

1 **Weighting and indirect effects identify keystone species in**
2 **food webs**

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23 **Running title:** Roles of Weighting and Indirect Effects

24 **Key-words:** centrality, carbon flux, energy budget, quantitative food web,
25 robustness, secondary extinction, sequential deletion, species loss

26 **Type of article:** Letter

27 **Content:** 149 words in the abstract, 4962 words in the main text, 50 references, 3
28 figures, 3 tables, and 0 text box.

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36 **Authorship:** HZ and GW were responsible for research design. LZ drafted the
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38 developed the modelling framework. LZ and WT performed numerical simulation.
39 EOG, LZ and AM analysed the results. All authors were involved in discussions and
40 editing.

41

42 **Abstract**

43 Species extinctions are accelerating globally, yet the mechanisms that maintain local
44 biodiversity remain poorly understood. The extinction of species that feed on or are
45 fed on by many others (i.e. ‘hubs’) has traditionally been thought to cause the greatest
46 threat of further biodiversity loss. Very little attention has been paid to the strength of
47 those feeding links (i.e. link weight) and the prevalence of indirect interactions. Here,
48 we used a dynamical model based on empirical energy-budget data to assess changes
49 in ecosystem stability after simulating the loss of species according to various
50 extinction scenarios. Link weight and/or indirect effects had stronger effects on food
51 web stability than the simple removal of ‘hubs’, demonstrating that both quantitative
52 fluxes and species dissipating their effects across many links should be of great
53 concern in biodiversity conservation, and the potential for ‘hubs’ to act as keystone
54 species may have been exaggerated to date.

55

56 **Introduction**

57 Biodiversity loss is a major threat to Earth's ecosystems (Barnosky *et al.* 2011) and it
58 is crucial to identify and conserve influential 'keystone' species or nodes, whose loss
59 would cause the cascading extinctions of many other species (Dunne *et al.* 2002;
60 Jordán 2009). Theoretical and empirical approaches to studying the importance of
61 interactions among species in maintaining biodiversity recognize that there is a bi-
62 directional component to every interaction that gauges the separate impacts of one
63 species on the dynamics of another (May 1972; Tang *et al.* 2014). For every direct
64 interaction, the consumer will have a negative effect on the resource and the resource
65 will have a positive effect on the consumer. Simple binary measures of interaction
66 strength have been used to identify 'hubs', i.e. highly connected nodes with a high
67 degree centrality (Dunne *et al.* 2002; Memmott *et al.* 2004; Dunne & Williams 2009).
68 Selective removal of nodes with the most trophic links in a network typically causes
69 more secondary extinctions than random removal of nodes (Dunne *et al.* 2002;
70 Memmott *et al.* 2004; Dunne & Williams 2009). However, this index of node
71 importance based on degree centrality ignores two major components of food webs:
72 the strength or weight of the links and indirect effects (Scotti *et al.* 2007). This can
73 lead to an inaccurate ranking of species importance, such that removing the most
74 connected nodes does not necessarily identify the most destructive extinction
75 sequence (Allesina & Pascual 2009).

76 There has been a tradition of binary descriptions in many network studies,
77 reflecting the relative ease of data collection, but there is a growing appreciation that
78 this qualitative network structure is often uninformative (Jordán *et al.* 2006). An
79 increasing number of studies now consider weighted networks in ecology (Jordán *et*
80 *al.* 2006; Borrett 2013; Ulanowicz *et al.* 2014), which can dramatically alter the
81 conclusions about node importance (Scotti *et al.* 2007; Jordán 2009). In many
82 quantitative food webs, link weights (i.e. the strength of trophic interactions) have
83 been estimated based on the biomass, numbers of individuals, or carbon flows
84 between species or compartments (Moore *et al.* 1993; Jordán *et al.* 2006; Borrett
85 2013). These quantitative approaches are arguably more robust than binary methods,
86 but are not without criticism (Paine 1980). For example, controlled removal studies
87 have demonstrated empirically that material flow does not always translate directly to
88 the impacts that interaction strength purports to capture (Woodward *et al.* 2005).

89 Indirect effects describe the impact of one species on another that is mediated
90 by a third species (Montoya *et al.* 2009), and their importance for the maintenance of
91 structure, stability, and biodiversity in food webs has been increasingly emphasised
92 (Bukovinszky *et al.* 2008; Woodward *et al.* 2008; Sanders *et al.* 2013). Both empirical
93 (Sanders *et al.* 2013) and theoretical (Stouffer & Bascompte 2011; Säterberg *et al.*
94 2013) studies show that secondary extinctions can occur even when a species is more
95 than one trophic link away from the primary extinction. Recent studies that used a
96 static structural approach showed that direct and indirect indices provide quite

97 different rankings of node importance in networks (Scotti *et al.* 2007; Jordán 2009)
98 and we do not know which of the indices performs best at identifying keystone
99 species for maintaining biodiversity.

100 There are two main approaches to simulating the cascading extinctions that
101 occur after primary removals: topological and dynamical analyses (Eklöf & Ebenman
102 2006). Both approaches have strengths and weaknesses: the former considers only
103 binary network structure and so is easier to parameterise, whereas the latter takes into
104 account both link structure and changes in species abundance through time
105 (Curtsdotter *et al.* 2011). In topological models, secondary extinctions emerge from
106 bottom-up cascades (Eklöf & Ebenman 2006). In a natural system, the loss of species
107 can also cause top-down extinction cascades (Elmhagen & Rushton 2007; Säterberg
108 *et al.* 2013), meaning that the full range of indirect effects are not covered and food
109 web robustness is often overestimated (Curtsdotter *et al.* 2011). We chose the
110 dynamical approach here and we simulated natural communities using parameter
111 values derived from empirical data, which should provide more realistic outcomes
112 than can be derived from simulating purely artificial communities (Curtsdotter *et al.*
113 2011). Furthermore, both top-down and bottom-up effects are possible in the
114 dynamical approach, therefore extinction cascades in both directions could be
115 detected. We expect the assessment of node importance indices using the dynamical
116 approach should bring new insights into the magnitude and extent of secondary
117 extinctions.

118 We compared the performance of four different ranking scenarios (considering
119 direct effects only, both direct and indirect effects, weighted direct effects only, and
120 weighted direct and indirect effects) at identifying taxa that maintain biodiversity.
121 Considering the importance of link weight and indirect effects, we expect the nodes
122 with large carbon flux or dissipating their effects across many nodes would be
123 influential. We hypothesised that the indices considering weighted links and/or
124 indirect effects would perform better than the more traditional measures: i.e. more
125 secondary extinctions will be caused in deletion sequences ordered by link weight,
126 direct plus indirect effects, or both.

127

128 **Materials and methods**

129 **QUANTITATIVE FOOD WEBS**

130 We analysed 20 of the 50 aquatic food webs from a recently published database (see
131 Table 1; Salas & Borrett 2011; Borrett 2013). The extraction criteria were as follows:
132 1) small networks (containing no more than 10 nodes) which are easily collapsed
133 were excluded; 2) each dataset was from a distinct study system to avoid
134 pseudoreplication of similar networks from the same location (e.g. we randomly
135 chose one web from Florida Bay Dry Season and Florida Bay Wet Season).

136 The data for each food web include a list of taxa, the carbon biomass of each
137 taxon (g C m^{-2}), the carbon per unit time of import, export, and respiration of each
138 taxon ($\text{g C m}^{-2} \text{ day}^{-1}$), and the carbon flux between a pair of taxa ($\text{g C m}^{-2} \text{ day}^{-1}$). The

139 dataset was archived in the ‘enaR’ package in R (Borrett & Lau 2014). Nodes
140 represent species, trophic guilds, functional groups, or non-living components of the
141 system in which matter is stored. Initially unbalanced food webs, i.e. energy entering
142 a taxon does not exactly balance the output, were balanced using the AVG2 algorithm
143 using established procedures in Matlab 7.12.0 (Allesina & Bondavalli 2003). Our
144 focal food webs exhibit a wide range of network complexity, indicated by taxon
145 richness ($S = 12-125$), binary directed connectance ($C = 0.094-0.366$), and weighted
146 directed connectance ($C_w = 0.029-0.184$), but all of these were within the range
147 reported for other recently described catalogues (see Table 1; *cf.* Williams & Martinez
148 2000; Ings *et al.* 2009). Binary directed connectance is a qualitative descriptor based
149 on binary networks, which measures the proportion of possible links between taxa
150 that are realized; weighted directed connectance C_w is a quantitative descriptor based
151 on Shannon’s entropy (Banašek-Richter *et al.* 2009; see Appendix S1 for details).

152 FOOD WEB DYNAMICS

153 The model was constructed based on energy budgets that index the carbon fluxes
154 entering and leaving each taxon. The imports and exports *via* animal migration and
155 water flows are considered to be in balance and not to influence the food web
156 dynamics, similar to many other dynamical models (Moore *et al.* 1993; Hudson &
157 Reuman 2013). Generally the taxa in the system can be divided into four categories
158 (see Fig. S1): producers, consumers, decomposers, and non-living compartments (i.e.
159 detritus).

160 The change in biomass of producers can be described as:

$$161 \quad \frac{dB_i}{dt} = r_i B_i G_i - \sum_{j=herbi} \Phi_{ij} B_j - d_i B_i \quad (1)$$

162 Here, ‘*herbi*’ are herbivorous taxa, r is the maximum specific or intrinsic growth rate,
 163 G_i is the growth model, following $G_i = 1 - \sum_{j=pro} B_j / K$. Here ‘*pro*’ are producer taxa,
 164 and K is the carrying capacity. The value of K is considered as the total initial
 165 producer biomass in the community multiplied by a term 10^{k_0} . The carrying capacity
 166 coefficient k_0 was set to follow the distribution $U[0, 3]$ (after Hudson & Reuman
 167 2013). Φ_{ij} is the functional response when taxon j consumes taxon i (see below for
 168 more details), and d is the specific death rate. The biomass of producer taxon i is
 169 increased by photosynthesis and decreased by inter-taxon competition, consumption,
 170 and non-predatory death.

171 The change in biomass of consumers (including herbivores and predators) can
 172 be depicted as:

$$173 \quad \frac{dB_i}{dt} = \sum_{j=res} a_i \Phi_{ji} B_j - \sum_{j=pred} \Phi_{ij} B_j - x_i B_i \quad (2)$$

174 Here, ‘*res*’ means resource taxon, ‘*pred*’ means predator taxon, a is the assimilation
 175 efficiency, and x is the respiration rate. The biomass of consumer taxon i is increased
 176 by assimilation of consumed resources and decreased by predation and respiration.

177 The change in biomass of decomposers can be depicted as:

$$178 \quad \frac{dB_i}{dt} = \sum_{j=det} a_i \Phi_{ji} B_j - \sum_{j=pred} \Phi_{ij} B_j - x_i B_i \quad (3)$$

179 Here, ‘*det*’ are detrital taxa. The biomass of decomposer taxon i is increased by
 180 assimilation of consumed detritus and decreased by predation and respiration.

181 In some food webs, detritus has been divided into separate compartments. For
 182 example, there are three detrital taxa in the Florida Bay ecosystem: water particulate
 183 organic carbon (POC), benthic POC, and dissolved organic carbon (DOC). The
 184 change in biomass of each detrital taxa can be described as:

$$185 \quad \frac{dB_i}{dt} = \sum_{j=pro} p_{ji} d_j B_j + \sum_{j=con} (p_{ji} e_j B_j \sum_{k=res} \Phi_{kj}) + \sum_{j=det} c_{ji} B_j - \sum_{j=dec} \Phi_{ij} B_j - \sum_{j=det} c_{ij} B_i \quad (4)$$

186 Here, ‘*con*’ are consumer taxa and ‘*dec*’ are decomposer taxa, p_{ji} is the proportion of
 187 converted detritus i to the total amount of detritus converted from taxon j , $e = (1 - a)$
 188 is the egestion rate, and c_{ji} is the conversion coefficient from detrital taxon j to detrital
 189 taxon i . Here we consider that the amount of faeces, i.e. the unassimilated fraction of
 190 prey killed, is proportional to the amount of predation (Moore *et al.* 1993; de Ruiter *et*
 191 *al.* 1995; Moore & de Ruiter 2012). The biomass stored in detrital taxon i is increased
 192 by the dead bodies of producer taxa, the faeces of consumer taxa, and the conversion
 193 from other detritus, and decreased by consumption of decomposer taxa and
 194 conversion to other detritus. The meanings and calculations of the parameters listed
 195 above (except the functional response Φ which was given below) can be found in
 196 Table 2.

197 FUNCTIONAL FORMS

198 The functional response Φ_{ij} was set to follow either a nonlinear form or a linear form.

199 The nonlinear form was set as follows (see Hudson & Reuman 2013):

200
$$\Phi_{ij} = \frac{y_j \omega_{ij} B_i^h}{H_j^h + q_j B_j H_j^h + \sum_{k=res} \omega_{kj} B_k^h} \quad (5)$$

201 Here y_j is the maximum consumption rate of taxon j and ω_{ij} is the preference of taxon
 202 j for taxon i . For a consumer j , $\omega_{ij} \propto F_{ij} / B_i^h$. F_{ij} is the carbon flux from taxon i to
 203 taxon j , which was contained in the empirical data. Given that $\sum_{i=res} \omega_{ij} = 1$, we can

204 calculate ω_{ij} as:

205
$$\omega_{ij} = \frac{F_{ij} / B_i^h}{\sum_{k=res} F_{kj} / B_k^h} \quad (6)$$

206 H_j is the half-saturation density, which was one order of magnitude either side of the
 207 mean of all biomasses in the community being simulated (Hudson & Reuman 2013).
 208 That means $H_j = 10^b \bar{B}$. Here b is a coefficient following the distribution U[-1, 1]. q_j is
 209 the predator interference coefficient, which was randomly chosen from 0 to 100
 210 (Hudson & Reuman 2013). h is the hill exponent that regulates the shape of the curve
 211 from Holling type II ($h = 1$) to Holling type III ($h = 2$). We chose the value of h
 212 randomly from 1 to 2.

213 Notice that $F_{ij} = \Phi_{ij} B_j$, combining Eq. 5, and we can calculate the value of y_j

214 by:

215
$$y_j = \frac{F_{ij} (H_j^h + q_j B_j H_j^h + \sum_{k=res} \omega_{kj} B_k^h)}{\omega_{ij} B_i^h B_j} \quad (7)$$

216 We ran 1,000 simulations for each food web. The values of parameter b , q , and h for
 217 each simulation were chosen randomly from their ranges, i.e. U[-1, 1] for b , U[0, 100]
 218 for q , and U[1, 2] for h .

219 To increase the generality of our model, we also applied the linear functional
220 response, i.e. the Holling type I. The linear form of the functional response Φ_{ij} is:

$$221 \quad \Phi_{ij} = f_{ij}B_i \quad (8)$$

222 Here f_{ij} is the feeding rate coefficient when taxon j consumes taxon i . The value of f_{ij}
223 can be got by:

$$224 \quad f_{ij} = \frac{F_{ij}}{B_i B_j} \quad (9)$$

225 SEQUENTIAL NODE DELETIONS

226 Following the framework of Scotti *et al.* (2007), but using the whole food web
227 dynamical model, we compared four different rankings based on the presence or
228 absence of information on indirect effects and weighted links. Here, we ordered nodes
229 by their: 1) maximum unweighted direct effect (Max.D); 2) maximum unweighted
230 direct plus indirect effect (Max.DI); 3) maximum weighted direct effect (Max.wD);
231 and 4) maximum weighted direct plus indirect effect (Max.wDI). Unweighted direct
232 effect is defined as the degree centrality of a node (i.e. the number of its direct
233 neighbours including both consumers and resources), while weighted direct effect of a
234 node is defined as the total amount of its inward and outward carbon fluxes. The
235 unweighted direct plus indirect effect is the mean of effects originating from one
236 taxon in a binary network, while weighted direct plus indirect effect has the same
237 meaning but in a weighted network.

238 The method for quantifying the direct plus indirect effects has been used in
239 both undirected (Jordán *et al.* 2006; Jordán 2009) and directed networks (Scotti *et al.*

240 2007). First, we calculated the direct plus indirect effects in unweighted networks. We
 241 defined $a_{n,ij}$ as the effect of taxon j on taxon i when i can be reached from j in n steps.
 242 The simplest case of calculating $a_{n,ij}$ is when $n = 1$:

$$243 \quad a_{1,ij} = \frac{b_{ij}}{\sum_{j=1}^D b_{ij}} \quad (10)$$

244 where b_{ij} is the element of the qualitative feeding matrix. Here $a_{1,i,j} = 1/D_{i,out}$ if
 245 species j is a consumer and $a_{1,i,j} = 1/D_{i,in}$ if species j is a resource. $D_{i,in}$ is the number
 246 of resources for taxon i while $D_{i,out}$ is the number of consumers for taxon i .
 247 Furthermore, we define the n -step effect originating from species i by the following
 248 formula:

$$249 \quad \sigma_{n,i} = \sum_{j=1}^S a_{n,ji} \quad (11)$$

250 The direct and indirect effects originating from species i up to n steps are considered
 251 as:

$$252 \quad DI_i^n = \frac{\sum_{m=1}^n \sigma_{m,i}}{n} = \frac{\sum_{m=1}^n \sum_{j=1}^S a_{m,ji}}{n} \quad (12)$$

253 which represents the sum of effects originating from species i up to n steps averaged
 254 over by the maximum number of steps considered. Here we considered a maximum of
 255 five-step long indirect effects, i.e. $n = 5$. As the strength of indirect effects decreases
 256 dramatically with distance (Berlow *et al.* 2009; Borrett *et al.* 2010; Stouffer &
 257 Bascompte 2011), up to five steps is sufficient to get their precise value (Scotti *et al.*
 258 2007; Borrett *et al.* 2010). For a weighted network, all the effects are defined in the

259 same way as above except that the value of b_{ij} is the amount of biomass flowing from
260 taxon i to taxon j .

261 We simulated taxon loss for each food web by sequentially removing taxa. We
262 used the Adaptive Runge–Kutta method with adaptive step sizes to perform numerical
263 simulations. In each simulation, the empirical biomass data were employed to give the
264 initial biomass values. 1,000 days were simulated first, to allow transient dynamics
265 caused by initial effects to settle down and let the system reach steady state (Hudson
266 & Reuman 2013). Then we started the sequential deletions, which can be seen as a
267 stepwise process: 1,000 days were simulated after each deletion, and secondary
268 extinctions during this time were recorded. Before adding a new step, the deletion
269 sequences were updated, as the extinctions in the former step would change network
270 structure and carbon fluxes among the surviving taxa. During the simulation, a species
271 was considered to be extinct if its biomass fell to $<10^{-30}$ g C m⁻² (Berlow *et al.* 2009).
272 We did not remove any detrital nodes in the extinction sequence (Staniczenko *et al.*
273 2010) to guarantee that energy cycling would occur during the simulations, which
274 thus continued until only detrital nodes were left in the web. Note that an established
275 food web may persist for a long period without autotrophs if detrital taxa have
276 accumulated sufficient carbon storage to sustain detritus-based organisms (see
277 Appendix S2).

278 MEASURES OF STABILITY

279 We employed two indices to characterize the stability of food webs: robustness (R_{50}),
280 and survival area (SA). Robustness was quantified as the proportion of species
281 subjected to primary removals that resulted in 50 percent of total species loss, which
282 is commonly used in such analyses (Dunne *et al.* 2002; Dunne & Williams 2009;
283 Curtsdotter *et al.* 2011). A higher value of R_{50} means fewer secondary extinctions and
284 thus higher stability. SA is the area under the curve resulting from plotting the number
285 of surviving taxa, N_p , having occurred at a specific number of primary deletions, p . SA
286 is calculated as

$$287 \quad SA = \frac{\sum_{p=1}^{S_l} N_p}{S_l^2} \quad (13)$$

288 where S_l is the number of living taxa in the original food web. The value of SA meets
289 the term $SA + EA = 1$, where EA means extinction area as used in prior studies
290 (Allesina & Pascual 2009; Curtsdotter *et al.* 2011). Here we chose SA rather than EA
291 because it exhibits a positive relationship with stability, i.e. a higher value of SA
292 indicates higher stability. All numerical simulations and calculations were carried out
293 in Matlab (version 7.12.0).

294 STATISTICAL PROCEDURES

295 We conducted 1,000 Monte-Carlo simulations for each web and for each node-
296 ordering index, with four parameters (h , k_o , b , and q) varying randomly in each
297 replicate (1,000 replicates \times 20 webs \times 4 indices = 80,000 simulations). We separately
298 compared the effects of the four indices (Max.D, Max.DI, Max.wD, and Max.wDI) on
299 R_{50} and SA using a linear mixed effects model (LME) with a maximum-likelihood

300 estimator (function ‘lme’ with ‘method = ML’ within the ‘nlme’ package in R 3.2.3).
301 Food web identity was included in the model as a random factor to correct for
302 differences between study systems. Post-hoc comparisons were applied using the
303 Tukey HSD test at $\alpha = 0.05$ level of significance (function ‘glht’ within the
304 ‘multcomp’ package). Since robustness and connectance are logarithmically related
305 (Dunne *et al.* 2002), we explored the relationship between stability and log
306 transformations of the measures of complexity (i.e. S , C , and C_w), using the functions
307 ‘lm’ and ‘cor’ in the ‘stats’ package.

308

309 **Results**

310 With the nonlinear functional response, the four deletion orders produced
311 significantly different values of R_{50} (Fig. 1a, LME: $F_{3, 57} = 13.07$, $P < 0.001$). Deletion
312 orders Max.DI, Max.wD, and Max.wDI had significantly lower values of R_{50} than
313 order Max.D (Tukey test, see Table S1). There was no significant difference of R_{50}
314 among the three deletion orders Max.DI, Max.wD, and Max.wDI (Tukey test, Table
315 S1). The four deletion orders also produced significantly different values of SA (Fig.
316 1b, LME: $F_{3, 57} = 12.072$, $P < 0.001$). Again, the three new indices led to significantly
317 lower values of SA than Max.D (Tukey test, Table S1). Using a linear functional
318 response led to significantly lower stability than the nonlinear form (LME: $F_{1, 79} =$
319 98.974 , $P < 0.001$ for R_{50} ; $F_{1, 79} = 101.338$, $P < 0.001$ for SA). The comparison of the
320 four deletion orders produced similar results to the nonlinear functional response,

321 however, with significantly different values of R_{50} (Fig. S2a, LME: $F_{3, 57} = 12.520$, P
322 < 0.001) and SA (Fig. S2b, LME: $F_{3, 57} = 25.048$, $P < 0.001$), while Max.DI, Max.wD,
323 and Max.wDI led to significantly lower stability than Max.D (Tukey test, Table S1).

324 Further analyses showed that different values of the four free parameters (h , k_0 ,
325 b , and q) in the nonlinear functional form did not alter our major conclusion for both
326 R_{50} and SA (Fig. S3-S6), i.e. deletions in Max.D led to significantly higher stability
327 than the three new indices in all groups (Tukey test). With the linear functional
328 response, the change of the only free parameter (k_0) also did not alter this conclusion
329 (Fig. S7).

330 There was no significant difference in the connectivity of nodes that went
331 secondarily extinct compared with the average value of those that remained (Fig. 2a;
332 $t_{19} = 0.31$, $P = 0.762$ for Max.D; $t_{19} = 0.44$, $P = 0.667$ for Max.DI; $t_{19} = 1.65$, $P =$
333 0.115 for Max.wD; and $t_{19} = 1.44$, $P = 0.167$ for Max.wDI). There was a significant
334 difference in the link weight of nodes that went secondarily extinct compared with the
335 average value of those that remained (Fig. 2b; $t_{19} = -14.47$, $P < 0.001$ for Max.D; $t_{19} =$
336 -12.66 , $P < 0.001$ for Max.DI; $t_{19} = -19.03$, $P < 0.001$ for Max.wD; and $t_{19} = -18.40$, P
337 < 0.001 for Max.wDI). Most (54-71%) secondary extinctions were caused by indirect
338 effects (the pink, yellow, and purple groups in Fig. 2c). Bottom-up cascades, which
339 are the only cause of collateral losses in the topological approach, accounted for about
340 40% of secondary extinctions (the red and pink groups in Fig. 2c).

341 Across all 20 food webs, the stability indicated by R_{50} and SA under the four
342 deletion orders with the nonlinear functional response varied significantly with S and
343 C_w , but rarely with C (Table 3 and Fig. 3). More specifically, R_{50} and SA decreased
344 with increasing $\text{Log } S$ (except SA in Max.D) and with decreasing $\text{Log } C_w$ (Table 3).
345 There was no significant effect of the different deletion orders on the slopes of Log
346 R_{50} versus $\text{Log } S$ (Two-way ANOVA: $F_{3,72} = 0.31$, $P = 0.821$) and $\text{Log } C_w$ ($F_{3,72} =$
347 0.07 , $P = 0.977$). Similarly, there was no significant effect of the different deletion
348 orders on the slopes of $\text{Log } SA$ versus $\text{Log } S$ ($F_{3,72} = 0.34$, $P = 0.795$) and $\text{Log } C_w$
349 ($F_{3,72} = 0.09$, $P = 0.968$). The same patterns emerged from the dynamical models
350 based on a linear functional response (Fig. S8). Although food web stability increased
351 with decreasing food web size, we found that the inevitable decrease in the size of a
352 food web during the deletion process seldom affected our conclusion (see Appendix
353 S3).

354

355 **Discussion**

356 In the last few decades, the influence of random loss of nodes ('error') and selective
357 loss of the most-connected nodes ('attack') has been investigated in many real-world
358 networks, e.g. the Internet (Albert *et al.* 2000). All of these networks exhibit high
359 fragility against the removal of the most-connected nodes (i.e. 'hubs'), which in an
360 ecological context suggests these nodes would represent keystone species that play an
361 important role in maintaining biodiversity (Dunne *et al.* 2002; Memmott *et al.* 2004;

362 Dunne & Williams 2009). However, this conclusion is drawn based on topological
363 approaches that always underestimate the amount of secondary extinctions
364 (Curtisdotter *et al.* 2011). Recent studies using a static structural approach have found
365 that node ordering would be altered when considering link weight or indirect effects
366 (Jordán *et al.* 2006; Scotti *et al.* 2007; Bauer *et al.* 2010), suggesting the possibility of
367 more useful centrality indices. Using a food web dynamical model derived from
368 empirical energy budget data, we found that network stability was significantly lower
369 when deletions were ordered by indirect effects, link weight, or both, compared with
370 the ordering by unweighted degree centrality (see Fig. 1). Furthermore, poorly-
371 connected nodes faced the same extinction risk as highly-connected nodes, while
372 nodes with low link weight were more likely to go extinct secondarily (see Fig. 2a-b),
373 indicating the failure of degree centrality and the importance of weighted indices.
374 Over 50% of secondarily extinct nodes were not directly connected to the removed
375 nodes (see Fig. 2c), emphasizing the need to consider indirect effects. These findings
376 suggest that indices considering link weight and indirect effects are better descriptors
377 of centrality in food webs than the traditional binary, direct-link measure. Moreover,
378 our findings were robust to different forms of the functional response and different
379 values of the hill exponent, carrying capacity coefficient, half-saturation coefficient,
380 and predator interference coefficient, suggesting a high level of generality.

381 The uneven distribution of interaction strengths in food webs (O'Gorman *et al.*
382 2010) provides a cautionary note when interpreting results derived from analyses of

383 simple binary networks (Banašek-Richter *et al.* 2009). It is generally assumed that
384 specialised species tend to have strong connections while generalised species have
385 weak interactions (Wootton & Emmerson 2005) and hence weaker net effects
386 (Montoya *et al.* 2009; O'Gorman *et al.* 2010) and different contributions to network
387 structure and stability relative to poorly connected species. We found that species
388 removals ordered by link weight led to a >30% reduction in network stability relative
389 to direct unweighted orderings. This conclusion is important because it suggests that
390 studies focused solely on direct, unweighted indices for identifying key species in
391 food webs may have severely overestimated the relative importance of degree
392 centrality and, while successfully identifying topologically important nodes, they may
393 fail to detect functionally important ones. Notice that considering weights did not add
394 anything to the conclusion as long as indirect effects were considered, which might be
395 caused by the significant correlation between Max.DI and Max.wDI in 18 of the 20
396 food webs (Spearman rank correlation = 0.557 ± 0.037 ; mean \pm SEM).

397 Most empirical studies only contain qualitative food web data due to logistical
398 constraints in collecting quantitative information on link weights, although the
399 situation is improving (Ings *et al.* 2009). Our results show that food web stability is
400 significantly lower after removals ordered by both unweighted direct and indirect
401 effects than by direct effects alone. Thus, in the absence of quantitative data, an
402 understanding of indirect effects will give a more realistic view of species importance
403 than in a network constructed solely from direct link information. This is perhaps

404 unsurprising, given that indirect effects can often be stronger than direct effects in
405 food webs (Werner & Peacor 2003; Salas & Borrett 2011). Trophic cascades and
406 apparent competition are the best known examples of indirect effects (Montoya *et al.*
407 2009). Indirect effects have also been regarded as important drivers of secondary
408 extinctions in a recent empirical study (Sanders *et al.* 2013). In our study, indirect
409 effects accounted for over 50% of the secondary extinctions (Fig. 2c). This implies
410 that not only neighbouring links, but also neighbours of neighbours need to be
411 considered to better understand how species losses propagate. For example, in the
412 well-studied Chesapeake ecosystem, zooplankton have the most direct links to other
413 taxa, whereas bacteria in sediment POC have the strongest direct plus indirect and
414 weighted effects (see Table S2 for the other food webs).

415 The hypothesis that diversity may give rise to ecosystem stability has led to
416 more than half a century of heated debate in ecology (May 1972; Tilman *et al.* 2006).
417 Many experiments have shown that higher diversity is associated with a reduction in
418 temporal variability (i.e. increased temporal stability; Tilman *et al.* 2006; Cardinale *et*
419 *al.* 2009), but the opposite may be true when considering other measures of stability
420 (Donohue *et al.* 2013). Our study demonstrated a negative relationship between
421 species richness and the robustness of food webs to secondary extinction under all
422 four of the deletion scenarios, suggesting that even species-rich ecosystems can be
423 vulnerable to cascading extinctions. A possible explanation for this is density
424 compensation, i.e. population densities decrease with increasing species richness

425 because of the increased intensity of interspecific competition (Borrvall & Ebenman
426 2008; Kaneryd *et al.* 2012). Our data showed a strong negative correlation between
427 average biomass densities and taxon richness (Fig. S9, Pearson correlation coefficient
428 $r = -0.95$, $P < 0.001$), which supported this hypothesis. As a consequence, species are
429 more easily excluded because they are closer to their extinction threshold, a finding
430 consistent with previous dynamical-analyses (Borrvall & Ebenman 2008; Kaneryd *et*
431 *al.* 2012).

432 We found a strong positive relationship between weighted directed
433 connectance, C_w , and food web stability, but a surprisingly weak relationship with
434 binary directed connectance, C . This stands in contrast to earlier topological analyses
435 (Dunne *et al.* 2002; Dunne & Williams 2009) conducted on binary networks of direct
436 links. When topological approaches are used, highly connected communities are
437 robust to species loss because species with many binary links are unlikely to become
438 isolated and thus go extinct. Using a dynamical approach, however, highly connected
439 nodes face a similar extinction risk as poorly connected nodes (Fig. 2a). In this case,
440 the density of weighted carbon flows plays an increasingly important role, where the
441 loss of a particularly strong link may result in a node receiving insufficient energy to
442 persist in the network, even if it retains several weak connections to other nodes.
443 Therefore the nodes with lower link weight would have a significantly higher risk of
444 going secondarily extinct (Fig. 2b). This is also consistent with recent findings that
445 increasing the energy threshold for consumer secondary extinction would nullify the

446 previously positive relationship between robustness and binary directed connectance
447 (Thierry *et al.* 2011; Bellingeri & Bodini 2013). The dynamical approach, through the
448 weighting of links refines our understanding of the factors affecting network stability
449 in ways that topological analyses cannot do because they assign equal importance to
450 all connections in the network (Eklöf & Ebenman 2006; Curtsdotter *et al.* 2011).

451 Moreover, in the topological approach, nodes are considered to be extinct only
452 when they lose all their resources, so all secondary extinctions emerge from bottom-
453 up cascades (Eklöf & Ebenman 2006). In dynamical approaches, however, a node
454 cannot persist if it receives insufficient energy, even though it still has resources. This
455 is in agreement with a recent study (Bellingeri & Bodini 2013), which investigated the
456 effects of the thresholds of minimum energy requirement for species survival on the
457 robustness of food webs. Top-down effects and other effects mediated by exploitative
458 and apparent competition can also play an important role (Elmhagen & Rushton 2007;
459 Säterberg *et al.* 2013). In our study, bottom-up effects only accounted for about half
460 of all the secondary extinctions (Fig. 2c), highlighting the potential for dynamical
461 analyses to identify a significant proportion of secondary extinctions that would
462 otherwise be missed with topological approaches.

463 As we enter the age of the sixth mass extinction (Barnosky *et al.* 2011), we
464 need efficient indices to quantify the relative importance of species to develop new
465 management policies for prioritising key populations to be conserved (Waldron *et al.*
466 2013). Our study contributes towards potential solutions and may help ecologists to

467 outline a better conservation policy based on the functional importance of species,
468 rather than qualitative metrics such as rarity or ‘hubs’. By quantifying link weights (or
469 in the absence of quantitative link data, by considering indirect effects) we can
470 improve the accuracy of keystone species identification (Jordán *et al.* 2008). The
471 extent to which our methods help in detecting more accurate indices remains to be
472 seen, but we posit that it will improve the designs of subsequent experiments or
473 dynamical simulation studies.

474

475 **Data Accessibility**

476 All data used in this paper are available in the ‘enaR’ package (Borrett & Lau 2014)
477 in R (<https://cran.r-project.org/web/packages/enaR/index.html>).

478

479 **Acknowledgements**

480 This study was financially supported by the National Special Water Programs (No.
481 2009ZX07210-009, No. 2015ZX07203-011, No. 2015ZX07204-007), Department of
482 Environmental Protection of Shandong Province (SDHBPJ-ZB-08), the China
483 Scholarship Council (No. 201206730022), the Chinese Natural Science Foundation
484 (No. 39560023), NERC grants NE/L011840/1 and NE/I009280/2, and Imperial
485 College London’s Grand Challenges in Ecosystems and the Environment initiative.

486

487 **References**

488 Albert R., Jeong H. & Barabási A. (2000). Error and attack tolerance of complex
489 networks. *Nature*, 406, 378-382.

490 Allesina S. & Bondavalli C. (2003). Steady state of ecosystem flow networks: A
491 comparison between balancing procedures. *Ecol. Model.*, 165, 221-229.

492 Allesina S. & Pascual M. (2009). Googling food webs: can an eigenvector measure
493 species' importance for coextinctions? *PLoS Comput. Biol.*, 5, e1000494.

494 Banašek-Richter C., Bersier L., Cattin M., Baltensperger R., Gabriel J., Merz Y.,
495 Ulanowicz R.E., Tavares A.F., Williams D.D. & Ruitter P.C. (2009). Complexity in
496 quantitative food webs. *Ecology*, 90, 1470-1477.

497 Barnosky A.D., Matzke N., Tomiya S., Wogan G.O., Swartz B., Quental T.B.,
498 Marshall C., McGuire J.L., Lindsey E.L. & Maguire K.C. (2011). Has the Earth's
499 sixth mass extinction already arrived? *Nature*, 471, 51-57.

500 Bauer B., Jordán F. & Podani J. (2010). Node centrality indices in food webs: Rank
501 orders versus distributions. *Ecol. Complex.*, 7, 471-477.

502 Bellingeri M. & Bodini A. (2013). Threshold extinction in food webs. *Theor. Ecol.-*
503 *Neth.*, 6, 143-152.

504 Berlow E.L., Dunne J.A., Martinez N.D., Stark P.B., Williams R.J. & Brose U.
505 (2009). Simple prediction of interaction strengths in complex food webs. *Proc. Natl.*
506 *Acad. Sci. U.S.A.*, 106, 187-191.

507 Borrett S.R. (2013). Throughflow centrality is a global indicator of the functional
508 importance of species in ecosystems. *Ecol. Indic.*, 32, 182-196.

509 Borrett S.R. & Lau M.K. (2014). enaR: An R package for Ecosystem Network
510 Analysis. *Methods Ecol. Evol.*, 5, 1206-1213.

511 Borrett S.R., Whipple S.J. & Patten B.C. (2010). Rapid development of indirect
512 effects in ecological networks. *Oikos*, 119, 1136-1148.

513 Borrvall C. & Ebenman B. (2008). Biodiversity and persistence of ecological
514 communities in variable environments. *Ecol. Complex.*, 5, 99-105.

515 Bukovinszky T., van Veen F.F., Jongema Y. & Dicke M. (2008). Direct and indirect
516 effects of resource quality on food web structure. *Science*, 319, 804-807.

517 Cardinale B.J., Srivastava D.S., Duffy J.E., Wright J.P., Downing A.L., Sankaran M.,
518 Jouseau C., Cadotte M.W., Carroll I.T., Weis J.J., Hector A., Loreau M. & Michener
519 W.K. (2009). Effects of biodiversity on the functioning of ecosystems: a summary of
520 164 experimental manipulations of species richness. *Ecology*, 90, 854-854.

521 Curtsdotter A., Binzer A., Brose U., de Castro F., Ebenman B., Eklöf A., Riede J.O.,
522 Thierry A. & Rall B.C. (2011). Robustness to secondary extinctions: Comparing trait-
523 based sequential deletions in static and dynamic food webs. *Basic Appl. Ecol.*, 12,
524 571-580.

525 de Ruiter P.C., Neutel A. & Moore J.C. (1995). Energetics, patterns of interaction
526 strengths, and stability in real ecosystems. *Science*, 1257-60.

527 Donohue I., Petchey O.L., Montoya J.M., Jackson A.L., McNally L., Viana M., Healy
528 K., Lurgi M., O'Connor N.E. & Emmerson M.C. (2013). On the dimensionality of
529 ecological stability. *Ecol. Lett.*, 16, 421-429.

530 Dunne J.A. & Williams R.J. (2009). Cascading extinctions and community collapse in
531 model food webs. *Philos. Trans. R. Soc. B*, 364, 1711.

532 Dunne J.A., Williams R.J. & Martinez N.D. (2002). Network structure and
533 biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.*, 5,
534 558-567.

535 Eklöf A. & Ebenman B.O. (2006). Species loss and secondary extinctions in simple
536 and complex model communities. *J. Anim. Ecol.*, 75, 239-246.

537 Elmhagen B. & Rushton S.P. (2007). Trophic control of mesopredators in terrestrial
538 ecosystems: top-down or bottom-up? *Ecol. Lett.*, 10, 197-206.

539 Hudson L.N. & Reuman D.C. (2013). A cure for the plague of parameters:
540 constraining models of complex population dynamics with allometries. *Proceedings*
541 *of the Royal Society B: Biological Sciences*, 280.

542 Ings T.C., Montoya J.M., Bascompte J., Blüthgen N., Brown L., Dormann C.F.,
543 Edwards F., Figueroa D., Jacob U. & Jones J.I. (2009). Ecological networks – beyond
544 food webs. *J. Anim. Ecol.*, 78, 253-269.

545 Jordán F. (2009). Keystone species and food webs. *Philos. Trans. R. Soc. B*, 364,
546 1733-1741.

547 Jordán F., Liu W.C. & Davis A.J. (2006). Topological keystone species: measures of
548 positional importance in food webs. *Oikos*, 112, 535-546.

549 Jordán F., Okey T.A., Bauer B. & Libralato S. (2008). Identifying important species:
550 linking structure and function in ecological networks. *Ecol. Model.*, 216, 75-80.

551 Kaneryd L., Borrvall C., Berg S., Curtsdotter A., Eklöf A., Hauzy C., Jonsson T.,
552 Münger P., Setzer M. & Säterberg T. (2012). Species-rich ecosystems are vulnerable
553 to cascading extinctions in an increasingly variable world. *Ecol. Evol.*, 2, 858-874.
554 May R.M. (1972). Will a large complex system be stable? *Nature*, 238, 413-414.
555 Memmott J., Waser N.M. & Price M.V. (2004). Tolerance of pollination networks to
556 species extinctions. *Proc. R. Soc. Lond. B*, 271, 2605-2611.
557 Montoya J.M., Woodward G., Emmerson M.C. & Solé R.V. (2009). Press
558 perturbations and indirect effects in real food webs. *Ecology*, 90, 2426-2433.
559 Moore J.C. & de Ruiter P.C. (2012). *Energetic food webs: an analysis of real and*
560 *model ecosystems*. Oxford University Press, Oxford.
561 Moore J.C., De Ruiter P.C. & Hunt H.W. (1993). Influence of productivity on the
562 stability of real and model ecosystems. *Science*, 261, 906-906.
563 O'Gorman E.J., Jacob U., Jonsson T. & Emmerson M.C. (2010). Interaction strength,
564 food web topology and the relative importance of species in food webs. *J. Anim.*
565 *Ecol.*, 79, 682-692.
566 Paine R.T. (1980). Food webs: linkage, interaction strength and community
567 infrastructure. *J. Anim. Ecol.*, 49, 667-685.
568 Salas A.K. & Borrett S.R. (2011). Evidence for the dominance of indirect effects in
569 50 trophic ecosystem networks. *Ecol. Model.*, 222, 1192-1204.
570 Sanders D., Sutter L. & Veen F.J. (2013). The loss of indirect interactions leads to
571 cascading extinctions of carnivores. *Ecol. Lett.*, 16, 664-669.

572 Säterberg T., Sellman S. & Ebenman B. (2013). High frequency of functional
573 extinctions in ecological networks. *Nature*, 499, 468-470.

574 Scotti M., Podani J. & Jordán F. (2007). Weighting, scale dependence and indirect
575 effects in ecological networks: a comparative study. *Ecol. Complex.*, 4, 148-159.

576 Staniczenko P., Lewis O.T., Jones N.S. & Reed Tsochas F. (2010). Structural
577 dynamics and robustness of food webs. *Ecol. Lett.*, 13, 891-899.

578 Stouffer D.B. & Bascompte J. (2011). Compartmentalization increases food-web
579 persistence. *Proc. Natl. Acad. Sci. U.S.A.*, 108, 3648-3652.

580 Tang S., Pawar S. & Allesina S. (2014). Correlation between interaction strengths
581 drives stability in large ecological networks. *Ecol. Lett.*, 17, 1094-100.

582 Thierry A., Beckerman A.P., Warren P.H., Williams R.J., Cole A.J. & Petchey O.L.
583 (2011). Adaptive foraging and the rewiring of size-structured food webs following
584 extinctions. *Basic Appl. Ecol.*, 12, 562-570.

585 Tilman D., Reich P.B. & Knops J.M.H. (2006). Biodiversity and ecosystem stability
586 in a decade-long grassland experiment. *Nature*, 441, 629-632.

587 Ulanowicz R.E., Holt R.D. & Barfield M. (2014). Limits on ecosystem trophic
588 complexity: insights from ecological network analysis. *Ecol. Lett.*, 17, 127-136.

589 Waldron A., Mooers A.O., Miller D.C., Nibbelink N., Redding D., Kuhn T.S.,
590 Roberts J.T. & Gittleman J.L. (2013). Targeting global conservation funding to limit
591 immediate biodiversity declines. *Proc. Natl. Acad. Sci. U.S.A.*, 110, 12144-12148.

592 Werner E.E. & Peacor S.D. (2003). A review of trait-mediated indirect interactions in

593 ecological communities. *Ecology*, 84, 1083-1100.

594 Williams R.J. & Martinez N.D. (2000). Simple rules yield complex food webs.
595 *Nature*, 404, 180-183.

596 Woodward G., Papantoniou G., Edwards F. & Lauridsen R.B. (2008). Trophic trickles
597 and cascades in a complex food web: impacts of a keystone predator on stream
598 community structure and ecosystem processes. *Oikos*, 117, 683-692.

599 Woodward G., Speirs D.C. & Hildrew A.G. (2005). Quantification and resolution of a
600 complex, size-structured food web. *Adv. Ecol. Res.*, 36, 85-135.

601 Wootton J.T. & Emmerson M. (2005). Measurement of interaction strength in nature.
602 *Annu. Rev. Ecol. Evol. Syst.*, 419-444.

603

604

605 **Table 1** Original names and structural properties of the 20 empirical food webs

606 examined in the study.

Food web	Original name	S*	C†	C _w ‡
Bothnian Bay	Bothnian Bay	12	0.222	0.184
Baltic Sea	Baltic Sea	15	0.173	0.184
Ems Estuary	Ems Estuary	15	0.196	0.169
Swartkops	Swartkops Estuary	15	0.169	0.121
Crystal River	Crystal River (control)	21	0.186	0.070
Benguela	Northern Benguela Upwelling	24	0.208	0.101
Neuse Estuary	Neuse Estuary (late summer 1998)	30	0.138	0.062
Georges Bank	Georges Bank	31	0.354	0.162
Gulf of Maine	Gulf of Maine	31	0.345	0.148
Narragansett	Narragansett Bay	32	0.154	0.093
Atlantic Bight	Middle Atlantic Bight	32	0.366	0.156
New England	Southern New England Bight	33	0.347	0.154
Chesapeake	Chesapeake Bay	36	0.094	0.068
St. Marks	St. Marks Seagrass, site 1 (Feb.)	51	0.103	0.086
Graminoids	Graminoids (wet)	66	0.182	0.033
Cypress	Cypress (wet)	68	0.118	0.060
Lake Oneida	Lake Oneida (pre-ZM)	74	0.223	0.072
Bay of Quinte	Bay of Quinte (pre-ZM)	74	0.211	0.056
Mangroves	Mangroves (wet)	94	0.152	0.036
Florida Bay	Florida Bay (wet)	125	0.124	0.029

607 * number of taxa.

608 † binary directed connectance, L/S^2 ; where L is the number of trophic links.

609 ‡ weighted directed connectance (see Materials and Methods for calculation method).

610

611 **Table 2** Details of the parameters used in the model.

Symbol	Meaning	Value	Unit
r_i	Maximum specific or intrinsic growth rate	$(GPP_i - R_i) / [B_i(1 - 1/10^{k_0})]$	day ⁻¹
K	Carrying capacity	$10^{k_0} \sum_{j=pro} B_i$	g C m ⁻²
d_i	Natural specific death rate	$\sum_{j=det} F_{ij} / B_i$	day ⁻¹
a_i	Assimilation efficiency	$1 - \sum_{j=det} F_{ij} / \sum_{j=res} F_{ji}$	proportion (unitless)
x_i	Respiration rate	R_i / B_i	day ⁻¹
p_{ji}	Proportion of converted detritus i in all the converted detritus from producer or consumer taxon j	$F_{ji} / \sum_{k=det} F_{jk}$	proportion (unitless)
e_i	Egestion rate	$1 - a_i$	proportion (unitless)
c_{ji}	Conversion coefficient from detritus j to detritus i	F_{ji} / B_j	day ⁻¹

612 Our data (see Table 1) contain the values of GPP_i (gross primary production), R_i (respiration),
613 B_i (biomass), and F_{ij} (carbon flux when taxon j consumes taxon i). k_0 is an undetermined
614 parameter. Considering that carrying capacity K was within three orders of magnitude of total
615 primary producer biomass in the community being simulated (Hudson & Reuman 2013), we
616 assumed k_0 follows the distribution U[0, 3]. We ran 1,000 separate simulations for each food web,
617 using different values of k_0 , chosen randomly from this distribution.

618 **Table 3** Stability of food webs under four different species deletion sequences as a
 619 function of three measures of food web complexity.

Stability	Deletion sequences	<i>Log S</i>			<i>Log C</i>			<i>Log C_w</i>		
		Slope	<i>P</i>	<i>r</i> ²	Slope	<i>P</i>	<i>r</i> ²	Slope	<i>P</i>	<i>r</i> ²
<i>R</i> ₅₀	Max.D	-0.067	0.043	0.21	0.201	<0.001	0.69	0.096	0.008	0.33
	Max.DI	-0.092	0.002	0.41	0.081	0.141	0.12	0.076	0.040	0.21
	Max.wD	-0.072	0.022	0.26	0.065	0.238	0.08	0.085	0.016	0.28
	Max.wDI	-0.094	0.007	0.34	0.112	0.065	0.18	0.106	0.008	0.33
SA	Max.D	-0.053	0.083	0.16	0.186	<0.001	0.71	0.082	0.013	0.30
	Max.DI	-0.083	0.001	0.45	0.096	0.035	0.22	0.078	0.010	0.31
	Max.wD	-0.064	0.030	0.23	0.065	0.209	0.09	0.081	0.015	0.29
	Max.wDI	-0.081	0.012	0.30	0.107	0.051	0.20	0.095	0.009	0.33

620 Linear regressions of robustness, *R*₅₀ (the fraction of species that have to be removed in order to
 621 induce ≥50% total species loss), and survival area, SA (the area under the curve resulting from
 622 plotting the number of survival taxa), of 20 food webs to species loss following four deletion
 623 sequences as a function of the logarithm of taxon richness (*S*), binary directed connectance (*C*),
 624 and weighted directed connectance (*C_w*). Significant results (*P* < 0.05) are shown in bold.
 625

626 **Figure Legends:**

627

628 **Figure 1** Stability of the 20 food webs to species loss in 4 deletion sequences (mean \pm
629 SEM). Here, stability is represented by (a) robustness, R_{50} , the fraction of taxa that
630 have to be removed in order to induce $\geq 50\%$ total taxon loss, and (b) survival area,
631 SA, the area under the curve resulting from plotting the number of surviving taxa. The
632 stars directly above the error bars denote significant differences in stability between
633 the focal deletion orders and the control order (Max.D): *** $p < 0.001$; ** $p < 0.01$; * p
634 < 0.05 ; and NS, not significant.

635

636 **Figure 2** (a-b) Comparison of the types of nodes that went secondarily extinct with
637 those surviving. The nodes going secondarily extinct were significantly different
638 (denoted by stars) from the surviving nodes in (a) number of links or (b) link weight if
639 the confidence intervals around the logarithm of the ratio between the value of the
640 secondarily extinct nodes and the average value of all surviving nodes did not overlap
641 with zero. (c) Trophic categories of nodes that caused the secondary extinctions. The
642 percentage of secondary extinctions for each trophic category across the 1,000
643 simulations of all 20 food webs is shown, along with an illustration of what each of
644 the trophic categories imply.

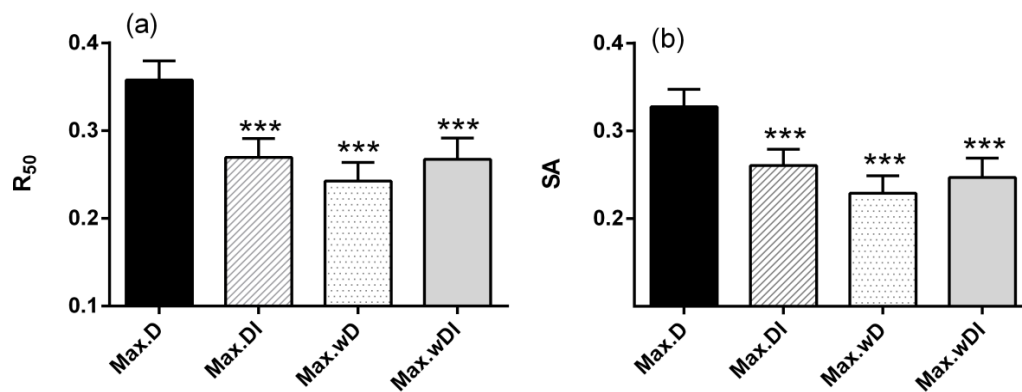
645

646 **Figure 3** Stability in nonlinear functional response simulations indicated by

647 robustness, R_{50} (top panels), and survival area, SA (bottom panels), as a function of
648 the taxon richness, S (left panels), and weighted directed connectance, C_w (right
649 panels), of each food web. Logarithmic fits to the four datasets are shown, with
650 different colours and markers indicating different deletion orders.

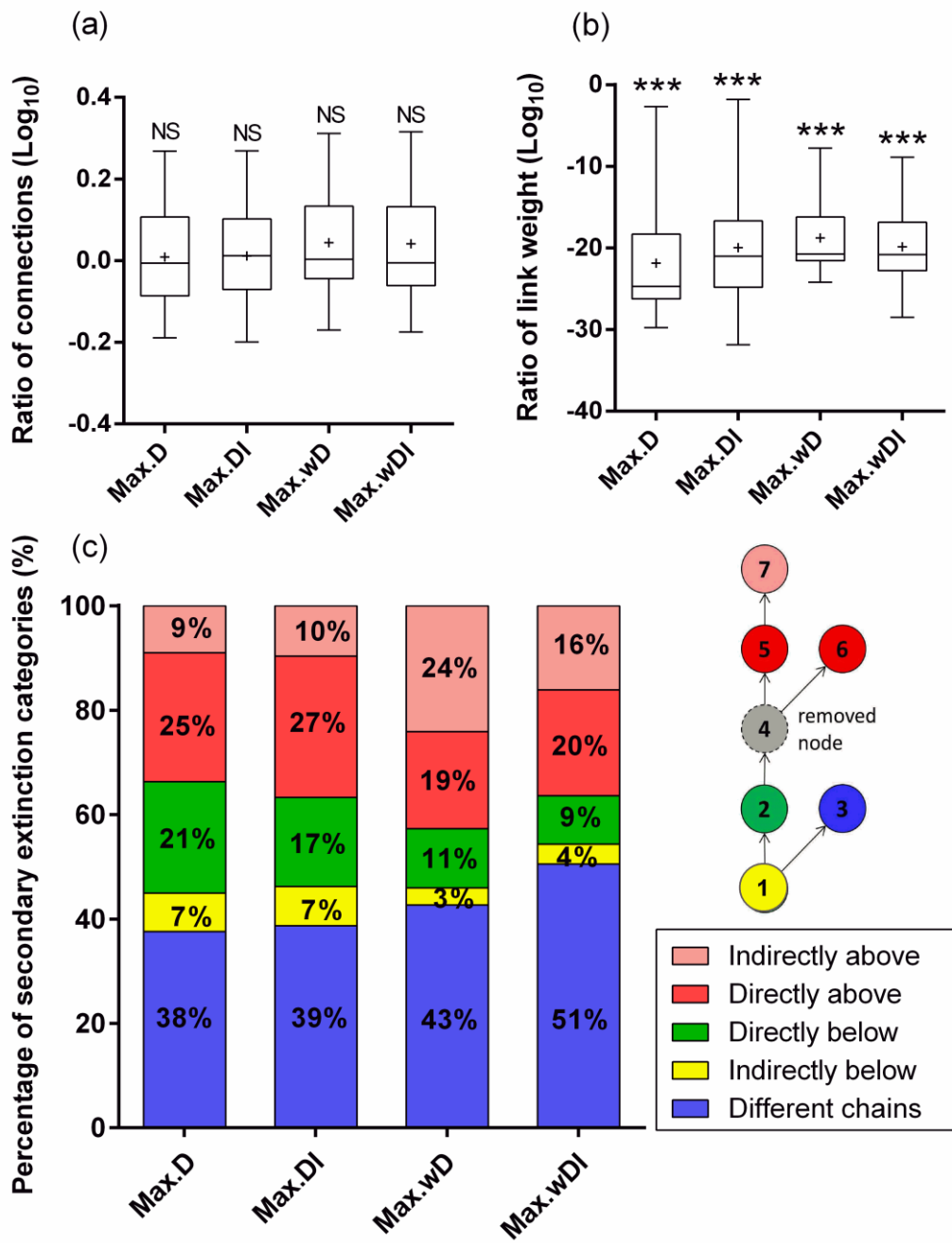
651

652 **Figure 1**



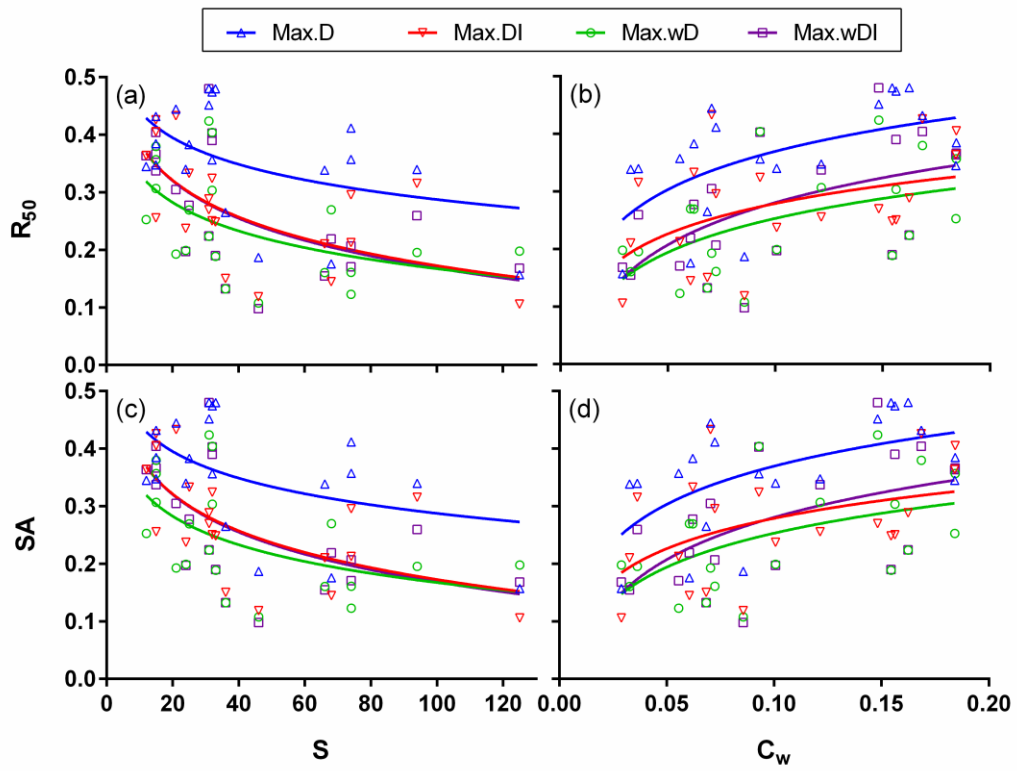
653

654 **Figure 2**



655
656

657 **Figure 3**



658