11 The Ecoweb

"There is something I do not understand here. Why are you writing about ecosystems after the world market and the whole of human history? So far I thought we were going from small to big." And you were right, Spite! We are still going from small to big. Humankind with all its global glory and a few thousand years of written history only occupies a part of Gaia's ecosystem, which has been developing for almost 4 billion years (Schidlowski, 1988; Holland, 1997). On our seventh and last trip into Netland, we shall learn about the properties of the oldest and biggest network of all: the ecoweb.

11.1 Weak Links and the Stability of Ecosystems

The ecoweb is not a birthday party. Here links are built between predators and prey, consumers and food. You either eat – or you are eaten.[1] Ecowebs display the usual network characteristics, such as small-worldness and scale-freeness, but differently. When we eat, we get really close to each other: the now proverbial six degrees of separation of human societies go down to two degrees of separation in ecowebs (Williams et al., 2002). However, path length and other small-world characteristics, like clustering of ecowebs, do not typically differ from those of random graphs (Dunne et al., 2002a). A bona fide scale-free behavior can only be demonstrated for smaller ecowebs with low connectivity or for modules of larger ecological networks. In fact, many ecowebs display a degree distribution with a single characteristic degree, which makes them similar to random graphs (Dunne et al., 2002a; Jordan and Scheuring, 2002; Jordano et al., 2003; Montoya and Sole, 2003).

[1] We usually consider ourselves to be at the top of the food chain. However, if we really think about it, the King of Nature is the pit bull. (Pit bulls occasionally consume humans. On the other hand, oriental cuisine has other dog delicacies than pit bulls, as far as I know. The same cannot be said for sharks, which consume us more systematically, but may also end up on our table on an unlucky day in the history of sharks.)

The large variability in these network properties may be explained by the differences in size, connectivity and complexity of the ecowebs studied. However, the topological phase transitions of networks we saw earlier (Sect. 3.4) (Derenyi et al., 2004; Palla et al., 2004) may also work here. The characterization of resource-rich or resource-poor states has not yet been systematically addressed in the ecoweb analysis. The random-like, scale-free and high-connectance, few-node networks of Dunne et al. (2002a) may actually correspond to the random, scale-free and fully connected subgraph phases of Derenyi et al. (2004), showing a response to increasing stress. Even if this assumption is not valid, it would be interesting to see whether a random-like ecoweb structure can be shifted to a scale-free-type network if resources are curtailed.

Another type of ecoweb scaling emerges from the transportation network analogy due to Garlaschelli et al. (2003). By decomposing the loops of ecowebs in a renormalization-type operation, they constructed a tree-like energy flow connecting the various foods and consumers, starting from the external environment. After this transformation, the ecowebs become similar to the fractal-type transport systems we saw in Sect. 7.2, and show the general scale-free behavior of the allometric scaling laws (Sect. 2.2) (Kleiber, 1932). Although the exact value of the scaling exponent has recently been debated, all authors agree that food webs are very efficient resource transportation systems (Barbosa et al., 2005; Camacho and Arenas, 2005; Garlaschelli et al., 2005b).

Ecowebs show a rather complex dynamism. I have already mentioned the synchronization of hare and lynx populations fluctuating in sync over millions of square kilometers in Canada (Blasius et al., 1999). The variation in population size as well as in the lifespans of bird species both display a scale-free distribution, which also invokes cooperative behavior (Keitt and Stanley, 1998).

As is generally true for non-random, scale-free systems (Albert et al., 2000), the removal or addition of an element to an ecoweb may lead to a wide variety of consequences. The removal of a keystone species which may bridge separate eco-modules or may have many connections, can be catastrophic. On the the other hand, a random failure does not cause secondary extinctions in most cases. Sequential damage often shows a threshold, beyond which the system displays extreme sensitivity to removal of any further species. A rather simple rule of nature conservation may follow from this: We should find the very few keystone species and protect them, and then we may kill the rest. Fortunately, this is not so easy. A seemingly redundant species playing only a minor role in a particular ecosystem may suddenly assume the role of the keystone species as environmental conditions change. The unpredictability of keystone species status resembles the yeast metabolic network, where 40% of the genes become essential under special conditions only (Papp et al., 2004). Facultative essentiality is a general feature of complex networks and reflects the same stabilizing power as weak links. As an additional warning sign, it is extremely difficult to predict the sensitivity threshold of ecowebs. In other words, we never know whether the ecosystem will become completely unbalanced after the extinction of the second or fifth species (Allesina and Bodini, 2005; Dunne et al., 2002b; Holling, 1973; Ives and Cardinale, 2004; Jordan and Scheuring, 2002; Jordan et al., 2002; Montoya and Sole, 2003; Paine, 1969). Since we cannot put the Earth into an incubator, we need to preserve its diversity to protect the ecosystem under a variety of possible conditions.

Ecological systems are by definition diverse. Diversity may further increase due to either immigration or specitation. In bacterial communities, a large part of diversity is microdiversity, i.e., an abundance of genetically almost identical species (Acinas et al., 2004). Bacterial diversity is fine-tuned by the vivid lateral transfer of DNA (Ochman et al., 2000) between various bacteria. Diversity and especially microdiversity invoke differential contacts between system elements, which give rise to strong and weak links. Symbioses, like that of the mycorrhiza fungi with terrestrial plants may – weakly – link whole forests (Wiemken and Boller, 2002). Weak links are also perceived in ecowebs as indirect, higher order interactions (Abrams, 1983). Indeed, data analysis of food webs suggests that most interactions in complex ecowebs may be weak (Berlow, 1999; McCann et al., 1998; Montoya and Sole, 2003; Paine, 1992).[2]

Molecular sources of ecological diversity in situations of need. Stress induces an increased variability of ecosystems (Warwick and Clarke, 1993). As one of the possible reasons for this, when an ecosystem becomes unbalanced, participants begin to consume unusual foods. This is a perfect scenario for acquiring unusual viruses and prions, which often cross the species barrier (Scott et al., 1999). These and perhaps other mechanisms change the genetic or epigenetic status of the reorganized ecoweb and open new ways to unleash a surge in diversity (see Sect. 6.3). As a conse-

[2] I am grateful to Márton Tóth for many of these ideas.

quence, diversity helps to stabilize the ecoweb and promotes its survival, by increasing its netsistance.

The dangers of partial extinctions: The distribution of genetic diversity is highly uneven. Diversity is not uniform. We may feel this from the uneven distribution of diversity at the phenotype level. As an example of this, think of the human-made monocultures of wheat or corn. However, the really important diversity of diversity lies at the genetic level, since this forms the basis for future stability and changes, the evolvability of the species, as described in Sect. 6.3. Rauch and Bar-Yam (2004) showed that the distribution of genetic diversity is scale-free. Thus, most of the potential future development of a species may be concentrated in a tiny environment. Moreover, the borders of diversity sanctuaries are often not visible. Therefore, a 'small', 'negligible' partial extinction may wipe out most of the reserves in genetic diversity and may lead to a dangerously low chance of survival for the whole species in the long run.

Top predators stabilize diversity. Sergio et al. (2005) found that the presence of five different predators (the goshawk and 4 owl species) was consistently associated with a higher diversity of birds, trees and butterflies in the Italian Alps. Their results justify conservation efforts concentrating on top predator species. In agreement with this, Bascompte et al. (2005) suggest that overfishing of the top predator sharks may have induced trophic cascades leading to the degradation of Caribbean reefs.

Recent data indicate that diversity enhances the stability of an ecosystem (Hughes and Stachowicz, 2004; McCann, 2000). However, this statement has had a rather eventful past, called the diversity–stability debate (McCann, 2000). Before the 1970s, ecologists believed that diversity enhanced the stability of ecological networks. The famous ecologist, Robert May (1973) and other colleagues challenged this view by showing that the more species the system has, the higher are the fluctuations that occur if we remove or add a constituent. May and others were partially right. The instability of overconnected systems is a well-documented effect, as mentioned in Sect. 3.3 (Fink, 1991; Siljak 1978; Watts, 2002). The establishment of new links is costly, since new territories must be explored for the new food, new hunting techniques have to be employed, etc. Therefore, it remains an open question whether real ecosystems ever reach the unbalanced, overconnected state.

May (1973) built his networks as random graphs and calculated their equilibrium. But links in the ecoweb are not random and ecosystems never reach equilibrium (McCann, 2000). If assessed by dynamic methods, weak links clearly dampen oscillations between consumers and resources and decrease the likelihood of extinction (Berlow, 1999; McCann et al., 1998).

On the basis of a large amount of data, diversity won the diversity–stability debate (McCann, 2000). Diversity does not only act over intervals of weeks or decades. The diversity of 3 300 biogenic reefs stabilized them over a 542 million year timescale (Kiessling, 2005). Diversity not only stabilizes ecosystems, but also gives them a greater potential for evolution (Earl and Deem, 2004). Functional and spatial diversity all help system stability – by using weak links. Strong and weak links may have complementary roles in ecowebs: while strong links build up the frame of the network, weak links provide its robustness (see Table 11.1) (Garlaschelli et al., 2003; McCann, 2000).

Our forests are superorganisms connected by invisible weak links. Trees in the forest are nursed by the wood-wide web of symbiotic fungi, called mycorrhiza. This concept was put forward more than a hundred years ago (Frank, 1885) and has been proven by recent studies. As an example of the multiple benefits, trees which are well-exposed to light feed trees growing in the dark by supplying assimilated carbon through ectomycorrhizal bridges between them (Wiemken and Boller, 2002). Mycorrhiza makes our forests into a superorganism which is stabilized by weak links.[3]

11.2 Omnivory

What is best for the stability of our ecosystem? Are we helping system survival more if we restrict our diet to three liters of fresh orange juice per day, or should we eat everything? As a first approximation to the answer, humans are by nature omnivorous animals (like pigs). In this section, I will use omnivory as a special case to enhance and extend our knowledge of the stabilizing role of weak links in the ecoweb.

Omnivorous animals are typically inefficient in consuming their prey (Sole et al., 2003a), which means a low-affinity interaction. Adaptive foraging generally leads to the development of a few strong and many weak links (Kondoh, 2003). The omnivore feeds largely on the

[3] I am grateful to Márton Tóth for this idea.

Table 11.1. Stabilizing effects of weak links on ecowebs

Weak links	Effect on stability	References
Weak predator effects in field experiment	Removal of weak links induces higher noise of network parameters	Berlow, 1999
Weakly coupled oscillation of hare and lynx populations	Resistance against perturbations	Blasius et al., 1999
Strong and weak link patterns together	An appropriate pattern of strong and weak links is needed for network stability	de Ruiter et al., 1995; Yodzis, 1981
Strong and weak link patterns together	Reduced trophic cascades	Bascompte et al., 2005
Loop-forming weak food fluxes	Network stability increases with the number of weak links	Garlaschelli et al., 2003; Neutel et al., 2002
Weak and intermediate strength links	Dampened oscillations of model web densities	McCann et al., 1998
Indirect effects	Approximately 40% of system stability is derived from these weak links	Menge, 1995

lowest trophic level. As a result, it has strong links to this trophic level and makes weaker and weaker links at higher and higher levels (Neutel et al., 2002). Thus omnivory helps the development of a wide range of weak links in ecological networks.

In parallel with the diversity–stability debate, the contribution of omnivory to ecoweb stability was also questioned over a long period. Pimm and Lawton (1978) concluded to a destabilizing role for omnivory, while Dunne et al. (2002b) found that omnivory and robustness are independent in ecosystems. On the other hand and in agreement with the stabilizing role of weak links, numerous studies reported that the presence of omnivory exerts a stabilizing force in the dynamics of ecosystems (Borrvall et al., 2000; Fagan, 1997; Holyoak and Sachdev, 1998; McCann et al., 1997; 1998). Omnivory reduces trophic cascades (Bascompte et al., 2005) and extends the range of topologies in which the food web remains stable (Kondoh, 2003). Omnivores, like typi-

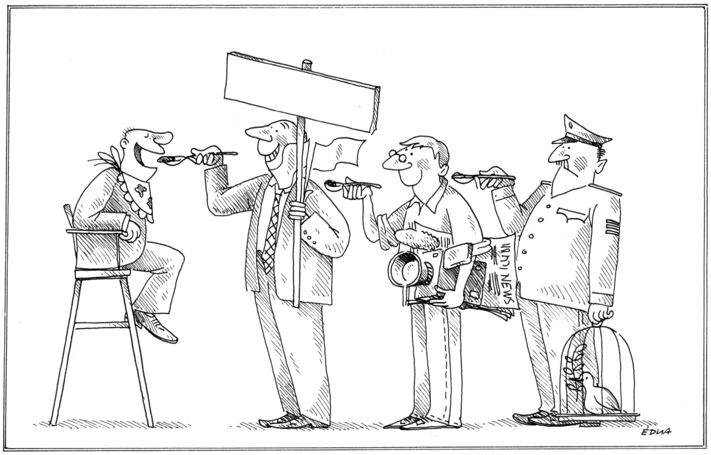

Fig. 11.1. Omnivory-induced system stability probably helped us to conquer this planet

cal weak-linkers, are thus reminiscent of water in Sect. 5.3 and may also smooth the saddles between local stability regions of the eco-landscape.

What can be the reason for the differences in the proposed or observed consequences of omnivory? Some of the discrepancies arises from the same sources already mentioned in the diversity–stability debate. Earlier models designed to monitor secondary extinctions lacked a detailed description of interaction strength and system dynamics. Moreover, overconnectedness (Sect. 3.3) may have overturned the stabilizing effect of omnivory in some systems. In reality, omnivory is often facultative, which means that an omnivorous animal may spend a long time being a vegetarian, for example, if there is plenty of fruit around. Additionally, an increased variability of data due to the increased system imbalance also disturbed the final conclusions.

Omnivory as our increased chance for survival. We eat everything possible and even more (watch TV or order fast food if you do not believe this). Omnivory-induced system stability probably helped us to conquer this planet. Had we been exclusively herbivorous or carnivorous species, system imbalance would have wiped us out a long time ago, or it would have forced the diversification of humans to herbivorous and carnivorous sub-types, generating a coexistence with our Neanderthal or other cousins and making human history an unending war between the two. Omnivory also provides us with a greater variety of plant toxins and other xenobiotics than a carnivorous or herbivorous diet, and this creates more weak links between these compounds and our cellular proteins. Omnivory seems to be a good strategy for staying well-balanced.

To answer the opening question of this section, it is better not to keep to strict promises in hard times. Eating our first fruit after years of all-burger days will both serve our own survival and help the ecosystem to get stabilized. On the other hand, the above scenario gives a good example of the nestedness of the ecoweb. In the long run, my choices from the eco-menu on the local level determine the survival of my species at the planetary level. The brave extension of existing knowledge and the discovery of large-scale, trans-network interactions led to the concept of Gaia described in the next section.

11.3 The Weak Links of Gaia

James Lovelock formulated the Gaia hypothesis at the end of 1960s. Gaia is the whole ecosystem of the Earth. Everything around and inside us belongs to it: the biosphere, atmosphere, oceans and soil, all making up a highly regulated complex network. At first, the self-regulating nature of the whole Earth ecosystem was received with skepticism. However, the increasing number of demonstrations had led to wide support by the end of the 1980s (Lovelock, 1979; 2003; Lenton, 1998).

"As it grows older, the Earth system weakens." Our Gaia network is "elderly and we should treat it with respect and care" (Lovelock, 2003). How can our aging Gaia be stabilized? Most of the existing examples of the self-regulation of Gaia involve negative feedback mechanisms (Lenton, 1998). However, it is quite clear that these are only the very first proofs of system stabilization at the global level. Gaia is the most complex network we have ever met, and has most probably developed a lot more stabilizing effects than we have ever found or even thought of. The extreme robustness and resilience of ecosystems (as discussed in Sect. 11.1) may encourage a general neglect with regard to preserving the stability of this largest ecosystem, Gaia herself. One often hears: "Without much care for the consequences, we should do what we need to do. If some species become extinct, we will find them elsewhere. If they become endangered worldwide, we can put them into sanctuaries or save videos and DNA samples until we can. The ecosystem will survive anyway. It has survived worse scenarios in the last 3 to 4 billion years." These assumptions are true. Gaia's resilience is indeed amazingly strong. However, there is an important point here. Does it make us happy to think that Gaia will survive – without us?

The stabilizing effect of weak links in ecosystems gives an additional, powerful argument for maintaining diversity. Diversity serves not only to preserve a larger genetic pool to combat future challenges, and it serves not only to prevent a general system crash at some time in the remote future. It serves also to avoid extreme fluctuations *today*. Pfefferkorn (2004) warns in his recent article on the Permian catastrophe: "Today we are living through another mass extinction." According to a recent estimate, climate warming scenarios may commit 15 to 37% of species to extinction (Thomas et al., 2003). If we pauperize ecowebs, they will be enriched in strong links. The depletion of weak links leads to larger oscillations and further extinctions, which may propel a downward spiral (Bascompte et al., 2005; McCann, 2000; McCann et al., 1998; Scheffer et al., 2001). Moreover, decreased diversity lessens the chances for degenerate functions which may substitute for one another during system fluctuations (Edelman and Gally, 2001; McCann, 2000). As a conclusion, we cannot risk the extinction of even a single species. Not only because of some altruistic, God-substituting pattern such as: "If we have become the rulers of the Earth, we should take care of her beings", but also because the more species vanish, the closer we get to unbearable fluctuations.

"I do share your thoughts, but let me ask a question here. You have already noted most of this in previous chapters, so why do you repeat it here? More pages, more money?" No Spite, fortunately this is not a string of sausages, but a book. Here the basic rule is almost the reverse: the more words it has, the less it may mean. Why do I stress the importance of diversity yet again? First, it is important. *If I am allowed to sum up only a single lesson from the stabilizing strength of weak links described in this book, then it should be the commitment to diversity*. However, the commitment to diversity is not only to preserve the ecosystem from large fluctuations. It has an even more serious reason. The concept of Gaia means that *all* these networks are connected. The anticipated extinction cascade due to climate warming will not only induce fluctuations in ecowebs. Eco-fluctuations will likely contribute to the destabilization of all other physicochemical networks around us. Among other things, it will make weather fluctuations wider. Larger weather fluctuations may induce an even larger imbalance in the ecosystem. We have another grim possibility here for a downward spiral.

I would make one more remark. Diversity here is not only the diversity of the species around us. Cultural diversity (Pagel and Mace, 2004) is also included. Cultural diversity is important, not only because it stabilizes societies and the social mega-net of our globalized world. Cultural diversity also makes weak links with the ecosystem. Our fast-conquering, omnipresent Western culture is not only pauperizing the cultural heritage that all previous generations have so far collected (Axelrod, 1997). It is also destabilizing the whole ecosystem, Gaia, around us. Population and economic growth may lead to a destabilized period around 2060–2080, according to some estimates (Johansen and Sornette, 2001). However, the situation might be worse. If we are truly unlucky, we may face a critical phase in the inherent growth of human networks, in the destabilized ecosystems, and in the destabilized complexity of Gaia all at the same time.

"Peter, you frighten me. Thinking about Pity, who is expecting, I am deeply concerned. We do want to take our responsibility for our future, for the largest known network, Gaia." Wow, a child! That was quick work, Spite. Congratulations to both of you! In Sect. 12.4, I will make some remarks as to whether Gaia is the largest known network or not. Apart from that, I am very happy to see your commitment. To end this chapter, let me list some advice.

Ecosystem management (I could say Gaia management) usually behaves as a human substitute for the Le Chatelier principle in thermodynamics. Has the equilibrium been changed? Too bad, we should add an extra measure to push it back to the original. Prevention of perturbations is a primary concern. This is wrong, and not only wrong, but fundamentally wrong. First of all, the system was not in equilibrium. It is not at all obvious that the previous state is more stable or more desirable under the present conditions. Secondly, as mentioned in Sect. 3.2, life is a relaxation phenomenon. If we reverse the change, we may prevent relaxation. Thirdly, even if we assume that the system was in a quasi-equilibrium, this equilibrium is not the simple equilibrium of the chemistry textbooks. The rules governing this equilibrium are much more complex than the Le Chatelier principle, and will be mentioned in the synthesis of Sect. 12.2. If we use simple logic and fight against the changes observed today, we may induce cascading changes leading to an even greater disturbance. Moreover, even if we are successful in our fight, this may not prevent the next perturbation occurring tomorrow at an unexpected point and level. *"Peter, by now I am not only frightened, I feel helpless. Was this your advice?"* Do not worry, Spite, there is more advice to come:

- **Learn system logic.** You are built from networks, you make networks, and you live in networks. You should understand how they work and how you can influence them.
- **Let it burn.** Once you have learnt how the system works, you should not block relaxation processes. If you do not take care over this, a netquake will follow with all the unpredictability I mentioned in Sect. 3.2. *"What is the 'burn' here?"* If you do not let small forest fires burn, much larger, devastating fires will follow (Malamud et al., 1998; Sornette, 2003). Similarly, you should leave mild illnesses untreated. Let your immune system relax. If you have a problem with someone, say so! Chronic resentment may cause a chronic disease. You may continue the list and help the easy relaxation of tensions wherever you go.
- **Redirect growth.** Since the beginning of our history all human networks have been expanding. Material growth may have approached the limits where it exceeds the resilience of the nesting network, Gaia. You should slow down, act less and think more. It is brainless logic to jump up and do everything you can. Patience and the strength of abstinence are sadly missing from our current world. However, stasis is not an alternative. You cannot stop growth. But you may redirect it. The Western world,[4] which consumes most of the world's resources, should make a shift from material growth to intellectual, artistic and spiritual growth. Knowledge is non-rivalling (Johansen and Sornette, 2001): you can share and develop it without exploiting the outer networks. You have to redirect your links, too. It is not your treasured goodies, but your fellow human beings who deserve your links. Caress your spouse, not the buttons of your computer. (*"Pity, don't you think he should stop writing here?"*) How can we accomplish all this? The West may learn from the traditions of the East and from some primitive societies. At least, while both still exist.
- **Protect diversity.** Diversity is the key to system stability and development. You should make every effort to protect it. If a complex system experiences trouble, it may begin to shift towards a star phase, and it may move towards collective and critical behavior. None of this helps diversity. If you get into trouble, stay calm and think. Remember the wisdom of hundreds of generations before, and remain independent. Do not go with the herd, and think twice before accepting the rules of a strict hierarchy. Like the foreign-

[4] And here I mean not only the USA, the EU and other G7 member countries, but more and more the fast-developing China and India, too.

Fig. 11.2. The West may learn from the traditions of the East and from some primitive societies. At least, while both still exist

ers, those who are different, those who are strange. Your tolerance will not only stabilize the many, but will also isolate the intolerable fanaticism of the few. If you can link future fanatics into your current networks, you have achieved real success. Stabilization of your present and future both require proper links: the last piece of advice and the main point of this book.

- **Balance your links.** Weak links help you to avoid unbearable fluctuations. However, you should not blindly start to make all the weak links possible. This will lead to an overconnected network, and will not decrease, but probably increase fluctuations. You should keep the delicate balance between a few strong and a lot of weak links. Moreover, you should make a few long-range links connecting social groups which were poorly connected before. The promotion of their understanding is your only ticket for a safe present and future. How can you do all these? Turn back to the first piece of advice and start again: learn system logic.

With this set of advice, we have reached the end of our last trip into Netland. I do not think I can give a better summary here. I can just ask you to take a deep breath, drink a glass of crystal clear water, relax, and most importantly: think about this advice. The next chapter will be the concluding chapter of the book. The coda I promised earlier.