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Who dominates whom in the ecosystem? Energy flow bottlenecks and cascading extinctions☆

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Abstract

In this paper, we investigate the problem of secondary extinction in food webs through the use of dominator trees, network topological structures that reduce food webs to linear pathways that are essential for energy delivery. Each species along these chains is responsible for passing energy to the taxa that follow it, and, as such, it is indispensable for their survival; because of this it is said to dominate them. The higher the number of species a node dominates, the greater the impact resulting from its removal. By computing dominator trees for 13 well-studied food webs we obtained for each of them the number of nodes dominated by a single species and the number of nodes that dominate each species. We illustrate the procedure for the Grassland Ecosystem showing the potential of this method for identifying species that play a major role in energy delivery and are likely to cause the greatest damage if removed. Finally, by means of two indices that measure error and attack sensitivity, we confirm a previous hypothesis that food webs are very robust to random loss of species but very fragile to the selective loss of the hubs.

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Keywords: Food web; Energy flow; Bottleneck; Graph theory; Dominator; Secondary extinction; Species removal

1. Introduction

An increasingly important focus of ecological research looks at environmental problems related to human activities (Laurance, 2001; Loreau et al., 2001; Tilman et al., 2001) such as biodiversity loss due to habitat destruction (Tabarelli et al., 1999; Coleman and Williams, 2002), climate change (Bawa and Markham, 1995) and introduction of allochthonous species (Shoener and Spiller, 1996; Da Silva and Tabarelli, 2000; Shea and Chesson, 2002). In this framework, the possibility that species loss may lead to cascades of further extinctions is of particular concern (Pimm, 1980; Greenwood, 1987). Although extinction and its effect on ecosystem has been framed in various contexts of ecological research, from the diversity–stability question (Tilman and Downing, 1994; McCann, 2000) to investigation on the relation between biodiversity and ecosystem functioning (Symstad et al., 1998; Ruesink and Srivastava, 2001), only studies aimed at understanding the role of keystone species (Spencer et al., 1991; Estes et al., 1998) considered the issue of secondary extinction specifically, although no general conclusion about patterns or mechanisms responsible for secondary extinction were among the objectives of the research.

At the heart of this question is the issue of species interdependence in ecosystems. Whenever a species that is eaten by another disappears, if the consumer has no alternative resource to exploit, it will also go extinct. In this paper we analyse secondary extinction as related to interdependence of species or guilds for energy. This is a simplified scenario as other factors may affect patterns of secondary extinction as well. For example interdependence is not only for food, but for any other factor that makes up each species' niche (i.e. chemical environment, shelter, habitat modifications and so forth) (Jones et al., 1997); also environmental variability greatly affects patterns of coexistence and extinction

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(Ripa et al., 1998) and the multiplicity of connections in an ecological community, through a variety of indirect effects, may either amplify or buffer effects of food-web alterations (Wootton, 2002). However, clarifying how food-web structure (i.e. reciprocal dependence for food) affect patterns of secondary extinction may add to the scientific debate on extinction.

Theoretical analysis of the problem of cascading extinctions has developed in two main directions: one based on demographic/dynamic models, the other focused on trophic or food-web models. The former, using generalized Lotka–Volterra equations, has produced various results: probability of secondary extinction may increase with community size (Lundberg et al., 2000), but, also, this risk is reduced with greater numbers of species per functional group (Borrvall et al., 2000). Dynamics-based models are shaped on a general template that fails to grasp the structural properties of real communities both in terms of species richness and topology. As such, they are useful to understand the consequences of certain general features such as redundancy, community size, distribution of interaction strength and so forth, but may often lead to contrasting results depending on the rules that are used to assemble the model (Jordán et al., 2002). Food-web models reconstruct the topology of trophic interactions observed or inferred in actual ecosystems. Using these models, patterns of secondary extinction (extinctions caused by the former disappearance of a species) have been investigated as a function of structural properties such as connectance (links/species^2) and species richness (Dunne et al., 2002a). Since interdependence relates to trophic connections, analysing connectance seems appropriate for understanding secondary extinctions. However, interdependence refers also to the position the species occupy within the flowing of matter and energy in the ecosystem, and that defines their role in concentrating and distributing the energy. In this respect connectance, which accounts for the number of links and not for their functional characteristics, may not fully embrace the problem of interdependence and, consequently, that of secondary extinctions.

In this paper, we investigate secondary extinctions in food webs by focusing on the concept of interdependence with the help of dominator trees (Lowry and Medlock, 1969; Lengauer and Tarjan, 1979; Aho et al., 1986). Matter and energy move in food webs from producers to consumers following complex pathways. Certain routes are obligatory when there are no alternative paths for energy to flow from one species to another. A dominator tree is the topological construct that groups the whole suite of these obligatory routes. Any species in these chains is said to dominate the followings, because they necessarily depend on it to satisfy their own energy requirement. This is the reason why these topologies are called dominator trees.

While assessing the effects of random species loss (*errors*) and targeted species removals (*attacks*) (Albert et al., 2000; Dunne et al., 2002a) through the use of specific indices, we show the potential of dominator trees to anticipate losses caused by species removal and to identify which nodes are likely to cause the greatest impact if removed. In this respect, dominator trees seem a promising approach for identifying keystone nodes in ecological food webs.

2. Materials and methods

2.1. Food webs and dominator trees

We analysed a set of 13 food webs chosen among those used in previous investigations on secondary extinction (Solé and Montoya, 2001; Dunne et al., 2002a). As representations of "who eats whom" relations, food webs describe how species depend on each other for their energy requirements. Extinction may have different cascading effects depending on where target species are positioned with respect to the flow of energy from producers to consumers. In linear food chains, the loss of a species causes all the others following it to go extinct. In food webs, the multiple reticulate connections create such a complex scenario that reciprocal dependence is inherently difficult to understand and, consequently, secondary extinctions very complicated to predict (Yodzis and Winemiller, 1999).

Dominator trees are topological structures in which nodes are sequentially connected based on their dominance relations. An example of a simple food web and its dominator tree is given in Fig. 1.

Node a is a dominator of b ($a = dom(b)$) if every path from r (representing the external environment or root) to b contains a: that is to say, a quantum of matter entering into the system cannot reach b without visiting a. From this definition it follows that every node

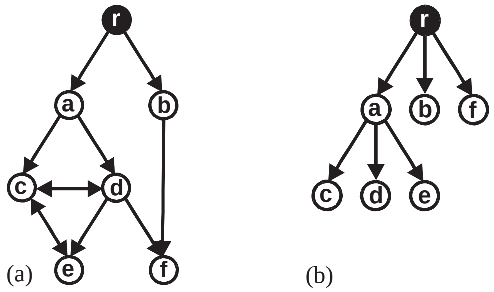

Fig. 1. Hypothetical network rooted in r (left side) and the corresponding dominator tree (right side). The node r represents the external environment the ultimate source of energy for all the species. The algorithm for constructing the dominator tree is given in the text.

dominates itself ($a = dom(a)$). Then we can define a "proper dominator": a is a proper dominator of b if $a = dom(b)$ and $a \neq b$. If $a = dom(b)$ and every other proper dominator of b ($c = dom(b)$, $c \neq a \neq b$) is also dominator of a ($c = dom(a)$), then a is the "immediate dominator" of b. One of the fundamental theorems of dominator trees (Lengauer and Tarjan, 1979) states "every node of a graph except r has a unique immediate dominator". Accordingly, in the dominator tree a link connecting a and b exists if and only if a is the immediate dominator of b.

With reference to Fig. 1a, species f receives energy along the pathways $r \rightarrow a \rightarrow d \rightarrow f$ and $r \rightarrow b \rightarrow f$, but Fig. 1b shows that only the root dominates f, because it is the only node in common between the two paths. When either a or d become extinct, species f may survive because at least one pathway remains at its disposal. All the energy available to e passes trough r and a, so that both are dominators of this node, and a is its immediate dominator.

We transformed the 13 food webs into rooted networks with N nodes: N-1 species or trophic species (species that share the same set of predators and prey) and the special node r, representing the root of the network, from which the energy enters the system. It stands for the external environment, the ultimate source of energy for any ecosystem; the nodes are connected with E edges (trophic links, representing flows of energy between nodes). We linked r to all basal species, nodes with no incoming edges. This choice seems not only plausible but also ecologically necessary. To survive, in fact, these nodes must receive medium from the outer environment. With no clear indications on where the external environment is linked to the system, basal species become the natural candidates for importing medium. The root's position affects the final outcomes, and should be decided according to ecological basis. For example in this work we kept into account nutrient pools, treating them as "normal nodes". We have done this to contrast our results with those of previous studies that utilized the same food webs. This approach is questionable and could be challenged when applying the methodology to real cases, for example in conservation biology issues. This problem will be discussed in detail elsewhere, when the same analysis proposed here will be carried out on ecological flow networks (Baird and Ulanowicz, 1989; Heymans et al., 2002), which define the nodes through which energy enters the system and, consequently, where the root has to be positioned (Allesina, manuscript in preparation).

For each network dominator tree was constructed by computing the set of dominators for each node. This was done using an algorithm that selects iteratively common nodes between pathways (Aho et al., 1986; see the Supplementary Data for a detailed description of the procedure).

2.2. Error sensitivity and attack sensitivity

After generating dominator trees for the 13 food webs, for each node i the size of the subset of its proper dominators was computed. Recalling that every node dominate itself this number can be written as ($|dom(i)| - 1$) (the root r is not counted because, if removed, the entire system would vanish). Then we calculated the probability that ith node would disappear after randomly removing a node (excluding r) from the web as according to the probability $(|dom(i)| - 1)/(N - 1)$. By averaging this probability among all nodes, we obtained a measure of the fraction of species that would go extinct following a random removal. In other words, we computed an index of "error sensitivity" (ES) (Albert et al., 2000), whose expression is given as

$$ES = \sum_{i \neq r} \frac{|dom(i)| - 1}{(N - 1)^2}. \tag{1}$$

The structure of the dominator tree affects this index. Consider the two configurations given in Fig. 2: a straight linear chain (2a) and a star-like structure (2b).

In 2a every species dominates all those that follow it in the sequence, whereas in the star-like structure all the nodes are dominated just by the root. Computation of ES yields in the two cases, respectively,

$$\begin{aligned} ES &= \sum_{i \neq r} \frac{|dom(i)| - 1}{(N - 1)^2} = \frac{1}{(N - 1)^2} + \frac{2}{(N - 1)^2} \\ &\quad + \ldots + \frac{N - 1}{(N - 1)^2} = \frac{N(N - 1)}{2(N - 1)^2} = \frac{N}{2(N - 1)} \approx \frac{1}{2}, \end{aligned} \tag{2}$$

$$\begin{aligned} ES &= \sum_{i \neq r} \frac{|dom(i)|}{(N - 1)^2} = \frac{1}{(N - 1)^2} + \frac{1}{(N - 1)^2} + \frac{1}{(N - 1)^2} \\ &\quad + \ldots + \frac{1}{(N - 1)^2} = \frac{N - 1}{(N - 1)^2} = \frac{1}{N - 1}. \end{aligned} \tag{3}$$

On average, in a linear structure we expect a single node removal to cause half of the nodes to disappear (maximum sensitivity). In the star-like topology no secondary extinction is expected and this is expressed by the value $1/(N - 1)$. Linear chains and star-like structures are extreme configurations that define the range of variation for ES. While ES takes into account

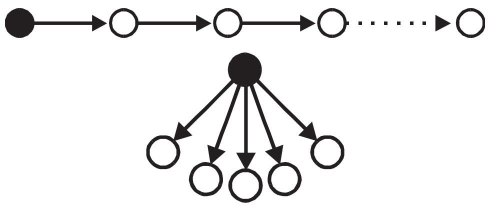

Fig. 2. Extreme configurations for dominator trees: linear chain (upper) and star-like architecture (lower). The black node is root r.

effects of random removals, another index is needed to account for the removal of nodes that play a pivotal role in passing energy, and that likely can cause many secondary extinctions. We measured this "attack sensitivity" (AS) (Albert et al., 2000) by the maximum damage that we can make with a single node removal, or

$$AS = \max\left\{\frac{|dom(i)| - 1}{(N - 1)}\right\} \forall i \neq r. \tag{4}$$

AS ranges between 0 and 1. In a linear dominator tree the percentage of extinction when the basal node is removed is 100% (all species disappear). As with ES, no secondary extinction is expected in a star-like dominator tree. Low ES and low AS values pertain to error-tolerant and attack-tolerant systems, respectively.

3. Results

Table 1 list the 13 food webs used in this study.

An interesting case, particularly useful for understanding the method of dominator trees is that of the Grassland ecosystem (Martinez et al., 1999). It comprises a relatively small number of nodes and, at the same time, a sufficient number of hubs so that the problem of secondary extinction can be appreciated visually. Unfolding the food web of this ecosystem yielded the graph of Fig. 3 that clarify dominance relations between nodes.

A few nodes (e.g. 1, 2, 3, 4, …, 51, 53, 61 see figure caption for correspondence between numbers and species) are dominated by the root only: these species cannot be extinguished by removing other taxa. Nodes 4, 38, 51, 53, 61 do not dominate other species. The rest of the nodes linked directly to the root initiate a branch. Removing these nodes would make a variable number of species disappear. For example, removing node 3, *Elymus repens* would cascade up to nodes 13–15, that would vanish. In turn this secondary extinctions would propagate to nodes 30–33 and 52. This example shows how dominator trees can be utilized to predict the effects of species removals.

Table 1
Food webs ordered by increasing size

Food Web	N-1	C	Max D	Avg D	StDev D	AS	ES
BridgeBrook	25	0.171	4	1.160	0.624	0.160	0.046
Skipwith	25	0.315	25	1.960	4.800	1.000	0.078
Coachella	29	0.312	3	1.069	0.371	0.103	0.037
Chesapeake	31	0.071	5	1.290	0.902	0.161	0.042
StMarks	48	0.096	3	1.083	0.347	0.063	0.023
Grassland	61	0.026	10	2.262	2.294	0.164	0.037
Ythan2	83	0.057	30	1.446	3.209	0.361	0.017
ScotchBroom	85	0.031	3	1.329	0.585	0.035	0.016
LittleRock	92	0.118	19	1.272	1.928	0.207	0.014
Canton	102	0.067	3	1.029	0.221	0.029	0.010
Stony	109	0.07	2	1.009	0.096	0.018	0.009
Ythan1	124	0.038	27	1.323	2.384	0.218	0.011
ElVerde	155	0.063	8	1.142	0.669	0.052	0.007

Food Web is the name used in plots; N-1 is the original size (excluding r, source of energy for the system); C is the connectance (number of edges/(number of nodes)^2); Max D is the maximum number of nodes dominated by a single node; Avg D is the average number of nodes dominated by a single node; StDev D is the standard deviation of the distribution; ES and AS are the indices described in the text.

To test the error and attack resistance we firstly computed the set of dominators for each node, in all the 13 food webs. In particular, the calculation comprised the number of nodes every node dominates (D) and the size of dominators ($|dom(i)|$) set for each node (Dby). These values are presented in Tables 2 and 3, respectively.

Every food web contains a certain number of nodes that dominate at least another node ($D > 1$). In *Ythan1*, *Ythan2*, *Skipwith*, *LittleRock* ecosystems there are nodes that dominate many species. Once removed, they are likely to cause mass secondary extinction.

All food webs show similar Dby distribution (Table 4): the majority of species are dominated by two nodes (root and the node itself). Less species are dominated by three nodes, only a few have four dominators, while no one has five. This is because the number of trophic levels (distance from the root) bounds the maximum number of dominators (Post, 2002; Garlaschelli et al., 2003).

The distribution of D and Dby obtained by pooling together the nodes of all food webs confirms that self-dominance largely prevails, as 90.8% of the nodes dominate no species beside themselves. Only 5.2% would produce, if removed, a single secondary extinction. Highly dominating taxa account for 4% of the nodes: their removal would cause the extinction of 3–30 components. As for Dby, a large amount of taxa (75.9%) would not be affected by cascading extinction, while 19.8% has a dominator that, once removed, disconnects the node itself from the root. A small percentage of taxa (4.3%) are more prone to secondary extinction as they have 2 nodes whose removal would cause these species to extinguish.

The presence of a large amount of nodes with $Dby = 2$ can be explained by considering that this group is formed by: (a) nodes that are basal species directly attached to the root; (b) nodes that receive energy from a multiplicity of pathways of which at least two have no nodes in common beside the root and the terminal node.

All the food webs show the possibility of multiple extinctions: in *Skipwith* system there is just a basal species attached to the root and its removal will cause the complete extinction of the web. In *Ythan2* up to 30 nodes can go extinct after a single removal, 27 in *Ythan1*, 19 in *LittleRock* and 10 in *Grassland* (Tables 1 and 2).

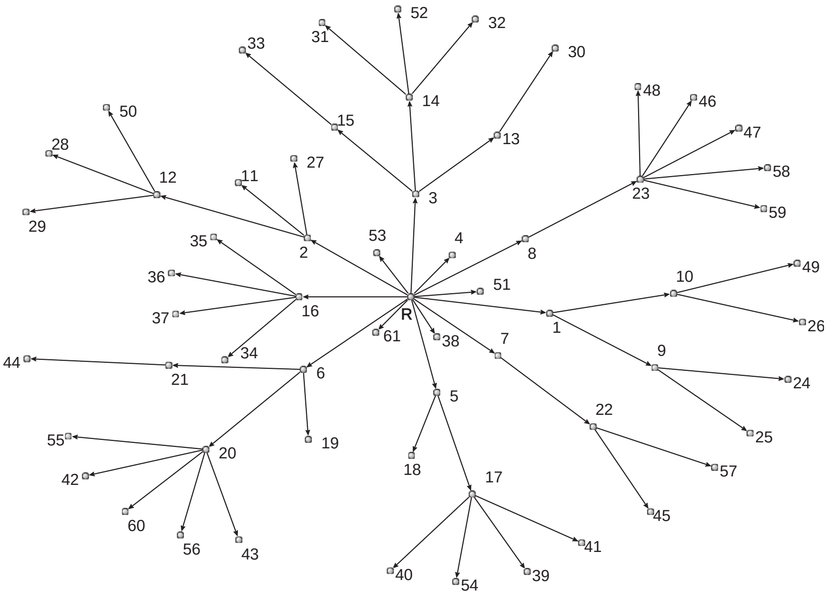

Fig. 3. Dominator Tree for the Grassland ecosystem (Martinez et al., 1999), which comprises grass species and their associated endophytic insects in Great Britain. Correspondence between numbers and species is as follows: R: root; 1: *Festuca rubra*; 2: *Alopecurus pratensis*; 3: *Elymus repens*; 4: *Ammophila arenaria*; 5: *Calamagrostis epigejos*; 6: *Deschampsia cespitosa*; 7: *Dactylis glomerata*; 8: *Phalaris arundinaceae*; 9: *Tetramesa brevicomis*; 10: *Tetramesa brevicollis*; 11: *Ahtola atra*; 12: *Tetramesa angustipennis*; 13: *Tetramesa linearis*; 14: *Tetramesa hyalipennis*; 15: *Tetramesa comuta*; 16: *Tetramesa eximia*; 17: *Tetramesa calamagrostidis*; 18: *Eurytoma* sp.; 19: *Eurytoma* sp.; 20: *Tetramesa petiolata*; 21: *Tetramesa airae*; 22: *Tetramesa longula*; 23: *Tetramesa longicomis*; 24: *Bracon* sp. + *Sycophila* sp.; 25: *Homoporus* sp. + *Eurytoma* sp.; 26: *Eurytoma* sp.; 27: *Chlorocytus pulchripes*; 28: *Sycophila* sp. + *Homoporus febriculosus* + *Endromopoda* sp.; 29: *Eurytoma tapio*; 30: *Sycophila* sp. + *Pediobius* sp. + *Eurytoma flavimana* + *Eurytoma* sp. + *Homoporus* sp.; 31: *Bracon erythrostictus*; 32: *Eurytoma roseni*; 33: *Chlorocytus agropyri* + *Pediobius alaspharus*; 34: *Eurytoma* sp.; 35: *Homoporus* sp. + *Sycophila* sp. + *Eurytoma danuvica*; 36: *Homoporus fulviventris*; 37: *Chlorocytus harmolitae*; 38: *Syntomaspis baudysi*; 39: *Bracon* sp. + *Homoporus luniger*; 40: *Endromopoda* sp.; 41: *Eurytoma pollux*; 42: *Eurytoma appendigaster*; 43: *Homoporus* sp.; 44: *Pediobius* sp. + *Chlorocytus* sp. + *Eurytoma castor*; 45: *Eurytoma erdoesi*; 46: *Bracon* sp.; 47: *Eurytoma phalaridis*; 48: *Endromopoda* sp.; 49: *Pediobius festucae*; 50: *Pediobius eubius*; 51: *Eupelmus atropurpureus*; 52: *Endromopoda* sp.; 53: *Macroneura vesicularis*; 54: *Pediobius calamagrostidis*; 55: *Pediobius deschampiae*; 56: *Endromopoda* sp.; 57: *Pediobius dactylicola*; 58: *Chlorocytus phalaridis*; 59: *Pediobius phalaridis*; 60: *Chlorocytus deschampiae*; 61: *Mesopolobus graminum*.

Table 2
Number of dominated nodes in all food web (D)

Dominated Nodes	Bridge-Brook	Canton	Chesapeake	Coachella	ElVerde	Grassland	Little-Rock	Scotch-Broom	Skipwith	StMarks	Stony	Ythan1	Ythan2
1	23	100	27	28	142	42	88	62	24	45	108	114	77
2	1	1	2	—	10	3	1	18	—	2	1	7	4
3	—	1	—	1	1	3	1	5	—	1	—	1	—
4	1	—	1	—	1	3	—	—	—	—	—	—	—
5	—	—	1	—	—	2	1	—	—	—	—	—	1
6	—	—	—	—	—	2	—	—	—	—	—	1	—
7	—	—	—	—	—	4	—	—	—	—	—	—	—
8	—	—	—	—	1	—	—	—	—	—	—	—	—
9	—	—	—	—	—	1	—	—	—	—	—	—	—
10	—	—	—	—	—	1	—	—	—	—	—	—	—
19	—	—	—	—	—	—	1	—	—	—	—	—	—
25	—	—	—	—	—	—	—	—	1	—	—	—	—
27	—	—	—	—	—	—	—	—	—	—	—	1	—
30	—	—	—	—	—	—	—	—	—	—	—	—	1

This is the number of extinctions expected due the removal of a single node.

Finally, we accounted for proneness to errors and attacks by computing ES and AS values for all the food webs (Table 1). ES varies from 0.007 (*El Verde*) to 0.078 (*Skipwith*), with average $\mu = 0.027$ and standard deviation $\sigma = 0.021$. Maximum AS value is that for *Skipwith* (1—the whole food web can be extinguished with a single removal). Minimum value for AS, 0.018, has been obtained for *Stony*. Mean and standard deviation for this index are $\mu = 0.197$ and $\sigma = 0.25$.

Table 3
Number of dominators for each node (*Dby*)

Node's Dominators	Bridge-Brook	Canton	Chesapeake	Coachella	ElVerde	Grassland	Little-Rock	Scotch-Broom	Skipwith	StMarks	Stony	Ythan1	Ythan2
2	21	99	23	27	134	13	69	60	1	44	108	87	49
3	4	3	7	2	20	19	21	22	24	4	1	34	31
4	—	—	1	—	1	29	2	3	—	—	—	3	3

This can be seen as the number of "bottlenecks" the matter find when flowing from root to the examined node.

Table 4
Distribution of dominators among all food webs (969 nodes excluding roots)

D	%	*Dby*	%
1	0.908	2	0.759
2	0.052	3	0.198
$\geqslant 3$	0.04	4	0.043

D is the number of nodes dominated by a single node, *Dby* is the number of nodes that dominate each node.

Error sensitivity (ES) appears inversely related to food web size. We examined log(*ES*) as a linear function of (*N-1*) and found a significant negative relationship ($R^2 = 0.871$, $F = 81.93$, $P = 1.98 \times 10^{-6}$). This means that proneness to random removal exponentially diminish with the number of taxa.

In the 13 examined food webs, on average, single species random removal results in 2–3% species loss, an effect due to prevailing self-domination. These food webs possess a high degree of tolerance against a single random extinction event, a typical property of scale-free networks (Albert et al., 2000). In contrast, attack sensitivity (*AS*) appeared to have no relation with size. In certain food webs secondary extinction due to removal of targeted species is not very different from random removal. This holds for *Stony*, *Scotch*, *Canton* and *StMarks*, which can be considered highly resistant to secondary extinction regardless of what species is removed.

In some case, ecosystems resistant to the effect of random removal show very high sensitivity when the most dominating species is lost. In *Skipwith* a single removal can destroy the whole web, while in other food webs can cause enormous damage (*Ythan2*: 36% species loss; *Ythan1*: 21%; *LittleRock*: 20%).

The relationships of *ES* and *AS* with species richness (inverse exponential; no relationship) contradicts results obtained using demographic models which suggest that probability of secondary extinction increases with species richness (Lundberg et al., 2000).

To be sensitive to attacks but error resistant is attributed to scale-free networks, inhomogeneous systems in which the majority of the nodes possess a few edges but some of them have a large number of connections (Albert et al., 2000). However, we must point out that the same food webs analysed here have been classified as non-scale-free networks (Dunne et al., 2002b). Further investigation on the organizing principles that govern network structures (Ravasz and Barabàsi, 2003) would contribute to clarify this point.

We reiterate that the position occupied by the root greatly affects the final outcomes (as shown for *Skipwith*, where the presence of a single basal species makes $AS = 1$). This key node should not be imposed, but carefully positioned according to ecological rules.

4. Discussion

Looking at food webs response to extinctions is not novel in ecological literature. The conclusion that loss of random species is likely to precipitate few extinctions, whereas there are structurally dominant taxa whose loss can lead to bigger impacts has been drawn first by Solé and Montoya (2001). Dunne et al. (2002a) generalized these conclusions by publishing the results of removal experiments conducted on a larger set of food web networks. Our paper confirms these results, but corroborating previous findings using a different method is not the main purpose of this exercise. Rather it is the method presented here in itself that allows further insights.

Previous studies targeted selective extinctions to the most connected species (Solé and Montoya, 2001; Dunne et al., 2002a). Their results showed that in some food webs (*St. Martin*, *St. Marks*, *Lake Tahoe*, *Mirror*, *Bridge Brook*, *Coachella*, and *Skipwith* food webs, Dunne et al., 2002a, Fig. 1) secondary extinction begins to be significant after several removals of the mostly connected species. The fact that connectance is not synonymous of functional dependence or control, and a species that has few connections may have a greater impact than another with many links may explain this outcome. In other words, the statement that the more links one species has the more potential it might have to affect community structure holds, but only on average. The number of links may be a misleading measure of the positional importance of species (Jordán, 2002). Comparing the connectance-based approach with that based on dominator trees, presented in this article, reveals that the former approach is of limited predictive value, as species that will be lost by a single removal cannot be anticipated. Dominator trees, on the other hand, are elegant, highly informative structures that allow to identify in advance which nodes are likely to cause the greatest impact on the web if removed. The example of the Grassland ecosystem is particularly informative in this respect.

The above considerations lead immediately to practical questions. It is common wisdom that keystone species have large effects on other species in the community (Mills et al., 1993). Accordingly, much more attention should be devoted to the conservation of these taxa and methods suitable for their a priori identification have been called for (Power et al., 1996). Dominator trees have much to offer because they simplify food webs so that keystones may be easily identified.

Dominator trees frame the problem of keystone species in a bottom-up perspective. Cascading extinction certainly occurs also in a top-down direction and we are aware that approaches based on dominator trees underestimate secondary extinction. Using dominator trees extinctions occur when a species is disconnected from its source of energy. Predator's extinction, on the other hand, leaves its preys without a flow of regulatory effects but this does not imply extinction of the prey. A reliable method that treat the question from a top-down perspective must include necessarily dynamical features of species interaction (Jordán et al., 1999, 2002), which is beyond the scope of this paper and will be discussed in another work.

Tracking multiple extinction events through dominator trees requires rebuilding the tree after every single deletion. This is certainly a limitation of the method in comparison with the approach that removes the most connected species. However in the latter case, we cast doubts about the possibility that after removing the species involved in the extinction events (main removal and its secondary effects) the remaining species maintain the same pattern of interactions as in the original food web. Likely, when mass secondary extinction occurs due to a removal, patterns of interaction may change substantially, leading to food web reshaping. This requires recalculating patterns of connectance as well. Unfortunately, the shape of the new food web is difficult to predict if not impossible, and assessing the effects of multiple extinction events looses its ecological value. This strengthens the value of calculating, through index AS presented in this paper, the maximum possible damage that a single extinction can produce in a food web. We stress, however, that this number of extinctions produced does not take into account the top-down dynamical effects (e.g. lack of regulatory effects as specified in the previous paragraph). In this context AS accounts for the damage that would surely occur for lack of nutrient inflow, not the maximum damage that could occur de facto.

Nodes in the food webs analysed here represent either single species or groups of species sharing the same trophic ecology (same set of preys and predators). We maintained the same structure to compare our result with the outcomes of previous investigations on secondary extinction (Dunne et al., 2002a). However, we are aware that the probability of extinction of a node that corresponds to a single species is not the same than that of a vertex including a set of species. This might have major effect on the computation of indices presented here, although this does not weaken the value of the methodology presented in the paper.

As a final remark we point out that the concept of dominator trees, although of large use in other fields of science, has never been used before in food-web studies. From this first application the potential is promising: it could help identifying structurally important taxa in a fairly simple, powerful way; it can be utilized to calculate the maximum possible damage occurring to a food web through a single removal; it can provide an alternative representation of food webs to investigate structural properties of ecosystems.

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