612	9.71	0.157	Heymans et al. 2002
Everglades Graminoids Wet Season ó Florida	63	612	9.71	0.157	Heymans et al. 2002
Florida Bay Dry season, Florida-USA	121	1799	14.87	0.124	Ulanowicz et al. 1998
Florida Bay Wet season, Florida-USA	121	1767	14.60	0.122	Ulanowicz et al. 1998
AlteSchwentine stream, Germany	14	34	2.43	0.187	Poepper 2003
Gulf of California, Mexico	25	121	4.84	0.202	Arreguin-Sanchez et al. 2002
Gulf of Salamanca, Colombia	17	86	5.06	0.316	Duarte and Garcia 2004
HuizacheóCaimanerolagooncomplex	25	159	6.36	0.265	Zetina-Rejon et al. 2003
Palude della Rosa, Lagoon of Venice	15	40	2.67	0.190	Carrera and Opitz. 1999
Lake Santo 1972, Italy	23	118	5.13	0.233	Bondavalli et al. 2006. Unpublished draft, University of Parma
Lake Scuro 1991, Italy	19	77	4.05	0.225	Bondavalli et al. 2006. Unpublished draft,

					University of Parma
Lake Michigan, USA	33	127	3.85	0.120	Krause et al. 2009
Mangrove estuary Dry season, Florida-USA	90	1149	12.77	0.143	Ulanowicz et al. 1999
Mangrove estuary Wet season, Florida-USA	90	1151	12.79	0.144	Ulanowicz et al. 1999
Mondego estuary, western coast of Portugal	42	271	6.45	0.157	Patricio and Marques 2006
Narraganset Bay (MA, USA)	31	113	3,65	0.122	Monaco and Ulanowicz. 1997
Southern Plateau, New Zealand	17	46	2.71	0.169	Bradford-Grieve et al. 2003.
Steina mountain stream, Germany	18	90	5.00	0.294	Meyer and Poepperl 2004
St. Marks, Florida-USA	48	216	4.50	0.096	Baird et al. 1998
Terminos Lagoon, south-western Gulf of Mexico	19	127	6.68	0.371	Manickchand-Heileman and Arreguin-Sanchez 1998

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452 **Table 2:** length of MLST, MWST, MinWST, RWST, extracted from the 30 food webs.

453 Explanation for how length was computed is in Figure 1 caption. ; %MWST indicates the

454 percentage of random trees which showed average trophic step lower than MWST; %MinWST

455 indicates the percentage of random trees which showed average trophic step lower than

456 MinWST; the column labelled as RWST reports for every food web the mean length calculated

457 over the 1000 tree extracted from each network; MMR (Mean Max Resource) indicates the

458 fraction of energy that, on average, the best resources (strongest incoming link) deliver in eah

459 food web. It describes the average fraction of energy a single link of maximum magnitude can

460 transfer.

461

	MLST	MWST	MinWST	RWST	%MWST	%MinWST	MMR
Benguela	2.38	2.5	3.19	3.04	0.5	77	0.62
Caetemangrove	2.22	2.5	3.00	2.70	18	93	0.61
Caribbean	2.27	3.22	3.10	3.24	51	8	0.67
Maspalomas	1.77	2	1.80	1.95	78	18	0.41
Chease lower	1.97	2	2.10	2.17	5	11	0.43
Chease middle	2.13	2.42	2.80	2.52	36	90	0.46
Chease upper	2.26	2.29	3.20	2.61	0	94	0.48
Crystal river	2	2.25	2.50	2.38	20	82	0.56
Cyp dry	2.2	2.65	2.81	2.71	36	80	0.41
Cyp wet	2.2	2.65	3.00	2.69	38	99	0.41
Ever dry	2.22	2.33	3.00	2.92	0	72	0.52
Ever wet	2.22	2.38	2.90	2.93	0	56	0.51
Flo dry	2.39	3.15	3.10	3.14	59	24	0.32
Flo wet	2.39	3.07	3.20	3.15	39	79	0.35
Germ low stream	1.64	1.79	2.00	1.96	12	80	0.48
Gulf california	2.16	2.84	3.50	2.87	55	00	0.52
Gulfsalamanca	2.35	3.06	3.70	3.39	24	81	0.45
HuizaCaimanero	2.12	2.56	3.40	2.91	3	99	0.45
Venicelagoon	1.93	2.27	2.60	2.29	55	88	0.55
Lake Santo	1.91	1.96	2.13	2.13	0	73	0.47
Lake Scuro	1.89	1.89	2.11	2.095	0	70	0.5
Lake Michigan	2.32	2.77	3.10	2.82	49	92	0.44
Mangrove Dry	2.35	3.13	3.80	3.43	8	97	0.42
Mangrove wet	2.35	3.15	3.80	3.43	9	89	0.44
Mondego	1.79	2.26	2.04	2.19	83	10	0.45

Narraganset	2.26	2.45	3.40	3.07	0.5	85	0.49
New Zeland	2.41	3.41	3.50	3.3	68	78	0.51
Steina Mountain	2	2.17	3.30	2.57	0.5	99	0.49
St Mark	2.10	2.38	3.20	2.65	1	98	0.49
Terminos Lagoon	2	2.41	3.20	3.17	12	53	0.42

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465 **Figure Legend**

466

467 **Figure 1:** (a) Benguela ecosystem binary (qualitative) food web, $S=16$, i.e. the links mean only
468 presence-absence of trophic interactions among species; (b) Benguela ecosystem weighted food
469 web where the magnitude of energy transfer is associated to the links; (c) Benguela food web
470 MWST; (d) Benguela food web MLST; (e) Benguela food web MinWST; (f) one Benguela food
471 web RWST. The length of the trees is computed as the average of the distances that separate the
472 nodes in the web from the root. In practice this distance, that we called trophic steps ($\langle TS \rangle$),
473 counts the number of links that keep each node apart from root. This number is zero for the root
474 itself ($TS=0$); 1 for species that are connected directly to the root ($TS=1$, likely primary
475 producers); 2 for consumers that feed on these latter speices ($TS=2$), and so forth. For
476 example, for species 4 in (c) is $TS=2$ and for species 13 in (e) it is $TS=5$.

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478 **Figure 2.** Average fraction of energy that the strongest incoming link can carry to consumer
479 species in each of the 30 food webs.

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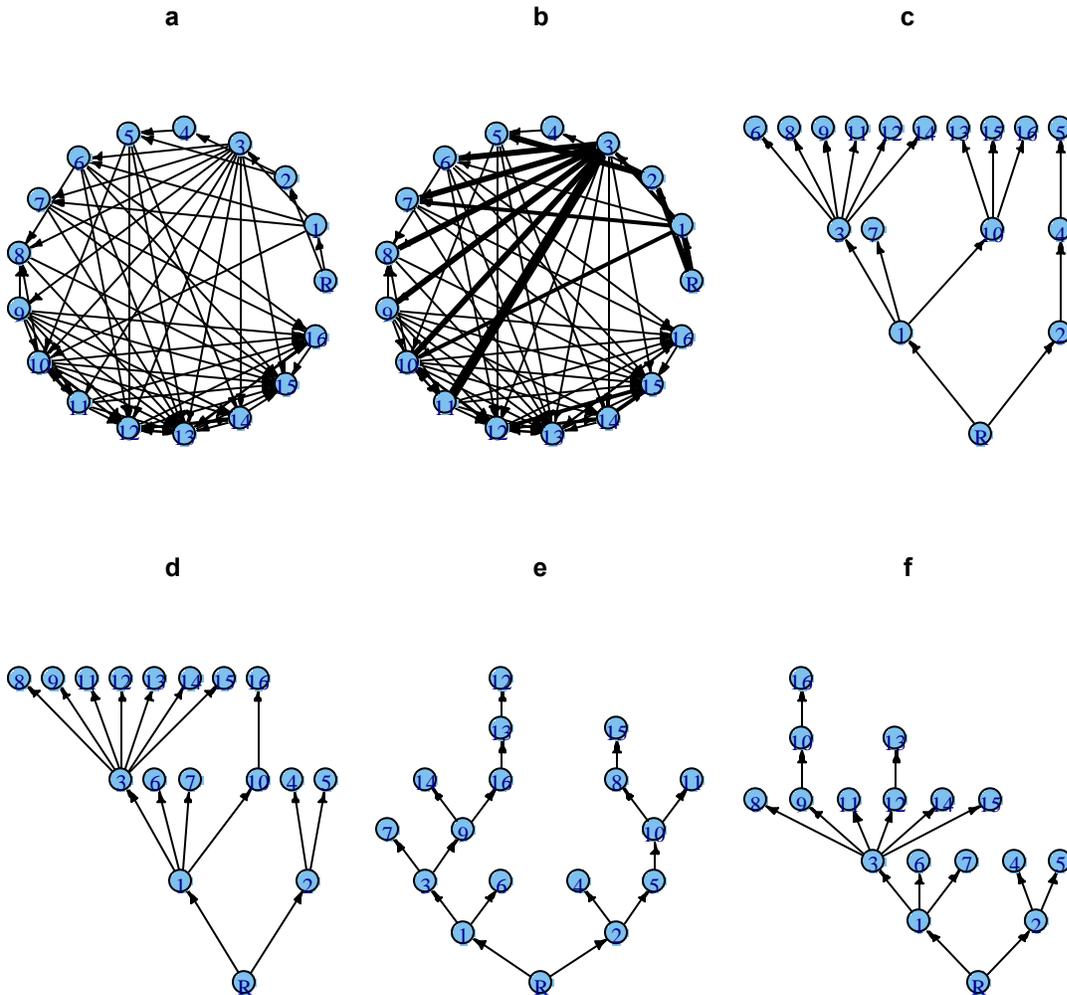
481 **Figure3.** Departure from random expectation shown by the mean length of the MWST in the 30
 482 selected food webs plotted against connectance ($p=0.006$, $R^2= 0.22$), with parameters $y= 1.4 x -$
 483 0.014 (a) and the mean length of the MWST plotted against the mean length of the
 484 RWST ($p<0.001$, $R^2= 0.76$), with parameters $y= 0.85 x + 0.2$ (b).

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486 **Figures**

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488 **Figure 1**



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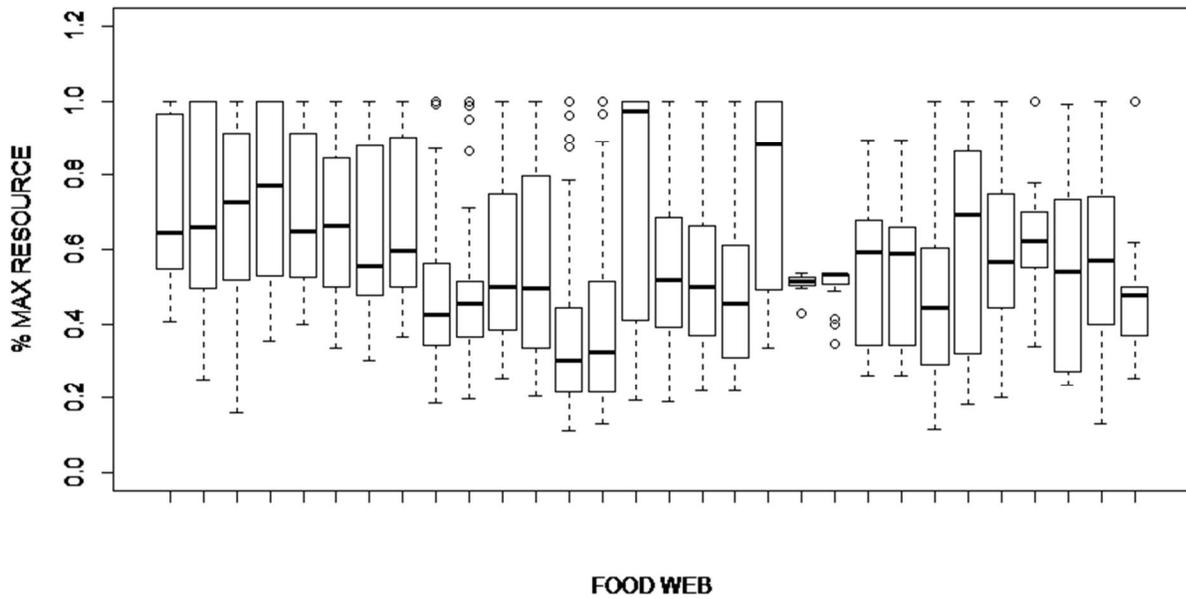
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495 **Figure 2**



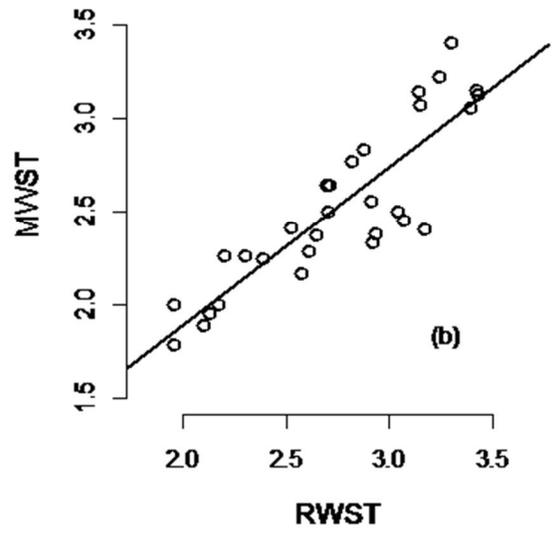
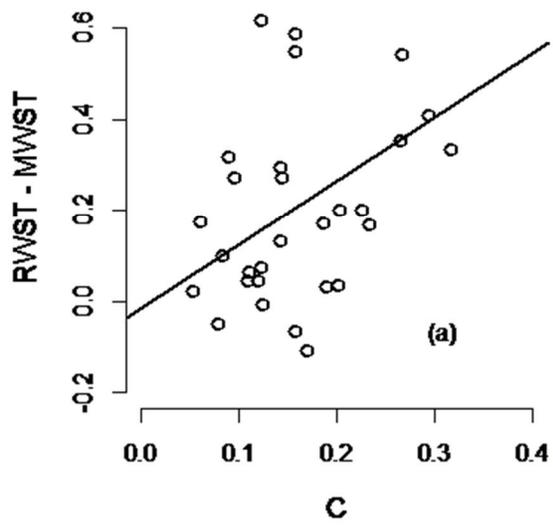
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497 **Figure 3**

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508 **Appendix**

509 **Chu-Liu/Edmonds Algorithm**

510

511 For a weighted directed graph G of N nodes and L links, we can produce the MWST using the
512 Chu-Liu and Edmonds algorithm.

513 The procedure is:

514 1) For each node other than the root, select the entering link with the highest magnitude.

515 2) Let the selected $N-1$ links be S the set of links composing the MWST.

516 3) If no cycle formed, $G(N, S)$ is a MWST. Otherwise, continue.

517 4) For each cycle formed, contract the nodes in the cycle into a pseudo-node (k), and modify the
518 magnitude M of each link which enters a node (j) in the cycle, from some node (i) outside the
519 cycle, according to the following equation:

520

521

$$522 \quad M(i,k)=M(k,j)-M(i,j) \quad (1)$$

523

524 where $M(k,j)$ is the magnitude of the link in the cycle ingoing the node j .

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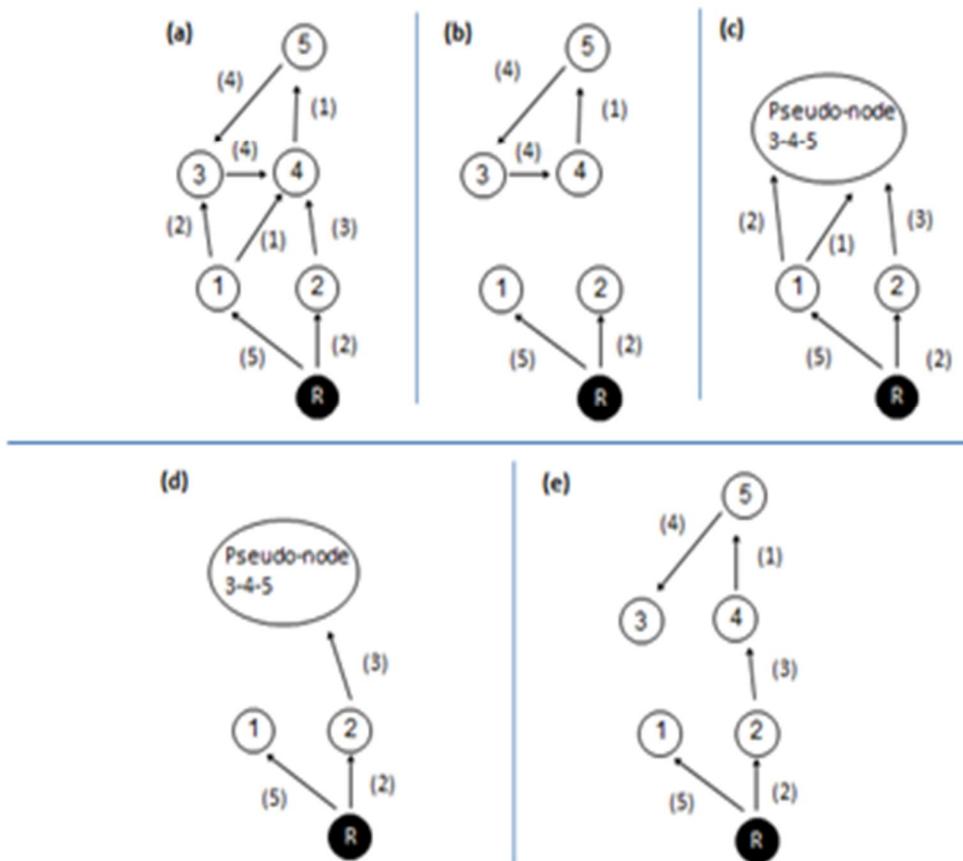
526 5) For each pseudo-node, select the entering link which has the smallest M .

527 6) Replace the link which enters the same real node in S by the new selected link.

528 7) If there are other cycles, goes to step 2 with the contracted graph. Else, the MWST is done.

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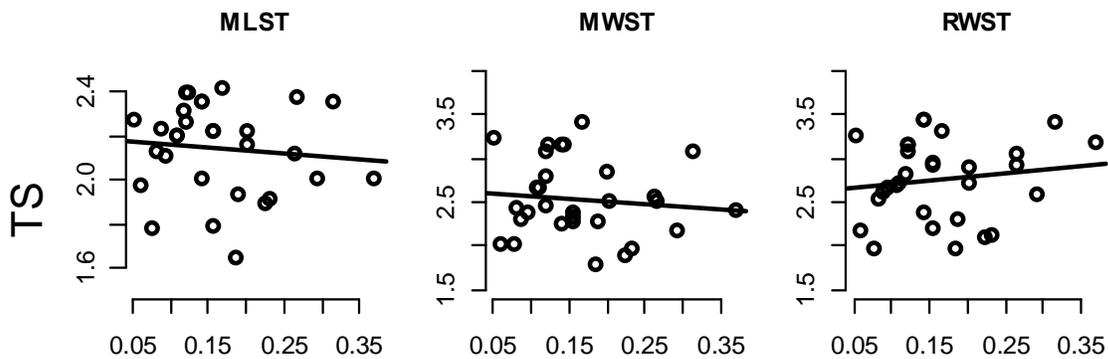
530 The main idea of the algorithm is to find the replacing link(s) that produces the minimum
 531 decrease in the total magnitude to eliminate cycle(s) if any. The equation (1) computes the
 532 associated decrease in the magnitude substituting links. The following Figure 1 shows an
 533 example of the algorithm.
 534



535
 536 **Figure A1:** (a) hypothetical weighted directed graph; (b) resulting MWST after the selection of
 537 the highest magnitude link for each node; (c) we contract the nodes in the cycle (3-4-5) in a
 538 pseudo-node; (d) according to equation (1) we computed the difference in magnitude between

539 ingoing links within the pseudo-node and the ingoing link outside and to the pseudo-node (in this
 540 case, we compute $M(1,k)=M(5,3)-M(1,3)=2$, $M(1,k)=M(3,4)-M(1,4)=3$, $M(2,k)=M(3,4)-$
 541 $M(2,4)=1$; then we select the link ingoing the pseudo-node with lower M , and subsequently the
 542 lowest reduction in magnitude, e.g. link from node 2 to pseudo-node; (e) we replace the link in
 543 the cycle (link 3-4) with the link outside the cycle entering from node 2 to node 4 from (link 2-
 544 4).

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548

549 **Figure A2:** average trophic step ($\langle TS \rangle$) for each type of tree as a function of the connectance
 550 (C) of the food web. The linear regression are not significant: MLST (p-value= 0.5929), MWST
 551 (p-value: 0.5936), RWST (p-value= 0.4433).

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