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Complexity and Fragility in Ecological Networks

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A detailed analysis of three species-rich ecosystem food webs has shown that they display scale-free distributions of connections. Such graphs of interaction are in fact shared by a number of biological and technological networks, which have been shown to display a very high homeostasis against random removals of nodes. Here we analyse the response of these ecological graphs to both random and selective perturbations (directed to most connected species). Our results suggest that ecological networks are extremely robust against random removal but very fragile when selective attacks are used. These observations can have important consequences for biodiversity dynamics and conservation issues, current estimations of extinction rates and the relevance and definition of keystone species.

I. INTRODUCTION

Ecological research has widely demonstrated that community fragility is far from being understood. Issues as which species might be considered as specially relevant because of their strong effects on the community have lead to a heated debate since Paine's definition of keystone species (Jordán et al., 1999). Despite this and other discussed topics, it is commonly accepted that community fragility is related to how ecological communities are structured, specifically to how trophic links are distributed throughout the community (May 1974; Pimm 1991). But both the scarcity of high-quality data (Polis, 1991; Cohen et al., 1993; Williamson and Martínez,) and the lack of methods suitable for a detailed analysis of the complexity of food web organization (Cohen et al., 1993) leads to a lack of an unified picture of community fragility. A number of questions emerge from these studies: How are dynamic and static (graph-level) properties related?; How dependent is ecosystem fragility from graph architecture?

Recently, there has been an increasing interest in the organization of complex networks. These networks go from technological ones (Watts and Strogatz, 1998; Albert et al., 1999), to neural (Watts and Strogatz 1998; Amaral et al., 2000) or metabolic networks (Jeong et al 2000; Wagner and Fell, 2000). All these networks can be represented as a graph consisting of a set of nodes and the links connecting them.

Such complex networks share some topological features, as the so-called "small world" (SW) behavior (Watts and Strogatz 1998; Newman, 2000). Some of these webs also exhibit scale-free (SF) distributions of links. Specifically, the frequency of nodes with k connections follows a power law distribution $P(k) \approx k^{-\gamma}$, where most units are connected with few nodes and very few nodes are highly connected.

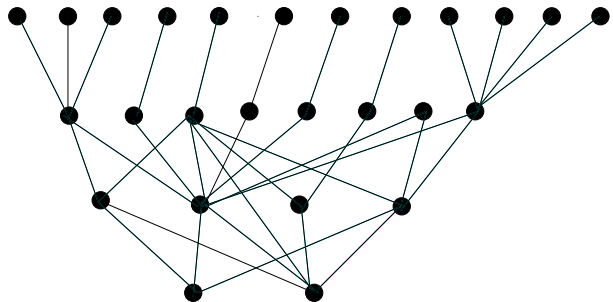


FIG. 1. Schematic representation of an ecological graph: few species have many links and many have just one or two. This leads to fat-tailed (scale free) distributions of connections. This particular example follows a power law $P(k) \approx k^{-1.2}$. This picture reflects the most common features observed in webs such as those reported here.

Networks exhibiting SW properties and SF distributions of connections present a characteristic response to the successive removal of their nodes, related to the way removals occur (Albert et al 2000; Jeong et al 2000). When nodes are removed at random, the network exhibit high homeostasis. By contrast, if most-connected nodes are successively eliminated, the structure of the network reveals an intrinsic fragility that eventually leads to a breaking into many small subgraphs. This behaviour is not shared by other networks, such as purely random ones, where $P(k)$ is Poissonian. It has been demonstrated that random networks are equally fragile to the way removal of nodes is produced.

The surprising and general nature of these results immediately suggests their application to ecological networks (figure 1), which have been recently shown to display SF behavior (Montoya and Solé, 2000). Here we examine the possible consequences for ecosystem stability against different types of species loss. As we will see, these networks display the robustness expected for long-tailed distributions of connections but also a high

fragility against selective species removal.

II. FOOD WEBS ANALYSED

Because of the limitations of the available data in terms of both taxonomic resolution and size (Polis, 1991; Cohen et al., 1993; Williams and Martinez, 2000) our study is limited to the three richest and best-described food webs available in the ecological literature (figure 2). These are: Ythan estuary web (Huxman et al. 1996), Silwood Park web (Memmott et al. 2000) and Little Rock Lake web (Martinez 1991).

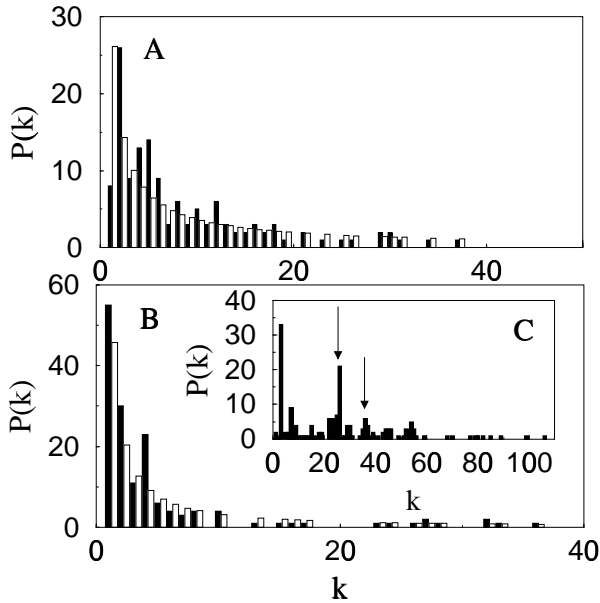


FIG. 2. Histograms showing the distribution of links (k) per number of species ($P(k)$) for the three networks analysed here (black bars): (A) Ythan estuary, (B) Silwood web and (C) Little Rock lake. Webs A and B are shown together with the best power-law fit (white bars, see table I for details). Little Rock web, shown in (C) displays several bumps (two of them indicated) due to low-level taxonomic resolution (Montoya and Solé, 2000).

Ythan estuary food web has $N_s = 134$ species, being the second largest documented web in the UK. Most nodes correspond to real species (88%) while the rest involve lower taxonomic resolution (all the species of Acarina or of Brown Algae are lumped together in the same node). It is one of the most reviewed food webs through ecological literature and the average number of links per species is $\langle k \rangle = 8.7$.

Silwood park food web is a very detailed sub-web (all nodes but one are real species) of those species associated with the Scotch broom *Cytisus scoparius* in a field site of 97 hectares. The average number of links per species is $\langle k \rangle = 4.75$. It includes 154 species: 60 predators, 66

parasitoids, 5 omnivores, 19 herbivores and one plant.

Finally, Little Rock Lake food web corresponds to a small lake. It is the largest of the three webs analysed here ($N_s = 182$), although it has less taxonomic resolution. Only 31% of nodes are real species, being most of the nodes genera-level (63%) and the rest corresponding to higher taxa. Here $\langle k \rangle = 26.05$.

By using these webs, we have a diverse representation of habitats: one food web from a terrestrial habitat (Silwood park), a freshwater habitat (Little Rock lake) and an interface environment (Ythan estuary). All of them have some features in common. In a previous study, we have shown that these networks display small-world properties (Montoya and Solé, 2000). In a graph with a small world (SW) topology, nodes are highly clustered yet the path length between them is small. In this sense a SW stands for a network whose topology is placed somewhere between a regular and a totally random distribution of connections. These networks display a number of surprising features and have been suggested to be of great relevance in different biological contexts (Watts and Strogatz, 1998; Jeong et al., 2000; Lago-Fernández et al., 2000).

In general, SW nets have been shown to provide fast responses to perturbations and thus provide a great source of homeostasis. However, two of these networks also display the power law distribution $P(k) \approx k^{-\gamma}$ (figure 2) thus belonging to the SF class of networks. Little Rock web is also fat-tailed but it displays deviations from the power law due to low taxonomic resolution (Montoya and Solé, 2000). For food webs displaying fat-tailed distributions, perturbations can have unexpected consequences, which are explored in the next section.

III. RESPONSE TO SPECIES REMOVAL

We have simulated two kinds of species removals: random and directed. These correspond to removal of an arbitrary or the highest connected node, respectively. Previous studies have shown that the eventual effect of removal is network fragmentation, which takes place in very different ways depending on the type of removal used (Albert et al., 2000; Jeong et al., 2000). Community fragility has been measured in different ways in relation to the fraction of species f that have been already removed (Figure 3). We have measured the fraction of species contained in the largest species cluster S for each f ; the average size of the rest of the species clusters $\langle s \rangle$ as the food web is being fragmented; and the fraction of species becoming isolated due to removals of other species on whom their survival depends, which are known in the literature as secondary extinctions, and can be used as measure of extinction rate (Pimm, 1991). Here f_c indicates the fraction of removed species at which the web becomes fragmented into many small sub-webs (figures 3a-c).

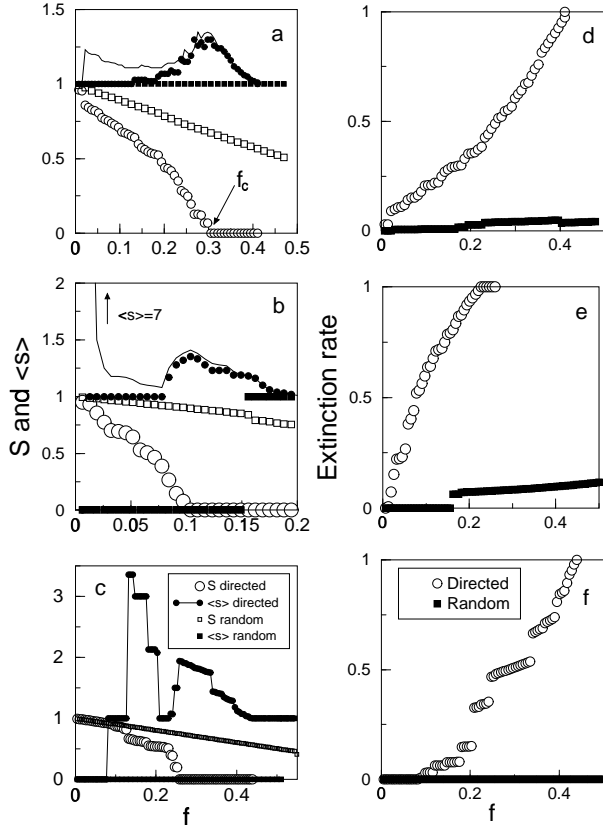


FIG. 3. Response of food webs under random (circles) and directed (squares) species removals. (a-c): relative size of the largest species cluster S (open symbols) and average size of the rest of the species clusters $\langle s \rangle$ (filled symbols) in relation to the fraction f of removed species for Ythan estuary, Silwood Park web and Little Rock lake food web, respectively. Critical thresholds f_c are indicated. In (a) and (b), continuous line consider a species cluster that appear quickly. This does not rest robustness to the observed trend, because it is similar to what happens for $\langle s \rangle$ and S near f_c if that cluster is not considered in the calculations. (d-f): extinction rate (fraction of secondary extinctions) as a function of f for the webs ordered as before.

The nature of the behaviour of the three food webs is very similar despite differences in f_c , S and $\langle s \rangle$ between them. They exhibit high homeostasis when random species removals occurs, showing slow, linear decrease in the fraction of species contained in the largest cluster S . The graph cannot be fragmented until extremely high removal has been introduced. This can be seen in the values of $\langle s \rangle$, which remain at 0 (no species clusters different from S), or 1 (due to very few isolated species). But what is more revealing is that extinction rates remain at low values even for high f , so secondary extinctions are almost nonexistent. In fact we can estimate the fraction of removed species required in order to get food web fragmentation from random removal (Cohen

et al., 2000):

$$p_c = 1 - \frac{1}{\kappa_0 - 1} \quad (1)$$

where κ_0 is estimated from:

$$\kappa_0 = \frac{\langle k^2 \rangle}{\langle k \rangle} = \frac{\sum_{k=1}^K P(k)k^2}{\sum_{k=1}^K P(k)k} \quad (2)$$

where K indicates the maximum connectivity. This value is shown in table I, where we can see that only totally unrealistic removals break the food web.

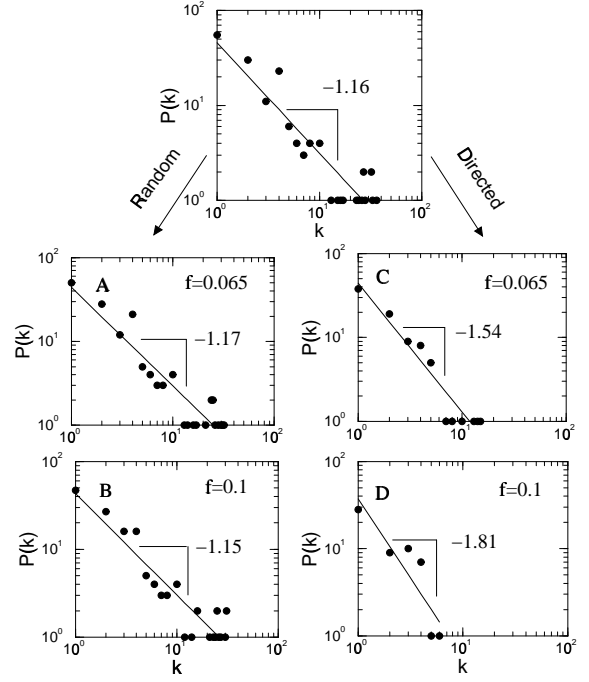


FIG. 4. Effects of random and directed removal on the connectivity distribution for the Silwood Park web for different fractions of removed species: $f = 0.065$ (10 removed species), and $f = 0.1$ (15 removed species). The estimated slopes are indicated ((a) $r^2 = 0.87$; $p < 0.01$; (b) $r^2 = 0.87$; $p < 0.01$; (c) $r^2 = 0.92$; $p < 0.01$; (d) $r^2 = 0.77$; $p < 0.01$).

However, what happens when most connected species are successively removed is clearly different. These webs are extremely vulnerable to such sort of removals. This fragility can be seen from: (a) the quick decay of S up to a critical fraction of removed species f_c (see table I); (b) the high fragmentation of the food webs into species clusters disconnected among them, giving maximum local values of $\langle s \rangle$ at critical points f_c where percolation takes place, and (c) the large fraction of isolated species occurring at low values of removed species, which reveal how fast secondary extinctions will occur (this is specially dramatic for our best defined web (Silwood), see figure 3.e). A measure of this phenomenon is given by π_c , the fraction of removed species that leads to an extinction

rate of one half. Although these are estimations based on a non-directed, non-weighted graph, other ingredients will presumably worsen this scenario due to other effects derived from indirect interactions (Yodzis, 1988; Stone and Roberts, 1991; Pimm, 1991) or habitat fragmentation processes (Solé and Bascompte, 2001).

	Ythan E.	Silwood P.	Little Rock
$\langle K \rangle$	8.71	4.78	26.15
γ	1.04	1.13	-
p_c	0.94	0.93	0.97
f_c	0.29	0.10	0.23
π_c	0.22	0.07	0.22

Table I: *Summary of the average properties of the ecological networks analysed (Due to the irregular shape of $P(k)$, no good power-law fit for Little Rock Lake can be obtained). (Here: (1) $r^2 = 0.83$; $p < 0.01$; (2) $r^2 = 0.79$; $p < 0.01$).*

We can make a simple division of the trophic nature of the species for each community into three groups: top predators, intermediate species and basal species (Polis, 1991). We find differences between analysed food webs in terms of the group that contains more highly-connected species, focusing in the set of species that are removed before reaching f_c . For Ythan estuary, these are mainly intermediate species (fishes and invertebrate organisms, 60%), few top predators (birds, 20%) and parasites (15%) that cannot be easily included in any of these three groups. For Silwood park, most of these species are herbivores (66%), that could be considered as basal species since only one plant (*Cytisus scoparius*), is present. Hemipterous omnivores are also important (26%), but, as happens with parasites at Ythan, they do not belong to any of the three trophic groups. Finally, for Little Rock no basal nodes are highly connected, being intermediate species belonging to zooplankton, benthic invertebrates (70%) and top predators (such as fishes, 24%) the most connected ones.

Another fundamental question related to the fragility of these communities is how species removals affect the distribution of links per species under each kind of simulated attack. In other words, do food webs maintain their SF distributions as species are successively deleted? Our analysis shows that indeed, SF distributions are stable up to high values of f (more than 50% of species eliminated in the three food webs) when random removals occur, while those particular distributions quickly disappear under directed removal. In Figure 4 we have represented this for the Silwood web. Under random removal, the long-tailed distributions show little variation. In contrast, that SF topology is lost when just few highly connected species are removed, which is likely to promote ecosystem collapse.

IV. DISCUSSION

The trophic organization of species-rich communities is similar to other complex network topologies (Albert et al 2000, Jeong et al 2000). They are extremely heterogeneous, being their topology dominated by few highly connected nodes around which the rest of the network is organized, with a scale-free distribution of connections. This complex organization entails some keys for ecological fragility. We have shown that SF food webs are very robust under random deletion of species. Secondary extinctions remain at low values because the probability of being removed decreases with k according to $P(k) \approx k^{-\gamma}$, so it is unlikely that a highly connected species will be deleted. Such robustness becomes weakness under removals directed to species with many connections. We find specially significant the differences in extinction rates between random and directed attacks, raising up to 95 times higher for removals of highly connected (keystone) species.

All the definitions of keystone species found in ecological literature share one feature: keystone species have large effects on other species in the community. The set of effects involved in each definition are very different. Those effects have been studied mainly qualitatively by the removal or introduction of species (see Jordan et al 1999 for a review). Quantitative approximations have used simulated food webs (Pimm 1991; Jordan et al 1999). In this respect, our approximation to the fragility of real, species-rich food webs through topological changes may help to design new quantitative methods for a priori identification of keystone species. We can identify keystone species as highly connected because of the effects of their removal in terms of secondary extinctions. The quick arrival to f_c and the high extinction rates corresponding to low values of f when those keystone species are removed stresses the importance of identifying and protecting highly connected species that maintain the stability of ecological communities.

By using this method, it is the topology of the food web instead of the trophic position of species what determines which species are keystone. In this respect, not only top predators must be considered as keystone species but also other organisms from different trophic levels, in agreement with previous studies (Bond 1993; Davic 2000). Making a simple division of species into the three classic trophic categories, we have seen that keystone species belong to different categories in each of the analysed networks. A common feature found in the two best taxonomically described food webs is that species that feed on more than one trophic level (omnivorous species and parasites, which in most cases could be considered as a special type of omnivory, Polis and Strong 1996) are a representative group in the set of keystone species, enhancing the importance of omnivorous species in the stability of ecological communities (McCann and Hastings, 1997).

Our results suggest that there are basic principles of ecological organization (not revealed by previous analyses) underlying the assembly process of diverse communities. These principles are in fact present at other scales: when a given spatial habitat is fragmented, there is a critical percolation threshold which leads to the breakdown of the habitat available into many small patches (Bascompte and Solé, 1996; Hanski, 1999). This threshold has very important consequences for metapopulation persistence and allows to define appropriate criteria for conservation in fragmented landscapes (Keitt et al., 1997).

Small-world and SF properties allows high food web complexity in terms of biodiversity. By one side, recent studies (Solow and Beet 1998; Montoya and Solé 2000) have shown that real food webs are more clustered from what would be expected from random wiring. These evidences support the hypothesis that compartmentalization (a characteristic of SW) is a way to enhance species coexistence in species-rich communities (May 1974). Besides, species that interact with a great number of species do so weakly. Conversely, species with strong interactions interact with few species of the community (May 1974, Paine 1992). Data on interaction strengths in natural food webs show that these networks are characterized by many weak interactions and very few strong interactions (Paine 1992; Raffaelli and Hall 1996). Recent studies also suggest that the balance of nature is related with those widespread weak interactions (McCann et al., 1998; Polis 1998). Thus highly connected species are important in promoting community stability and persistence. The detailed knowledge of this particular organization could lead to an improvement in the understanding of ecological assembly rules (Drake, 1990a; Drake 1990b).

This approximation to community fragility has obvious caveats derived from a lack of dynamics and taxonomic limitations. Besides, our findings are based on a non-directed, and non-weighted graph. Top-down and bottom-up effects due to species removals are considered together. A separate knowledge of these effects has been previously reported, arguing that whole community effects were more interesting and more relevant in the determination of keystone species (Jordan et al 1999). Preliminary analysis of model ecosystems suggest that our results are robust (Solé and Montoya, unpublished).

Current estimations of extinction rates are based on species-area relations, combined with estimates of habitat loss (May et al., 1995). The addition of secondary extinctions due to removal of keystone species, together with other indirect effects are likely to increase such projections. Food webs are described at a local scale, but the estimated extinction rates obtained from our study could be important in forecasting extinction rates at regional and global scales.

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1. Albert, R., Jeong, H. and Barabási, A-L. (2000) Error and attack tolerance of complex networks. *Nature* 406, 378-382.
2. Amaral, L.A.N., Scala, A., Barthelemy, M. and Stanley, H.E. (2000) Classes of small-world networks. *Proc. Nat. Acad. Sci. USA*, 97, 11149-11152.
3. Barabási, L-A. and Albert, R. (1999) Emergence of scaling in random networks. *Science* 286, 509-512.
4. Bascompte, J. and Solé, R. V. (1996) Habitat Fragmentation and Extinction Thresholds in spatially explicit models, *J. Anim. Ecol.* 65, 465-470
5. Bollobás, B. (1985) *Random Graphs*. (Academic Press, London)
6. Bond, W.J. (1993) Keystone species. Pages 237-253 in E-D. Shultze and H.A. Mooney, editors. *Biodiversity and ecosystem function*. Springer-Verlag, Berlin, Germany.
7. Cohen, J.E. et al. (1993) Improving food webs. *Ecology* 74, 252-258.
8. Cohen, R., Erez, K., ben-Avraham, D. and Havlin, S. (2000) Resilience of the Internet to random breakdowns. *Phys. Rev. Lett.* (in press)
9. Davic, R.D. (2000) Ecological dominants vs. keystone species: a call for reason. *Conservation Ecology* 4(1): r2 [online] URL: <http://www.consecol.org/vol4/iss1/resp2>
10. Drake, J. A. (1990a) The mechanics of community assembly rules. *J. Theor. Biol.*, 147, 213-233.
11. Drake, J. A. (1990b) Communities as assembled structures: do rules govern pattern?. *Trends Ecol. Evol.*, 5, 159-163.
12. Hanski, I. (1999) *Metapopulation Ecology*, Oxford U. Press.
13. Huxman, M., Beaney, S. and Raffaelli, D. (1996) Do parasites reduce the chances of triangulation in a real food web?. *Oikos*, 76, 284-300.
14. Jeong, H., Tombor, B., Albert, R., Oltvai, Z.N. and Barabasi, A-L. (2000) The large-scale organization of metabolic networks. *Nature* 407, 651-654.

15. Jórdan, F., Takács-Sánta, A. and Molnár, I. (1999) A reliability theoretical quest for keystones. *Oikos* 86, 453-462.
16. Keitt, T.H., D.L. Urban, and B.T. Milne. (1997) Detecting critical scales in fragmented landscapes. *Conservation Ecology* 1, 4.
17. Lago-Fernández, L. F., Huerta, R., Corbacho, F. and Sigüenza, J. A. (2000) Fast response and temporal coherent oscillations in small-world networks. *Phys. Rev. Lett.* 84, 2758-2761.
18. McCann, K. and Hastings, A. (1997) Re-evaluating the omnivory-stability relationship in food webs. *Proc. R. Soc. Lond. B.* 264, 1249-1254.
19. McCann, K., Hastings, A. and Huxel, G.R. (1998) Weak trophic interactions and the balance of nature. *Nature* 395, 794-798.
20. Martinez, N.D. (1991) Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecol. Monog.*, 61, 367-392.
21. May, R.M. (1974) *Stability and complexity in model ecosystems*. Princeton U. Press.
22. May, R.M., Lawton, J.H. and Stork, N.E. (1995). Assessing extinction rates, in *Extinction Rates* (Lawton, J.H. and May, R.M., eds.) pp. 1-24. Oxford U. Press.
23. Memmot, J., Martinez, N.D. and Cohen, J.E. (2000) Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *J. Anim. Ecol.*, 69, 1-15.
24. Montoya, J. M. and Solé, R. V. (2000) Small world patterns in food webs. Submitted to *J. Theor. Biol.* Also: Santa Fe Institute Working Paper 00-10-059.
25. Newman, M. E. J. (2000) Models of small worlds: a review. *J. Stat. Phys.* 101, 819-841.
26. Paine, R.T. (1966) Food web complexity and species diversity. *American Naturalist* 100, 65-75.
27. Paine, R.T. (1992) Food-web analysis through field measurement of per capita interaction strength. *Nature* 355, 73-75.
28. Pimm, S. L., Lawton, J. H. and Cohen, J. E. (1991) Food web patterns and their consequences. *Nature (Lond.)* 350, 669-674.
29. Pimm, S. L. (1991) *The Balance of Nature*. Chicago Press.
30. Polis, G.A. (1991) Complex trophic interactions in deserts: an empirical critique of food web theory. *American Naturalist*, 138, 123-155.
31. Polis, G.A. and Strong, D.R. (1996) Food web complexity and community dynamics. *American Naturalist* 147, 813-846.
32. Polis, G.A. (1998) Stability is woven by complex webs. *Nature* 395, 744-745.
33. Raffaelli, D.G. and Hall, S.J. in *Food Webs: Integration of Patterns and Dynamics* (eds. Polis, G.A. and Winemiller, K.O.), 185-191. Chapman and Hall, New York.
34. Solé, R. V. and Bascompte, J. (2001) *Complexity and Self-organization in Evolutionary Ecology*, Monographs in Population Biology. (Princeton U. Press) (to appear)
35. Stone, L. and Roberts, A. (1991) Conditions for a species to gain advantage from the presence of competitors. *Ecology* 72, 1964-1972.
36. Yodzis, P. (1988) The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* 69, 508-515.
37. Wagner, A. and Fell, D. (2000) The small world inside large metabolic networks, *Santa Fe Institute Working Paper* 00-07-041.
38. Watts, D.J. and Strogatz, S.H. (1998) Collective dynamics of "small-world" networks. *Nature* 393, 440-442.
39. Williams, R. J. and Martinez, N. D. (2000) Simple rules yield complex food webs. *Nature (Lond.)* 404, 180-183