

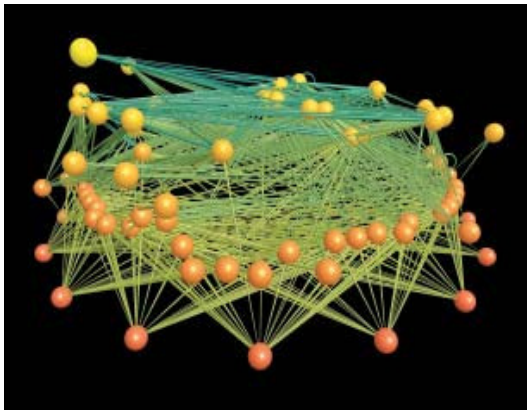
lated to environmental quality factors. It is configured as a network, though it tends to turn into a tangle, of desires, possibilities and limitations. A complex network that can be translated into artistic representation (beyond art that requires interfaces that are created, convenient for all its users).

If graphic media use photos to explain reality, the visual artist should be able to use the socio-ecological network as inspiration. There is a universe of gestures, departments and flows in socio-ecological management. Viewed properly, it consists of the management of relations between humans and their environment, and among humans, fighting for control over their environment. This epic has an unquestionably artistic dimension. Satellite sensors have glimpsed part of it as it is expressed through territory, which is configured in and translated to networks and fractals. New creators of new contemporary visual arts will have to interpret it in their own way. That interpretation will surely be beautiful and will also contribute to a better understanding of what it represents. Art has always done that.

## The architecture of nature: complexity and fragility in ecological networks\*

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Ecosystems today are characterized by their accelerated loss of biodiversity. 100,000 years from now, a palaeontologist would classify our era in the history of the earth as a time of mass extinctions. Some direct effects of this loss of biodiversity — for example, the reduction of primary productivity — are relatively well known. Others, which are more indirect but no less significant, are still practically unknown. We are referring to the complex network of ecological interactions. This article discusses some direct and indirect effects, recently discovered based on trophic interactions. These ecological networks are very fragile in the face of disturbances that eliminate the most closely connected species, with the result of a large number of co-extinctions of other species from the ecosystem. We discuss the implications these observations may have in terms of: 1) understanding the organization of ecosystems and their response to disturbances; 2) the relevance and definition of key species; 3) improving estimates of current rates of extinction, and 4) defining objectives within conservation biology.



**Figure 1.** Trophic network at Little Rock Lake (Wisconsin, United States of America). Trophic levels are ordered from bottom to top, from the basal level (primary producers, mainly phytoplankton) up to predators at the top of the food chain (mainly fish). The species (spheres) that have a connection with themselves are considered cannibal species, and are relatively abundant; in this network, 14% of the species are cannibal, but in the network at the desert in Coachella Valley (United States of America), this percentage is over 60%. Three-dimensional representation courtesy of Richie Williams and Neo Martínez (San Francisco State University, United States of America).

## Introduction

On what does the fragility of an ecosystem depend? Does the network of relations among species determine their response when faced with different types of disturbances? How does the extinction of one species affect the rest of the community? Are some species more important to the stability and persistence of an ecological system? If that is true, what characteristics do they share? The search for general reliable answers to these questions takes on a special significance today, given the sixth great extinction in the history of the earth that we are provoking and witnessing. The architecture of nature, the framework of ecological interactions, can provide some keys to these questions. E.O. Wilson, in his magnificent book *The Diversity of Life*, illustrates

how disturbances are propagated through the ecological network:

Jaguars and pumas in the scarce intact forests in Central America and South America prey on a great number of species, in contrast to the more selective behaviour of African cheetahs or wild hunting dogs. When the jaguars and pumas disappeared from Barro Colorado Island (Panama) due to the reduction of the size of the tropical forest, the population of their prey multiplied tenfold. The majority of their prey prefers large seeds from the forest treetops. Other species of trees with seeds too small to interest these animals benefited from the lack of competition. After a few years, the composition of the forest changed in their favor. Animal species specialized in the seeds of these trees increased their populations, as did the predators who fed on those animals, the fungi and bacteria that lived as parasites on the trees from the small seeds and the animals who distributed them, microscopic animals who fed on those fungi and bacteria, and the predators of those micro organisms, and so forth throughout the trophic network [Wilson, 1992].

Species relate to each other in different ways, which leads to complex interaction networks. Depending on the type of interaction that we observe, we find networks of competitors, trophic networks, mutual networks, facilitation networks, etc. The structure of ecological networks determines many of the functions of the ecosystems they represent. The recycling of nutrients, water and carbon flows, among many other functions, are altered when the architecture of these networks are lost (Schulze and Mooney, 1994; Levin, 1999).

The graphic representation of an interaction network — its nodes and connections — is called a graph. Knowing the architecture of the graphs of ecological networks will allow us to answer some aspects of the questions with which we began this article. As we will see, the architecture of these networks has points in common with other biological and technological networks, which supports the universality of certain organizational and functional principles in complex systems (Solé and Goodwin, 2001). The consequences of those architectures are surprising and involve a new view of the organization of ecosystems.

#### Toward a universal architecture of complex networks: the case of trophic networks

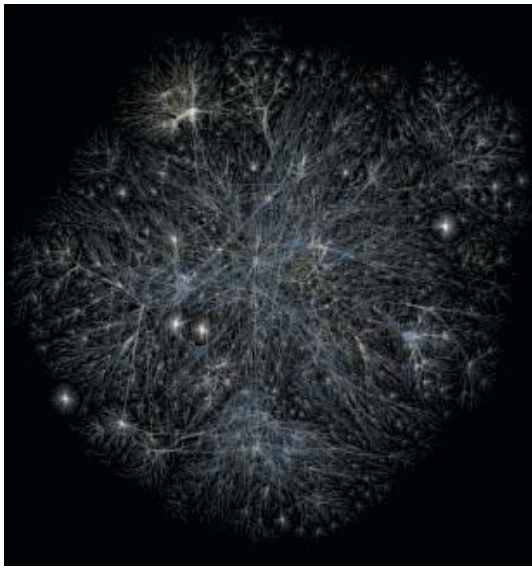
Does a universal architecture of ecological interactions exist? Trophic networks (that is, who eats whom) are the type of ecological network that have received the most attention from ecologists. In the words of Stuart Pimm and collaborators (Pimm *et al.*, 1991), “trophic networks are the highwaymen through the tangled universe of Darwin.” A trophic network shows all possible food sources for each of its constituent species [fig. 1]. Since the pioneering work of Lindeman (1942) great efforts have been made to find regularities among trophic network and different ecosystems (for the latest compilation, see Williams and Martínez, 2000).

For example, in wide collections of descriptions of trophic networks, similar values have been found for many variables, such as the average number of connections per species, the average and maximum longitude for trophic chains, the percentages of basal, intermediate and predator species, and the percentages of omnivo-

rous or cannibal species. However, there was also a great controversy that arose based on the publication of an article in 1991 by the recently deceased ecologist Gary A. Polis. In that article, the author indicates that the data on which regularities in trophic networks had been inferred were incomplete, biased, and difficult to compare with each other (see Polis, 1991, and Cohen *et al.*, 1993, for the criteria data should meet to be valid). Since then, detailed reliable trophic networks have been published on the basis of which some of these regularities are being verified, others abandoned and other new ones discovered. Most interesting of all is the development of an entire field of research on the response of the systems to different types of disturbances, observing and understanding the direct consequences of these disturbances on the network, and the indirect effects that may be caused by their propagation through the network.

Recently new techniques have been developed to analyze the complexity of a large number of natural and technological networks (for a review of the subject, see Strogatz 2001). These techniques have shown that there is a great similarity in the structure and response to disturbances and networks of very different types, which indicates a universal architecture within complex system. This perspective may constitute a true revolution in ecology, comparable to the introduction of mathematical models or multivariate analysis.

Networks, whether ecological or not, can be represented by the graph  $G(N,C)$ , where  $N$  represents the nodes in the network and  $C$  the connections among the nodes. Among others, cellular and metabolic networks have been studied (where  $N$  represents enzymes or substrata, and  $C$ , metabolic reactions; Jeong *et al.*, 2000);



**Figure 2.** Internet. The topology is quite similar to the trophic network represented in Figure 1. More connected nodes and less connected nodes can be seen (What is the node corresponding to “Ecosystems” like?).

the neural network of the *Caenorhabditis elegans* worm (in this case  $N$  represents neurons and  $C$ , synapses; Watts and Strogatz, 1998); social interaction network (for example, the network of scientific collaborations, where the nodes are the scientists, and a connection exists if they have published some joint work; Strogatz 2001); Internet, the www (Albert *et al.*, 2000) [fig. 3] and other technological networks. All of these networks share the widely known “small world” phenomenon. Basically, this phenomenon has two manifestations: 1) a high degree of component medicalization with respect to what is observed in a network where connections are distributed randomly among nodes, that is, in a network there are groups of nodes highly connected to one another (small worlds) but with very few connections to other groups of nodes, and 2) the minimum number of connections to connect two elements of the network is very low and quite similar

to that obtained for a network built randomly (for formal descriptions of these measures, see Montoya and Solé, 2001). Actually, networks with small world properties are halfway between completely ordered, regular networks and completely random networks.

Why is it so important to know the structure of networks? Simply because structure always affects function. For example, the topology of small worlds on the Internet facilitates the transmission of information in a much more efficient way than other types of topologies and, in general, this type of interaction architecture confers a great recovery capacity to systems faced with disturbances of various types.

This seemingly universal architecture is also observed in ecological networks. Two of us have found proof of this universal structure of small worlds in the three most species-rich and best described trophic networks to date (Montoya and Solé, 2001). These networks correspond to the Ythan Estuary, in the United Kingdom (134 species); Little Rock Lake, in the United States of America (182 species), and the land ecosystem associated with *Cytisus scoparius* around Silwood Park (England), with 154 species (for more details on the three trophic networks, see Solé and Montoya, 2001). Prior studies carried out by other authors had already suggested that trophic networks are usually more compartmentalized than random organization would lead one to expect, although the measurements used in those studies analyzed the trophic similarities among species, that is, groups of species that share a certain percentage of prey and predators (Solow and Beet, 1998). Does the topology of small worlds affect basic properties of the ecosystem such as their fragility or persistence? The answer is yes, but before we examine the matter in depth, we will

consider another characteristic of some complex networks, including ecological networks: the distribution of connections among species.

Many networks with small worlds show a distribution of connections via nodes of the potential type. In other words, in these networks, there are many nodes with very few connections and very few nodes with a large number of connections. The metabolic networks of many organisms and the Internet are examples of networks with this type of distribution. Two of the above-mentioned ecosystems show a potential distribution of trophic connections by species (the Ythan Estuary and the Silwood Park sub-network), and with respect to Little Rock Lake, although its amounts are not significant, it does show a distribution with a very long tail [fig. 4]. This type of distribution is very different from those in which the connections are randomly distributed through the network, which results in a Poisson distribution [fig. 1].

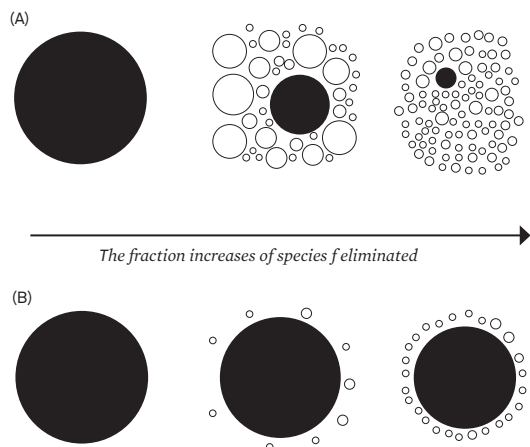
Networks with small worlds that also have distributions of connections by potential nodes show a duality between robustness and fragility based on the kind of disturbance they suffer. We identify disturbance with the successive disappearance of nodes and therefore of the connections of those nodes with other nodes within the network. Let's imagine two types of disturbance: a non-selective one that eliminates nodes randomly and a selective one that affects the most connected nodes within the network. These networks show high homeostasis in the face of random removals, that is, they recover the conditions they had prior to the disturbance. However, when faced with the selective removal of the most connected nodes, the network is tremendously fragile. In the case of the Internet and the World Wide Web (the first system in which this type

of response was observed), a random attack has almost no effects on the structure and function of the network: a very high percentage of nodes could be removed without affecting the global transmission of information. To the contrary, an attack aimed at removing a very low percentage of the most connected nodes (for example, Google, Altavista, Yahoo, etc.) caused a lack of communication among parts of the network that were previously connected quite effectively (Albert *et al.*, 2000).

The most connected species as  
“keystone species”

Ecological networks also seem to be quite fragile when faced with the removal of the most connected nodes (species), whereas they are quite robust given the random disappearance of nodes (species). What do we mean when we speak of fragility in this context? We are referring to two essential aspects of the structure and function of ecosystems: 1) biodiversity associated with the removal of species, and 2) the fragmentation of the network into sub-networks disconnected from each other. With respect to the loss of biodiversity, a good measure of the degree of fragility is secondary extinctions, that is, extinctions of species that result from the removal of other species. Specifically, through simulations carried out by computer, we have calculated the fraction of species co-extinguished in relation to species removed ( $f$ ) in the trophic networks of the Ythan Estuary, Silwood Park and Little Rock Lake. Thus, we obtained a secondary extinctions may that can be compared among these three ecosystems.

The behaviour of the three trophic networks is quite similar. By successively removing species



**Figure 3.** Fragmentation of a network (with small world topology and potential distribution of connections) in sub-networks as the fraction increases of species  $f$  eliminated by: *A*) a selective attack on the most connected species, and *B*) through a non selective attack eliminating species randomly. The radii of the circles reflect the number of species contained in each sub-network. The blue circle refers to the most numerous group of species with ecological viability (in the trophic chain there is at least one basal species). The random elimination of species permits the network to stay connected – the small circles are the species we have eliminated and a few other species that become extinct at the same time (*B*) – while for a very small fraction of the elimination of highly connected species, the ecosystem fragments into various sub networks that are disconnected from each other (*A*). The more fragmented the network, the higher the risk of extinction for other species (see text).

at random, each network stays connected, and does not fragment into sub-networks. Most significant is the fact that the extinction rates are very low even when a large number of species have been removed. Something quite different happens when we successively remove the most connected species: secondary extinction rates rise very fast. For example, in the Silwood Park network, the removal of less than 10% of the most connected species (13 of the 154 in existence) causes the disappearance of all the species in the system. In addition, the network fragments into multiple sub-networks disconnected from each other [fig. 3].

The last result might lead one to think that it makes no difference whether there is one sole network with many species or many small sub-networks, each with only a few species, but in general, it does make a difference. The risk of extinction is much higher in the second case. The main reason is what is called the “effect of biological insurance”. Greater biodiversity increases the probabilities that an ecosystem will have: 1) species that can respond in different ways to different environmental conditions and disturbances, and 2) functional redundancy, that is, species that are able to replace the function of an extinct species. Moreover, higher levels of biodiversity in a non-fragmented network can maintain the functions of the ecosystem. Thus, in the case of a fragmented network with only a few species, many of those functions may be significantly disturbed (Schulze and Mooney, 1994; Levin, 1999; McCann, 2000).

We can conclude that the most connected species in an ecosystem from a trophic perspective are “keystone species”, given that their removal has significant effects on the stability and persistence of the network (Bond, 1994). Some prior studies corroborate the key role played by the most trophically connected species. Like Wilson’s observations quoted above related to jaguars and pumas on Barro Colorado Island, Owen-Smith (1987) mentions the effects that the extinction of large herbivores has had on various ecosystems, resulting in a new distribution of vegetation and the extinction of a large number of species. Omnivorous insects with a wide trophic niche reduce the population fluctuations of all their prey, which, in their absence, fluctuate greatly over time, which can lead to the the extinction of species (Fagan, 1997). In a work in progress on communities of parasitic insects (parasitoids) of other insects, we have observed the stabilizing role of

the most connected species (hyperparasitoids) on the basic resource (the herbivorous insect that produces plant galls). In these communities, the higher the number of connections of the hyperparasitoids, the lower the rate of parasitism on the herbivore. This ensures the persistence of the basic resource and, therefore, that of the entire community. These networks also show small-world type architecture of their connections. From a theoretical standpoint, through the construction of trophic networks on a computer, we have also observed the effects on a community of insects of removing species in terms of secondary extinctions. The primary result is that the removal of the generalist species, which prey on and are preyed upon by other species, leads to a larger number of extinctions of other species.

Given this definition, “keystone species” are determined by their topology in the network, not the trophic position of each species. Therefore, not only large predators should be considered keystone species, but also species at other trophic levels (Bond, 1994). Accordingly, we have found that the keystone species in the trophic networks at Ythan Estuary, Silwood Park and Little Rock Lake belong to different trophic types (Solé and Montoya, 2001). In the network at the Ythan Estuary, keystone species are primarily intermediate species (fish and invertebrate organisms, 60%), some predators (birds, 20%), the remainder being parasites. In the Silwood Park network, the majority of keystone species are herbivores (66%), that may be considered basal species, given that only one plant exists as a resource (*Cytisus scoparius*). The omnivorous hemiptera are also quite significant (26%). In the case of Little Rock Lake, none of the basal species is among the most connected. The most connected species are intermediate species of

zooplankton and benthic invertebrates (70%) and predators (like fish, 24%).

#### The sixth extinction

Some of the most widespread disturbances of anthropic origin which also have the greatest effect on the loss of biodiversity primarily affect the most connected species in an ecosystem. The process of destruction and fragmentation of habitat is one of the most obvious cases. This process has been seen to be especially harmful for large herbivores and predators with a diet based on a large number of prey (see the example on the disappearance of jaguars and pumas due to the fragmentation of the tropical forests at the beginning of this article). The great majority of species hunted intensely by human throughout the Pleistocene were highly connected species, whose extinction led to changes in the structure of ecosystems and a large number of secondary extinctions (Owen-Smith, 1987). Another type of disturbance, with less clear effects on the most connected species, but with some well-documented examples, is the invasion of exotic species. In some cases, it can also primarily affect the highly connected species within an ecosystem (Drake *et al.*, 1989). Protecting the most connected species, through a minimization of the disturbances that affect them, would guarantee the persistence of the ecosystems of which they form a part.

Many species considered at the greatest risk of extinction are keystone species from a trophic point of view in different ecological systems. Species do not interact randomly within ecosystems: they interact according to be certain complex architecture resulting from ecological succession (with the properties of small worlds and distribu-

Extinction	Loss of genera (observed)	Loss of species (estimated)
Late Ordovician (440 Ma)	60%	85%
Late Devonian (360 Ma)	57%	83%
Late Permian (250 Ma)	82%	95%
Late Triassic (210 Ma)	53%	80%
Late Cretaceous (65 Ma)	47%	76%

**Table 1.** Extinction rates for genera and species in the five mass extinctions during the Phanerozoic (*Ma* stands for millions of years ago; data from Jablonsky, 1991, and Solé and Newman, 2001). Estimates for the extinction of genera come directly from the analysis of the fossil record, while the loss of species is inferred from a technique called *inverse rarefaction*, widely used in palaeontology.

tions of potential connections among species). This architecture is shared by other biological systems (including social systems) and humans seem to have imitated it (consciously?) in the design of multiple technological systems. This structure provided great homeostasis to ecosystems in the face of random foreseeable disturbances that can provoke the random disappearance of some species. Given this architecture, random disturbances will primarily provoke the loss of less connected species, which will generally have little impact on the ecosystem. This is what seems to have happened mainly over the course of evolution: the extinction of species has had a very large random component, as demonstrated by extinction patterns deduced from the fossil record, which did not favour or harm specific species or groups of species (Raup, 1991; Solé and Goodwin, 2001). However, there were also five mass extinctions where the loss of biodiversity of families and genera was huge (Solé and Newman, 2001) [Table 1]. The origin of these mass extinctions could

be some extraordinary agent, such as the fall of a large meteorite or intense volcanic activity, but in some cases it is not necessary to turn to these catastrophic external events to explain the existence of a large extinction. A small disturbance could have effected primarily keystone species (the most connected ones, for example), serving as a catalyst for an entire series of extinction cascades through the network of interactions in ecosystems, resulting in high extinction rates inferred from the fossil record (Solé *et al.*, 1997).

An increasing number of studies show that the biosphere is immersed in a new mass extinction (Leakey and Lewin, 1997). In this case, the cause is clearly internal: disturbances of anthropic origin that are essentially unpredictable for the ecosystems involved, many of which affect keystone species. Current estimates of extinction rates, even the most optimistic, prove the devastating magnitude of this process. All these estimates are based on species-area relations combined with estimates of the predictable reductions that the planet's habitats will undergo (May *et al.*, 1995). A recent compilation of several field studies shows that in trophic networks of different types, extinction cascades are taking place. A drop in the population size of a species, or its extinction, leads to variations in the size of populations of other species within the trophic network which, in many cases, also leads to their extinction, and this continues with more and more secondary extinctions. The workings of this domino effect are often caused by alterations of human origin (Pace *et al.*, 1999). A consideration of secondary extinctions and other indirect effects could worsen the outlook of a loss of the biodiversity and functionality of ecosystems, increasing current estimates of extinction rates.

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## References

- ALBERT, R., H. JEONG, A.-L. BARABASI (2000): "Error and Attack Tolerance of Complex Networks", in *Nature*, N° 406, pp. 378-382.
- BOND, W.J. (1994): «Keystone Species», in E.-D. Schulze, H.A. Mooney (eds.): *Biodiversity and Ecosystem Function*, Springer, Berlin, pp. 237-253.
- COHEN, J.E., et al. (1993): "Improving Food Webs", in *Ecology*, N° 74, pp. 252-258.
- DRAKE, J.A., H.A. MOONEY, F. DI CASTRI, R.H. GROVES, F.J. KRUGER, M. REJMANEK and M. WILLIAMSON (eds.) (1989): *Biological Invasions: a Global Perspective*, John Wiley, London.
- FAGAN, W.F. (1997): "Omnivory as an Stabilizing Feature of Natural Communities", in *American Naturalist*, N° 150, pp. 554-567.
- JABLONSKY, D. (1991): "Extinctions: a Paleontological Perspective", in *Science*, N° 253, pp. 754-757.
- JEONG, H., B. TOMBOR, R. ALBERT, Z.N. OLTVAI and A.-L. BARABASI (2000): "The Large- scale Organization of Metabolic Networks", in *Nature*, N° 407, pp. 651-654.
- LAGO-FERNÁNDEZ, L.F., R. HUERTA, F. CORBACHO and J.A. SIGÜENZA (2000): "Fast Response and Temporal Coherent Oscillations in Small-world Networks", in *Physiology Review Letters*, N° 84, pp. 258-2761.
- LEAKEY, R. and R. LEWIN (1997): *La sexta extinción: el futuro de la vida y de la humanidad*, Tusquets, Barcelona.
- LEVIN, S. (1999): *Fragile Dominion*, Reading, Perseus Books, Massachusetts.
- LINDEMAN, R.L. (1942): "The Trophic-dynamic Aspect of Ecology", in *Ecology*, N° 23, pp. 399-418.
- MAY, R.M., J.H. LAWTON and N.E. STORK (1995): "Assessing Extinction Rates", in J.H. Lawton and R.M. May (eds.): *Extinction Rates*: Oxford University Press, pp. 1-24.
- MCCANN, K.S. (2000): "The Diversity-stability Debate", in *Nature*, N° 405, pp. 228-233.
- \* MONTOYA, J.M. and R.V. SOLÉ (2001): "Small World Patterns in Food Webs", in *Journal of Theoretical Biology*. Also: *Santa Fe Institute Working Paper*, 00-10-059.
- OWEN-SMITH, N. (1987): "Pleistocene Extinctions: the Pivotal Role of Megaherbivores", in *Paleobiology*, N° 13, pp. 331-362.
- PACE, M.L., J.J. COLE, S.R. CARPENTER and J.F. KITCHELL (1999): "Trophic Cascades Revealed in Diverse Ecosystems", in *Trends in Ecology and Evolution*, N° 14, pp. 483-488.
- PERSSON, L., J. BENGSTON, B.A. MENGE and M.A. POWER (1996): "Productivity and Consumer Regulation: Concepts, Patterns and Mechanisms", in G. A. Polis, K. O. Winemiller (eds.): *Food Webs: Integration of Patterns and Dynamics*, Chapman & Hall, New York, pp. 396-434.
- PIMM, S.L. (1980): "Food Web Design and the Effect of Species Deletion", in *Oikos*, N° 35, pp. 139-149.
- (1991): *The Balance of Nature*: Chicago Press.
- PIMM, S.L., J.H. LAWTON and J.E. COHEN (1991): "Food Web Patterns and their Consequences", in *Nature*, N° 350, pp. 669-674.
- POLIS, G.A. (1991): "Complex Trophic Interactions in Deserts: an Empirical Critique of Food Web Theory", in *American Naturalist*, N° 138, pp. 123-155.
- RAUP, D. (1991): *Extinction: Bad Genes or Bad Luck?*, W. W. Norton & Co., New York.
- SCHULZE, E.-D. and H.A. MOONEY (1994): "Ecosystem Function of Biodiversity: a Summary", in E.-D. Schulze, H.A. Mooney (dirs.): *Biodiversity and Ecosystem Function*, Springer, Berlin, pp. 497-510.
- SOLÉ, R.V. and B. GOODWIN (2001): *Signs of Life. How Complexity pervades Biology*, Basic Books Harper and Collins, New York.
- \* SOLÉ, R.V., S.C. MANRUBIA, M. BENTON and P. BAK (1997): "Self-similarity of Extinction Statistics in the Fossil Record", in *Nature*, N° 388, p. 764.
- \* SOLÉ, R.V. and J.M. MONTOYA (2001): *Complexity and Fragility in Ecological Networks. Proceedings of the Royal Society of London Ser. B* (forthcoming).
- \* SOLÉ, R.V. and M. NEWMAN (2001): "Patterns of Extinction and Biodiversity in the Fossil Record", in *Encyclopaedia of Global Environmental Change*.
- SOLOW, A.R. and A.R. BEET (1998): "On Lumping Species on Food Webs", in *Ecology*, N° 79, pp. 2013- 2018.
- STROGATZ, S.H. (2001): "Exploring Complex Networks", in *Nature*, N° 410, pp. 268-275.
- WATTS, D.J. and S.H. STROGATZ (1998): "Collective Dynamics of "Small-world" Networks", in *Nature*, N° 393, pp. 440-442.
- WILLIAMS, R.J. and N.D. MARTÍNEZ (2000): "Simple Rules Yield Complex Food Webs", in *Nature*, N° 404, pp. 180-183.
- WILSON, E.O. (1992): *The Diversity of Life*, Allen Lane/Penguin, London.

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