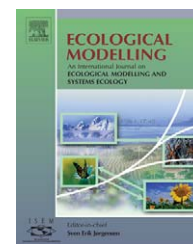


available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/ecolmodel

Secondary extinctions in ecological networks: Bottlenecks unveiled

Stefano Allesina^{a,b,*}, Antonio Bodini^a, Cristina Bondavalli^a

^a Department of Environmental Sciences, University of Parma, Parma, Italy

^b Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources Building, East Lansing, MI 8834, USA

ARTICLE INFO

Article history:

Available online 29 November 2005

Keywords:

Cascading extinctions

Secondary extinctions

Ecological networks

Bottlenecks

Error

Attack

Dominators

ABSTRACT

In ecosystems, a single extinction event could eventually precipitate in a mass extinction, involving species that may be several connections away from the target of the perturbation. This topic has been illuminated by recent studies on network mechanics, thanks to the concepts of hub, error and targeted removal, attack sensitivity, small world, and so forth. To forecast the effects of a species removal one can use an algorithm that unfolds a complex food web into a topologically simpler scheme, called its dominator tree. This structure is simple, elegant, and highly informative; all the bottlenecks and the effects of species removal are clearly traceable.

While food web studies are mostly qualitative, in this paper the use of the dominator tree is extended to weighted food webs, in which link magnitude is specified. These structures were obtained from ecological flow networks. In eight of these food webs, the analysis consisted in removing links that were weaker than a threshold of magnitude and building the dominator tree associated to the remaining structure. By progressively increasing the threshold up to the value that would make the graph disconnected, we had the opportunity to investigate patterns of dominance as a function of link magnitude.

© 2005 Elsevier B.V. All rights reserved.

1. Introduction

In ecosystems, feeding relations give rise to multiple reticulate connections between a diversity of consumers and resources. Such intricate web makes impacts spreading several links away from the affected taxon and a single extinction event may precipitate cascades of further extinction (Greenwood, 1987). Because this phenomenon, acknowledged by ecologists with the term “secondary extinction”, has important implications for the conservation of biodiversity (Spencer et al., 1991) unveiling its patterns and mechanisms is of fundamental importance.

Distant fields of science provided evidences that the anatomy of complex, web-like structures is the appropriate

locus of explanation for functions and dynamics. For example, the topology of social relationships may help assessing the magnitude of the health risk in human societies (Cohen et al., 2000); the anatomy of trade flows between countries may shed light on the dynamics of the global economic processes (Krempel and Plümper, 2003); the properties of metabolic networks can explain the tolerance of simple organisms to environmental modification or pharmaceutical interventions (Hartwell et al., 1999). It came, therefore, natural for ecologists to consider food web understanding crucial for a correct grasp of secondary extinction and to apply methodologies and algorithms that produced good results in other contexts. This cross-fertilization has developed in particular between theoretical ecology and the Internet’s structure exploration.

* Corresponding author. Tel.: +1 734 741 2370; fax: +1 734 741 2055.

E-mail address: allesina@msu.edu (S. Allesina).

Recently, Albert et al. (2000) introduced the analogy of biological extinctions into computer science studying how random or targeted disconnection of some servers would affect the connectedness of the Internet (cascading disconnections). Their results revealed that the Internet is very resistant to random disconnections (error tolerant) but attack prone, as a coordinate disconnection of a few very important nodes (hubs) could isolate entire branches of the net.

These features of the Internet network were tested on ecological food webs (Solé and Montoya, 2001; Dunne et al., 2002), which resulted to be error resistant and attack prone as well. In particular, they approached the question of attack sensitivity by simulating the removal of nodes in decreasing order of connectivity. However, node connectivity in scale-free networks (such as the Internet) plays a different role in comparison with non-scale-free structures (food webs) (Dunne et al., 2002). In the Internet system, in fact, removing the few hubs with the highest number of connections seriously hampers communication between the remaining nodes; in food webs, it is not necessarily so. In that case, the first few extinctions would produce huge cascading effects, but the “extinction curve” that accounts for secondary extinction events shows a sort of lag, meaning that the first few disconnections, which involve the most connected species, may not cause important effects (Allesina and Bodini, 2004). Although we maintain that studying food web architecture is fundamental to understand secondary extinction, we have the reason to believe that such study may be facilitated by the use of dominator trees. These trees are topological structures that make visible the linear pathways that are essential for energy delivery in complex food webs (Allesina and Bodini, 2004). By these structures, one can easily identify which nodes are likely to cause the greatest impact if removed. This is because dominator analysis illuminates which are the bottlenecks in the pathways that connect the fundamental source of energy (external environment) to any node (species or guild).

However, dominator tree analysis has been to date purely qualitative and dominance (i.e. interdependence) is calculated on the base of presence/absence of links between species. Links having different magnitude are considered equivalent in the computation. Nonetheless, interaction strength plays a major role in channeling energy through the vast array of pathways that makes up a food web, and this may affect patterns of interdependence and dominance between species. In this paper, the effect of interaction strength on dominance relations has been assessed on a set of eight real food webs. Because, likely, only links that are strong enough are essential to sustain the species in the food web, the search for dominator trees should be performed only considering these links, while neglecting the others. But this requires that one knows which links are important and which can be discarded from the analysis. Such knowledge is difficult to achieve, and almost impossible for large food webs. So, we followed an approach in which links that are weaker than an imposed threshold are removed, thus, assuming that they cannot provide enough energy to sustain the species. By progressively increasing this threshold, up to a value that would make the graph disconnected, and performing dominator tree search on the remaining links at every step, we created different scenarios for dominance in which secondary extinction has been

assessed, and indices of error and attack sensitivity were calculated. Results highlight that species that in the qualitative food web seemed to receive energy from a multiplicity of non-overlapping pathways, they might have few dominators when the magnitude of fluxes is considered. This modifies the patterns of food web resistance to errors and attacks in relation to a complete qualitative approach.

2. Materials and methods

2.1. Ecological networks and their properties

Trophic interactions in food webs may resemble the intricate web of routers and data-transfer lines by which computers are connected to each other in the Internet system. This analogy has suggested that ecosystems could be described, as the Internet, using un-weighted, un-oriented graphs (Solé and Montoya, 2001). The parallelism between computer networks and ecosystem could be, however, misleading, for a series of reasons that are summarized in the few points below.

2.1.1. Orientation-asymmetry

When two servers are connected with one another, the information can flow between the two in either ways; in ecosystems, instead, if one focuses only on matter and energy as currency, flows are bottom-up oriented (from resources to consumers). Accordingly, one can shape food webs as digraphs (directed graphs).

2.1.2. Mass conservation

Internet and food web topology have been described by un-weighted graphs. However, given the constraints imposed to natural systems by mass conservation, a more appropriate description of ecological webs should be based on weighted networks, leaving un-weighted networks for computer science, where information can be multiplied indefinitely. Any node (species) in an ecological network obeys the mass balance equation:

$$\frac{\partial B_i}{\partial t} = Z_i - E_i - D_i + T_{\cdot i} - T_i \quad (1)$$

in which the biomass variation of the i th component ($\partial B_i/\partial t$) is a function of matter entering the compartment from the outside environment (Z_i), increased by the quota of inflow from other species ($T_{\cdot i}$ where the dot sign stands for summation across all the species) and reduced by the fraction that is exported to the outer environment (E_i), dissipated (D_i), or fed to other species (T_i). If all nodes have null derivatives the system is at steady state. In this case, we can represent the ecosystem as a matrix, where every coefficient stands for the flux from the row to the column node (compartment).

2.1.3. Single-source and dissipation

In computer networks, every single machine can act as source of information; this does not hold for natural systems. The dissipative nature of ecological systems imposes that the outside environment provides a continuous supply of energy to the system. In graph theoretical language, this feature requires that ecological networks are rooted in a special

Table 1 – Statistics for each of the analyzed systems

Network	Nodes	Edges	Min edges	Min ES	Max ES	Min AS	Max AS	Max thres
Baydry	126	1987	300	0.008192	0.0096	0.024	0.048	0.1094574
Baywet	126	1956	259	0.008192	0.011136	0.024	0.096	0.1279146
Cypdry	69	574	114	0.015787	0.028114	0.058824	0.323529	0.1858526
Cypwet	69	565	111	0.015787	0.035251	0.058824	0.308824	0.1866415
Gramdry	67	798	89	0.01584	0.034435	0.030303	0.727273	0.2472287
Gramwet	67	798	108	0.01584	0.024793	0.030303	0.333333	0.2008547
Mangdry	95	1367	209	0.011091	0.012902	0.031915	0.085106	0.1342635
Mangwet	95	1368	229	0.011091	0.012336	0.031915	0.06383	0.1183497

For each of the analyzed systems (network), it shows: (1) the number of nodes including the root (nodes); (2) the number of edges in the original web (edges), and at the end of the procedure (Min edges); (3) the minimum error sensitivity (Min ES), that was calculated on the original configuration and maximum ES (Max ES) obtained in the very last step of the procedure; (4) attack sensitivity (AS), minimum and maximum, for the original network and the final structure, respectively. Max threshold (Max thres) is the value that if exceeded, would make the network disconnected. A detailed description of the analyzed networks can be found at the ATLSS website (<http://www.cbl.umces.edu/~bonda/ATLSS.html>).

node that represents the external environment as provider of energy/matter; this special node is called “root” or “source” node. Note that this representation takes into account the several ways energy/matters enter the system: flows of energy to primary producers, immigration, resuspension of nutrients, etc. All these flows are sketched as coming from the root node.

According to all the above considerations, we approached the study of secondary extinction in ecosystem using ecological flow networks instead of the typical empirical food webs employed in other studies (Solé and Montoya, 2001; Dunne et al., 2002). Flow networks, in fact, offer several advantages. They are depicted as oriented graphs so that building the topology of the associated food web is relatively straightforward; the compartments which import matter and energy (it occurs in the various forms, see the above paragraph) are clearly identified, so that connecting the system to the root node becomes straightforward; a magnitude is attached to each link (flow); this allows quantitative investigations.

In particular, we concentrated our efforts on the most resolved ecological networks up to date, which were produced for the ATLSS Project by the University of Maryland (<http://www.cbl.umces.edu/~bonda/ATLSS.html>). These networks represent four ecosystems (aquatic and terrestrial, namely the Florida Bay, the Cypress Wetlands, the Gramminoid Marshes, and the Mangroves Ecosystem) in two seasonal snapshots (dry and wet seasons). These networks have the advantage of being constructed with coherent and homogenous rules by the same team of scientists. Moreover, the networks comprise a great number of nodes and links (Table 1).

2.2. Bottlenecks and dominator trees

We represented the selected ecosystems as nodes (species/group of species) connected by weighted, directed links (carbon flows in $\text{mg C y}^{-1} \text{m}^{-2}$) to form a rooted network. The inputs in the original networks determined the way the root (external environment) is linked to the system variables. Tracing the consequences of a single extinction event was possible according to the idea that whenever a node is removed, all the nodes that rely on it for being connected to the source would go extinct as well. Secondary extinction may also be the consequence of variations in

top-down regulatory effect (e.g. removing a predator may lead to competitive exclusion of one its prey), but ecological flow networks allow investigating secondary extinction in the bottom-up perspective typical of the trophic-dynamics approach to ecosystem, so that this is the domain in which this work must be framed. Accommodating the two perspectives in a unique framework is not easy because they make use of different tools (Allesina and Bodini, 2004) and it is not among the objectives of this work. The main methodological tool used in this work is the dominator tree. It reduces any food web into a series of pathways that describe the linear sequence of steps through which energy is passed from one species to another in the ecosystem. By the use of dominator trees, one can identify without ambiguity which nodes are essential to the survival of other nodes. Any species along the branches of this topological construction is said to dominate those that follow it because these latter necessarily depend on the former to satisfy their energy requirement. In other words, this construction makes dominance relationships visible. Dominator trees are constructed by tracing a direct connection from any species to its immediate dominator, a species without which the former cannot survive. Consider the hypothetical food web depicted in Fig. 1 (graph on the left). Species E receives medium from species C and D, both of which, in turn, depend on A. The extinction of either C or D does not put E at risk of survival because at least one pathway remains at its disposal. On the contrary, extinction of A inevitably drives E (and B and D as well!) to extinction. Thus, A is the unique species necessary for E to survive and the dominator tree trace a direct connection from A to E. Given that A is essential for E and C as well the dominator tree depicts a direct connection from A to both these nodes. Because the dominator tree illustrates through its direct links only the dominance relations, there are no connections between C, D and E because none of these species is essential for the survival of any of the others.

We state that given a network G with N nodes ($N - 1$ species and the root) connected by E edges associated with weights W , a node A is a dominator of node B ($A = \text{dom}(B)$) if and only if every path from r (root of the network) to B contains A . According to this definition, every node dominates itself. A proper dominator C of a node B is defined as $C = \text{dom}(B)$, $C \neq B$. Every node has an immediate dominator; A is the immediate

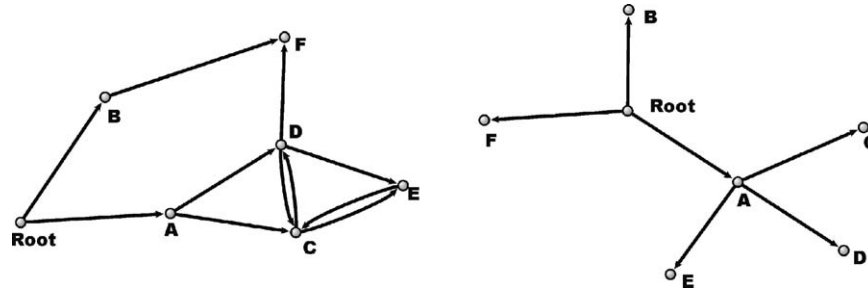


Fig. 1 – Sample network (left) and corresponding dominator tree (right). The removal of node A would cause the disconnection of nodes C–E, while the removal of any other node different from the root would cause no secondary extinction. The error sensitivity of this network (see below) would be $ES = 3/25 = 12\%$, while attack sensitivity ($AS = 3/5 = 60\%$). This means that a random extinction would make disappear another 12% of species on average, while a targeted removal can extinguish 60% of the network (maximum potential damage).

dominator of B if $A = \text{dom}(B)$ and every $C = \text{dom}(A)$ is also a dominator of B. Linking every node with its immediate dominator defines the so called dominator tree (Lengauer and Tarjan, 1979; see Allesina and Bodini, 2004 for a detailed description).

2.3. Errors and attacks

When a species goes extinct, one or more other species may disappear because they are left without connection to the root. Extinction events may be thought as of two types: random (Albert’s concept of “error”, Albert et al., 2000) and targeted (Albert’s “attack”), being the latter a term that defines removals that create as much damage as possible in terms of secondary extinction. We proposed (Allesina and Bodini, 2004) that network robustness to random losses and attacks could be tested by two indices calculated from the dominator tree. The so called error sensitivity index (ES), provides a measure of how robust ecological networks are with respect to random disconnections and it is calculated as the averaged sum of the number of proper dominators of every node i [$\text{dom}(i)$] divided by the overall number of nodes (the root node is always excluded from these calculations because its removal would trivially make the whole network disappear):

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

This index ranges from 0, as in the case of star-like dominator trees, where every node is directly attached to the root, to 0.5, that is the upper limit for chain-like dominator trees. In the former case, a single, random removal does not produce cascading extinction at all, because all the nodes directly depend on the root. In the latter, on average, a random disconnection will cause half of the nodes to disappear.

Targeted attacks will cause a cascading extinction if the node removed dominates at least another node. We can, therefore, measure the attack sensitivity (AS) as the maximum number of extinctions, we can cause by a single disconnec-

tion:

$$AS = \max \left\{ \frac{|\text{dom}(i) - 1|}{(N - 1)} \right\}, \quad \forall i \neq r \quad (3)$$

AS ranges from 0 (no secondary extinctions) to 1 (a single extinction leads all species to extinction). Indices of error and attack sensitivity are calculated in Fig. 1 for the network there represented.

2.4. Dominators on weighted networks

All the fluxes between nodes measured in a given period of time can be stored as coefficients of a matrix $T[t_{ij}]$. Because by dominator trees, we explore potential cascading extinctions due to energy shortage, we may expect that this phenomenon cannot be avoided whether nodes remain connected to the root through weak links. Only links that are strong enough (that carry enough currency) guarantee that species survive. In a purely qualitative dominator tree, this distinction is not taken into account, and it is sufficient that a species remains somehow connected to the root for not going to extinction, no matter how much energy it obtains through such connection. However, if we introduce flow intensity dominance patterns are likely to change. This can be intuitively appreciated using the same example proposed to describe dominator trees (see previous section). With reference to Fig. 1, if D received 90% of its requisite medium from C and the other 10% from B,¹ As a consequence, C becomes necessary for D, and it appears a dominator of this latter species, while in the qualitative case, only A played the role of dominator for D.

¹ If A–D were individuals, the entire amount of energy (100%) would be necessary for D to survive, so that even the lack of the weak flow would cause its death. Populations, instead, can survive with less energy at a lower number of individuals, unless this amount reduces population abundance below the minimum viable level.

In this study, we consider the magnitude of links as a key factor in defining dominance relation between species. The main idea is that only certain pathways guarantee that species receive enough energy. When these paths are interrupted because one node disappears, secondary extinctions occur, no matter whether the species remain connected to the root through other weak paths. In practice, the analysis has been performed according to the following procedure: we considered the original webs, removed links weaker than a certain threshold, thus, assuming that they could not guarantee the survival of the species they pointed to if left alone to provide energy, and build up the dominator trees on the remaining structure.² The value of the threshold was increased up to a value above which the graph became disconnected. For any step of this procedure, we investigated patterns of secondary extinction in the resulting dominator trees, while testing the network for sensitivity to errors and attacks. In summary, the entire procedure was conducted on matrix $T[t_{ij}]$ in the following way:

- we divided every non-zero coefficient by the row sum (every coefficient represents the fractional importance of each link with respect to food intake);
- we removed every link whose importance is below a given threshold;
- we computed dominator trees and relative statistics;
- we augmented the threshold and performed the above steps again.

The end point of this algorithm is the value for which the network becomes disconnected, isolating from the root at least one species/node.

3. Results

For the sake of simplicity, Figs. 2–5 provide a step-by-step reconstruction of the procedure as applied to the Gramminoid Marshes ecosystem (dry season). Fig. 2 depicts the original network and its corresponding dominator tree. All nodes but 2, 49, and 61 are attached directly to the root (node 1 in figure). This means that there exist at least two non-overlapping pathways connecting each node to the root, with the exception of

the ones specified above. In other words, only living sediment (2), rabbits (49), and nighthawks (61) obligatory require one intermediate node to be connected to the root. Link removal procedure started by imposing a threshold value of 0.1. That is to say all the links whose magnitude was less than 10% of each species' diet were removed from the original network. For the Gramminoid ecosystem, this yielded the web described in Fig. 3. Its corresponding dominator tree reveals a pattern of dominance not very different from the previous one. Seven nodes now rely on other species for their connection to the root but, still, most of the species remain connected directly to the root. At the end of this first step of the procedure, only 173 out of the 798 links that were present in the original web were retained.

Next, we increased the threshold to 15% of each species' diet (Fig. 4). The dominator tree now appears divided in two "sub-communities": species that are satellite of node 4 (*Periphyton*) and nodes that are directly attached to the root. Node 4 removal is expected to precipitate in a secondary extinction involving more than one third of the nodes. As the last step of the procedure, we considered as threshold for removal the maximum value that maintains the graph connected (no nodes are disconnected from the root). Such value for the Gramminoid ecosystem was equal to 0.247. That is we retained just the links accounting for at least 25% of each species' diet. The results are shown in Fig. 5. The remaining 89 links shape a structure whose dominator tree further emphasizes the importance of *Periphyton*; the energy intake of the majority of the nodes is channeled through this node.

Table 1 summarizes the statistics obtained for all the food webs.

Because the maximum value for the threshold was set up equal to the magnitude above which the graphs became disconnected, it was the specific architecture of any food web that defined such value. At one extreme lies the Florida Bay ecosystem, dry season, for which disconnection occurs when removal involves links whose magnitude is around 11% of each species' diet. At the opposite extreme, the Gramminoid Marshes ecosystem, previously discussed, remains connected up to when links accounting for 25% of each species' diet are removed. In the former case, relatively weak links are essential to maintain all nodes connected to the root, whereas in the latter this function is performed only by strong links. In all cases the number of links whose magnitude is above the threshold for disconnection is rather small. At most 20% of the links are essential to keep the graph connected (it is the case of the Cypress wetland ecosystem, 3rd row of Table 1), whereas only 11% of the original links are sufficient for the Gramminoid Marshes to stay connected with the root (Table 1, 5th row).

Error sensitivity and attack sensitivity increase as the weak links are progressively removed from the graphs. Still, the case of the Gramminoid ecosystem is particularly informative. In the original food web, the maximum possible damage as for secondary extinction is 3%, meaning that at most 3% of the species would disappear following an extinction event (Min AS). If we assumed that only links accounting for more than 25% of each species diet are important to deliver energy to all the nodes, a single extinction can drive 73% of species extinct (Max AS). Ecosystems that possess the greater threshold for disconnection are also those for which the difference

² Although it is logical that no single link of weak flow intensity could support a species alone an accumulation of a certain number of weak links could support a species. Our approach does not take into account the fact that an array of links of magnitude lower than the threshold could guarantee species' survival. We accepted this oversimplification because in this first attempt to study secondary extinction in food webs using the quantitative information on links we needed to keep things simple in order to understand the type of (general) behavior shown by the systems. In a future paper we will include this issue in the analysis. A possible way to tackle this problem is to consider possible combinations of existing links that, taken together, maintain global flows to the nodes that are greater than the thresholds. As we increase the threshold likely the number of such combinations will decrease. This approach will require substantial changes in the software that make this calculation (developed by the first author) and, perhaps, a different use of the flow matrices produced in network analysis.

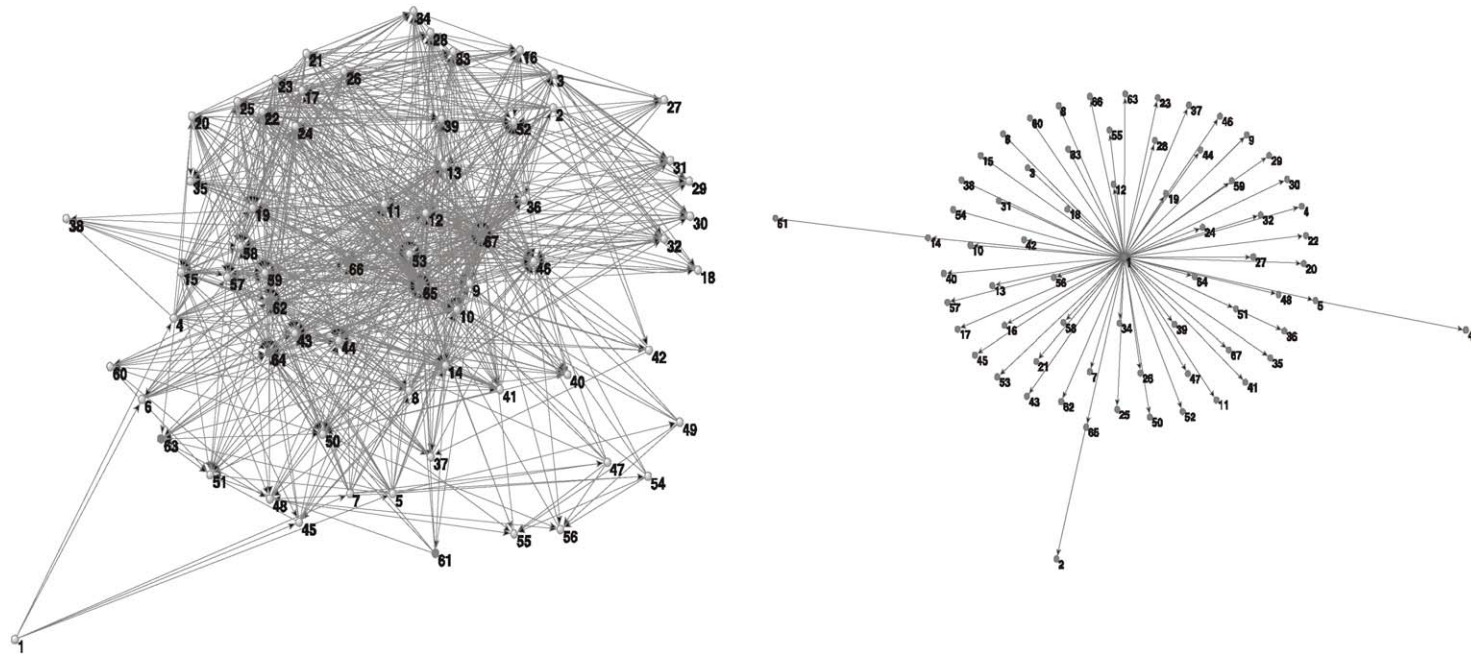


Fig. 2 – Gramminoid Marshes ecosystem, dry season (left), and corresponding dominator tree (right). Correspondence between nodes and species/group of species/pools: (1) root; (2) living sediments; (3) living POC; (4) *Periphyton*; (5) macrophytes; (6) *Utricularia*; (7) floating vegetation; (8) Apple snail; (9) freshwater prawn; (10) Crayfish; (11) mesoinvertebrates; (12) other macroinvertebrates; (13) large aquatic insects; (14) terrestrial invertebrates; (15) fishing spider; (16) Gar; (17) Shiners and Minnows; (18) Chubsuckers; (19) catfish; (20) flagfish; (21) Topminnows; (22) bluefin killifish; (23) killifishes; (24) Mosquitofishes; (25) Poecilids; (26) Pigmy sunfish; (27) bluespotted sunfish; (28) Warmouth; (29) dollar sunfish; (30) Redear sunfish; (31) spotted sunfish; (32) other Centrarchids; (33) largemouth Bass; (34) Cichlids; (35) other large fishes; (36) other small fishes; (37) salamanders; (38) salamander larvae; (39) large frogs; (40) medium frogs; (41) small frogs; (42) tadpoles; (43) turtles; (44) snakes; (45) lizards; (46) alligators; (47) muskrats; (48) rats and mice; (49) rabbits; (50) raccoons; (51) opossum; (52) otter; (53) mink; (54) white tail deer; (55) bobcat; (56) panthers; (57) grebes; (58) bitterns; (59) ducks; (60) snailkites; (61) nighthawks; (62) Gruiformes; (63) Cape Sable seaside sparrow; (64) Passerines; (65) sediment carbon; (66) labile detritus; (67) refractory detritus. For further information of species, please refer to the ATLSS website (<http://www.cbl.umces.edu/~bonda/ATLSS.html>). This network contains 67 nodes and 798 links. The network in its original form possesses: $ES = 1.584E-2$ and $AS = 3.0E-2$.

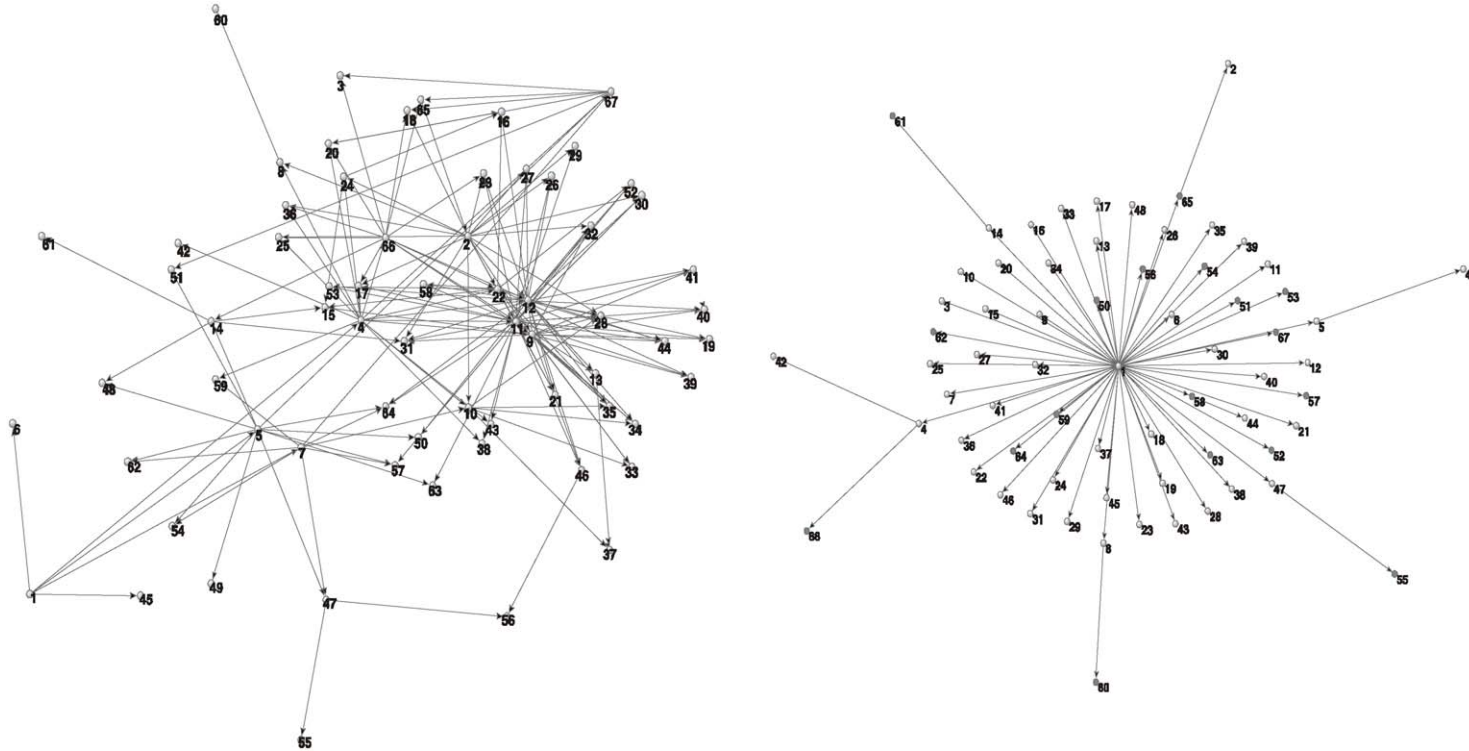


Fig. 3 – Gramminoid Marshes ecosystem, dry season, and corresponding dominator tree when the links with fractionary importance less than 0.1 are eliminated. In this case, the network would contain 173 links (out of 798). Consequently, the corresponding dominator tree possess more branches; this reflects in ES and AS values that becomes $1.68E-2$ and $4.54E-2$, respectively.

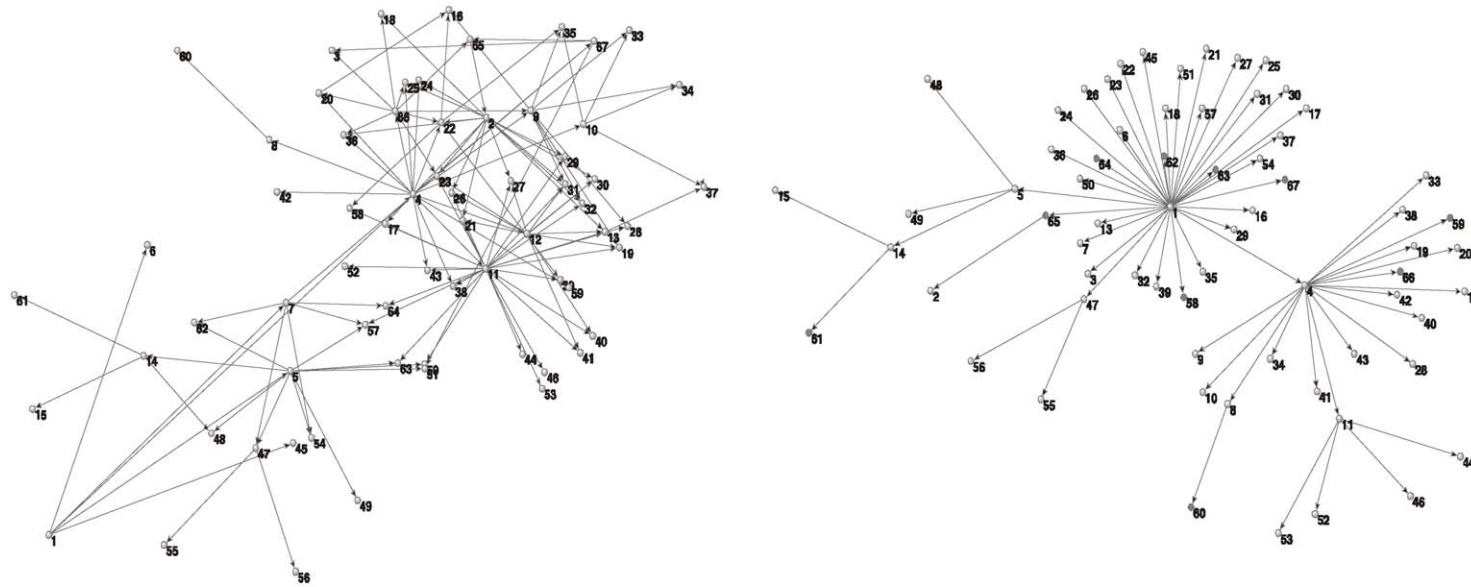


Fig. 4 - Gramminoid Marshes ecosystem, dry season, and corresponding dominator tree when the links with factionary importance less than 0.15 are eliminated. The network is further reduced to 127 links (out of 798): $ES = 2.36E-2$ and $AS = 3.48E-1$.

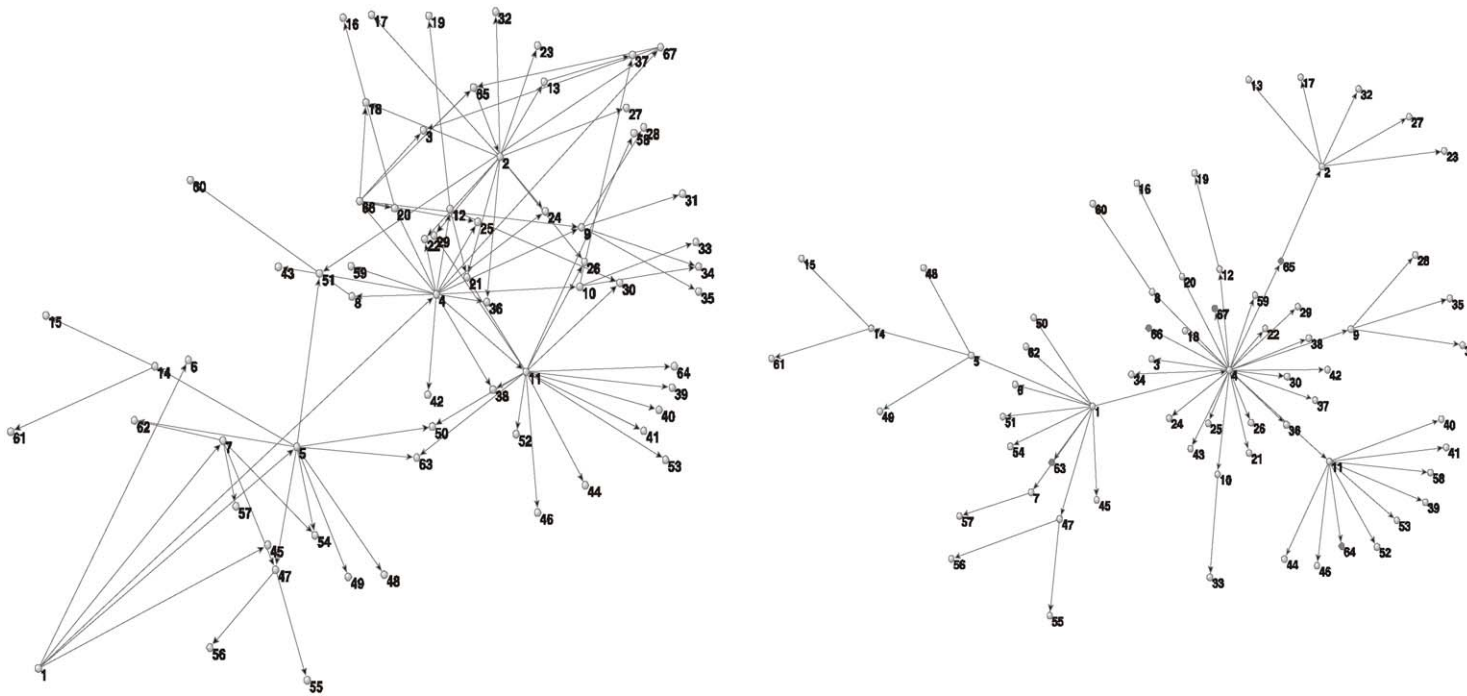


Fig. 5 – Gramminoid Marshes ecosystem, dry season, and corresponding dominator tree at the last step of the procedure. Any further removal of weak links would make the network disconnected. In this situation (89 links, threshold = 0.247): $ES = 3.44E-2$ and $AS = 7.27E-1$.

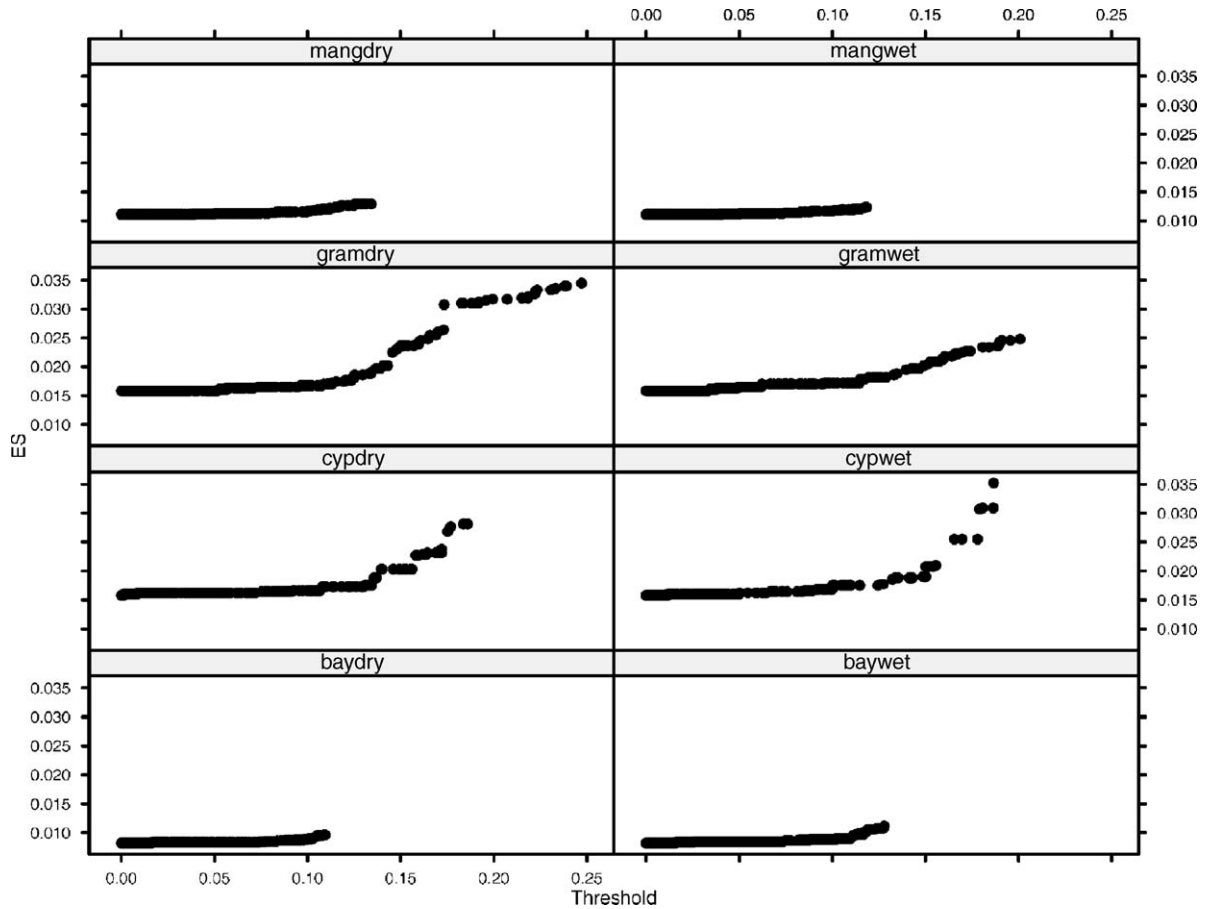


Fig. 6 – ES values for the considered networks in the two seasonal snapshots (left: dry season and right: wet season). Threshold values indicate the filter used for presence/absence of links. ES increase monotonically with the threshold until the value that makes the network disconnected is reached.

between Max AS and Min AS is the highest and can reach one order of magnitude (Cypress and Gramminoid ecosystems). Such a sharp difference does not characterize error sensitivity although also coefficient ES increases as links are removed. However, whereas Max AS gets close to its maximum possible value (1, extinction of 100% of the species) ES remains far from its maximum possible value (0.5) for all the networks but the Florida Bay (wet season). This means that after the majority of weak links are removed these webs resemble much more a star than a linear chain. Both ES and AS grow as step functions as shown in Figs. 6 and 7; link removal does not change the indices until a “critical” threshold is reached. Remarkably, all the curves possess the same shape, suggesting that this feature could be generalized.

The initial values for the two seasons do coincide for every network examined, but there are seasonal differences as for maximum values and curve shape. All the functions seem to possess a sort of “lag”; both ES and AS grow slowly up to a certain threshold. When this critical value is reached (see the Gramminoid ecosystem and the Florida Bay), ES and AS seem to grow exponentially. Because these indices cannot exceed the limit of 0.5 and 1, respectively, we can expect an inflection point (visible in Cypress–dry season curve).

4. Discussion

The idea that the loss of individual species may produce “domino extinctions” in ecosystems is not new. Pimm (1979, 1980) explored this issue in the framework of the diversity–stability debate and used rather simple food webs (maximum no. of species = 15, organized into chains of three species) that visualized multiple interactions governed by classical Lotka–Volterra equations. The same type of models was used more recently to explore secondary extinction in the context of biodiversity and its conservation (Lundberg et al., 2000). The majority of these dynamic models are multi-trophic assembly models rather than descriptions of real food webs; they were especially constructed to forecast the risk of secondary extinction in real communities as a function of general features, such as number of species per functional group, omnivory, intensity of competition. The effect of interaction strength seems to be such that risk of secondary extinction increases when the distribution of links magnitude changes from uniform to skew (Borrvall et al., 2000). In other words, communities with few strong links and many weak links would be more prone to secondary extinction.

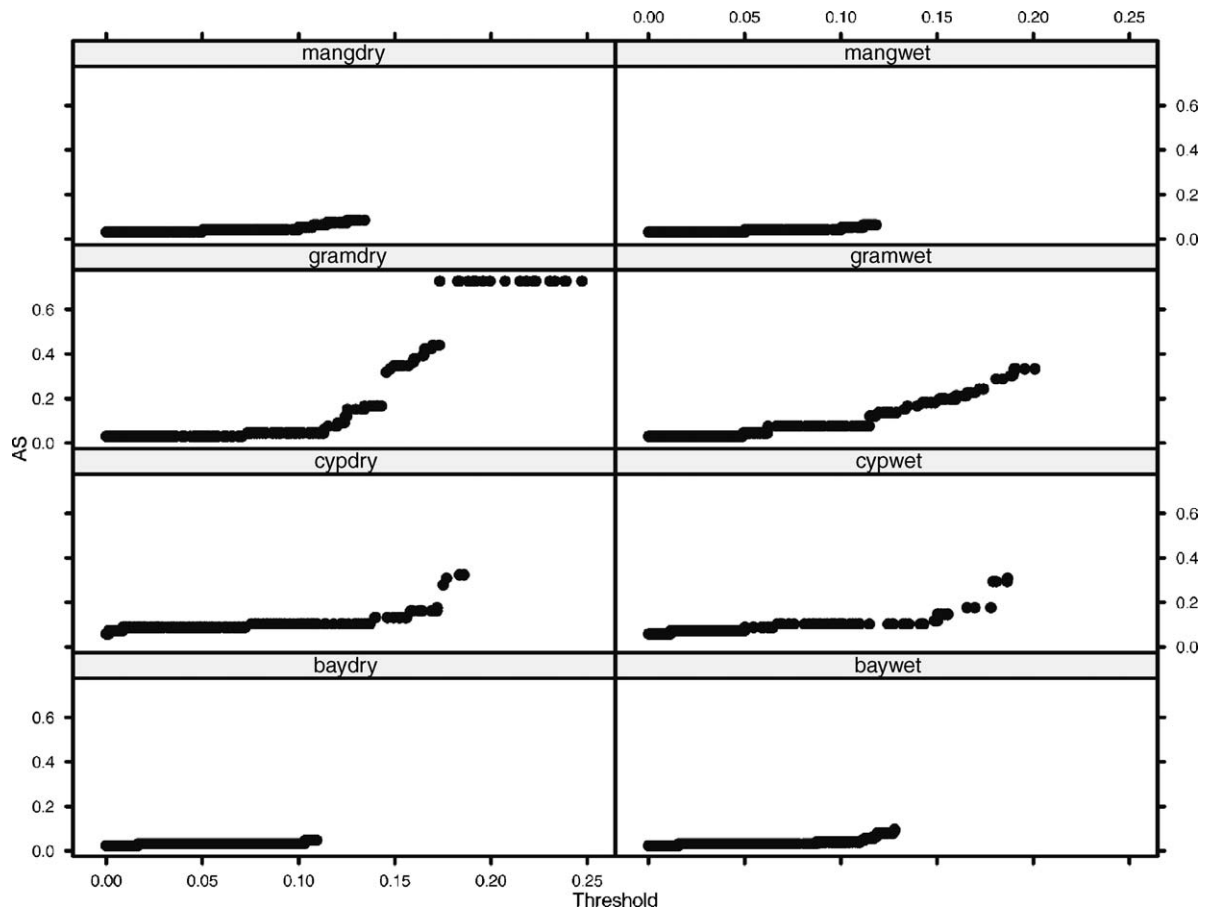


Fig. 7 – AS values for the considered networks in the two seasonal snapshots (left: dry season and right: wet season). Threshold values indicate the filter used for presence/absence of links. AS, as in the case for ES, increase with the threshold until disconnection of the network is produced.

Results presented here, although obtained studying energy flow networks instead of the dynamics of species interactions, recall those findings but from a different perspective. Figs. 2–5 show, for the Gramminoid ecosystem, that when the minimum amount of energy a single link must carry to function as a viable connection augments, the number of bottlenecks (node upon which other species obligatory depend for their energy requirements) increases, and so does the risk of secondary extinction. If species survival is guaranteed when they receive at least the energy delivered through pathways composed by strong links (those representing >25% of a species' food intake), this bulk of energy is concentrated in 89 out of the 798 original links and is channeled through fundamental nodes that are not visible when all links (and pathways) are considered equivalent (compare Fig. 5 with Fig. 2). In particular, these nodes are 4 (*Periphyton*), 11 (mesoivertebrates), 5 (macrophytes), 9 (freshwater prawn): their extinction would produce a cascade of secondary extinctions and they can be considered as keystone species in the Gramminoid ecosystem (Power et al., 1996; Allesina and Bodini, 2004). In general, the higher the threshold the more prone the networks become to random and selective extinctions, as shown by values of indices ES and AS in Table 1 and their trends in Figs. 6 and 7.

The qualitative food webs can be considered as special representations of networks with uniform distribution of interaction strength. When thresholds are imposed to select links on the base of their magnitude, we observed that most links are removed for rather low values of the filter. That is the majority of the links in the selected food webs are weak and strong interaction represent 10–20% of the total linkage patrimony of these ecosystems (see Table 1). In these food webs, distributions of link strength are clearly skewed (Ulanowicz and Wolff, 1991) and the dominator tree analysis shows a greater risk of secondary extinction, a result that matches with the outcomes of dynamic analysis. Also, these results support the idea that in real food webs there is a preponderance of weak interactions between species (Berlow, 1999; Kokkoris et al., 1999; Montoya and Solé, 2003).

Studies conducted on dynamics-based models revealed that the loss of species from lower trophic levels would cause greater risk of losing additional species (Borrvall et al., 2000). This matches with our results, although our approach, based on energy flow, is bottom–up in nature and does not consider the top–down perspective that is defined by the flow of regulatory effects due to predators (Allesina and Bodini, 2004). In the case of the Gramminoid ecosystem among the species that are likely to cause greater damage in term of secondary extinction

two are primary producers (*Periphyton* and macrophytes) and another two (freshwater prawn and mesoinvertebrates) feed at level 2.27 in a food web that counts up to five trophic levels (Heymans et al., 2002).

As a final remark, we point out that all the results discussed in this paper have been obtained without considering that species can modify their connections and switch to entirely different prey when the original source of energy becomes missing or scarcely available. Even though including switching would be very important, the collected food webs contain no data that would allow this kind of investigation.

Results of this analysis open up opportunities for research on structural features of food webs. Interestingly enough, the disconnection of the networks occurred when most of the links were removed (80–89% of links) and this means that stronger links (the backbone) of food webs are close to form a spanning tree (that would be composed by exactly $N - 1$ links, Garlaschelli et al., 2003), that is the collection of pathways that allow energy to reach all species at the minimum cost. In the Gramminoid food web the spanning tree would count as many as 66 links, while 89 links are required to maintain the network connected. This suggests that stronger, essential links are topologically arranged in such a way that delivery is somehow optimized. The issue is certainly promising and deserves to be further investigated.

Acknowledgements

Research supported partly by the European Commission (Project DITTY Contract No. EVK3-2001-00226) and partly by the Ph.D. Program in Ecology, University of Parma. SA would thank the ISEM for the bursary that allowed him to present this work to the ECEM.

REFERENCES

- Albert, R., Hawoong, J., Barbási, A.L., 2000. Error and attack tolerance of complex networks. *Nature* 406, 378–381.
- Allesina, S., Bodini, A., 2004. Who dominates whom in the ecosystem? Energy flow bottlenecks and cascading extinctions. *J. Theor. Biol.* 230 (3), 351–358.
- Berlow, E.L., 1999. Strong effects of weak interactions in ecological communities. *Nature* 398, 330–334.
- Borrvall, C., Ebenman, B., Jonsson, T., 2000. Biodiversity lessens the risk of cascading extinction in model food webs. *Ecol. Lett.* 3, 131–136.
- Cohen, S., Brissette, I., Skoner, D., Doyle, W., 2000. Social integration and health: the case of the common cold. *J. Soc. Struct.* 1 (3), 1–7.
- Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Food-web structure and network theory: the role of connectance and size. *Proc. Natl. Acad. Sci. U.S.A.* 99, 1222–12917.
- Garlaschelli, D., Caldarelli, G., Pietronero, L., 2003. Universal scaling relations in food webs. *Nature* 423, 165–167.
- Greenwood, S.R., 1987. The role of insects in tropical forest food webs. *Mar. Biol.* 16, 267–271.
- Hartwell, L.H., Hopfield, J.J., Leibler, S., Murray, A.W., 1999. From molecular to modular cell biology. *Nature* 402, 47–52.
- Heymans, J.J., Ulanowicz, R.E., Bondavalli, C., 2002. Network analysis of the South Florida graminoid marshes and comparison with nearby cypress ecosystems. *Ecol. Model.* 149, 5–23.
- Kokkoris, G.D., Troumbis, A.Y., Lawton, J.H., 1999. Patterns of species interaction strength in assembled theoretical competition communities. *Ecol. Lett.* 2, 70–74.
- Krempel, L., Plümper, T., 2003. Exploring the dynamics of international trade by combining the comparative advantages of multivariate statistics and network visualization. *J. Soc. Struct.* 4, 1–22.
- Lengauer, T., Tarjan, R.E., 1979. A fast algorithm for finding dominators in a flowgraph. *ACM Trans. Prog. Lang. Syst.* 1, 121–141.
- Lundberg, P., Ranta, E., Kaitala, V., 2000. Species loss leads to community closure. *Ecol. Lett.* 3, 465–468.
- Montoya, J.M., Solé, R.V., 2003. Topological properties of food webs: from real data to community assembly models. *Oikos* 102, 614–622.
- Pimm, S.L., 1979. Complexity and stability: another look at MacArthur original hypothesis. *Oikos* 33, 351–357.
- Pimm, S.L., 1980. Food web design and the effect of species deletion. *Oikos* 35, 139–149.
- Power, M.E., Tilman, D., Estes, J.A., et al., 1996. Challenges in the quest for keystones: identifying keystone species is difficult but essential to understanding how loss of species will affect ecosystems. *Bioscience* 46, 609–620.
- Solé, R.V., Montoya, J.M., 2001. Complexity and fragility in ecological networks. *Proc. R. Soc. Lond. B* 268, 2039–2045.
- Spencer, C.N., McClelland, B.R., Stanford, J.A., 1991. Shrimp stocking, salmon collapse and eagle displacement. *Bioscience* 41, 14–21.
- Ulanowicz, R.E., Wolff, W.F., 1991. Ecosystem flow networks: loaded dice? *Math. Biosci.* 103, 45–68.