On Volterra and D'Ancona's footsteps: The temporal and spatial complexity of ecological interactions and networks

M. Gatto

* Dipartimento di Elettronica e Informazione, Politecnico di Milano, Milano, Italy

Online Publication Date: 01 March 2009

To cite this Article Gatto, M.(2009)'On Volterra and D'Ancona's footsteps: The temporal and spatial complexity of ecological interactions and networks',Italian Journal of Zoology,76:1,3 — 15

To link to this Article: DOI: 10.1080/11250000802364657
URL: http://dx.doi.org/10.1080/11250000802364657
REVIEW ARTICLE

On Volterra and D’Ancona’s footsteps: The temporal and spatial complexity of ecological interactions and networks

M. GATTO*

Dipartimento di Elettronica e Informazione, Politecnico di Milano, Milano, Italy

(Received 9 July 2008; accepted 23 July 2008)

Abstract
In 1926, Vito Volterra published his monograph ‘Variazioni e fluttuazioni del numero d’individui in specie animali conviventi’ in the Memorie dell’Accademia dei Lincei, and the article ‘Fluctuations in the abundance of a species considered mathematically’ in the journal Nature. The quantitative ecology of complex trophic interactions was born in that year. However, he would have never considered the problem without the stimulus of a great zoologist and ecologist, his son in law Umberto D’Ancona. Following the footsteps of Volterra and D’Ancona, I will outline the research progress in the area of complex ecological interactions. Ecosystems can be viewed as spatial networks, in which local populations are connected by dispersal, or food webs, in which different species are connected by trophic interactions. Most of the scientific progress in the past century has been made by studying these two aspects. I will discuss that progress considering the following specific topics in a historical perspective: the role of space in consumer–resource interactions, population fluctuations and the predator’s functional response, bottom-up and top-down control in the trophic chain, the network structures of ecosystems, the link between stability and ecosystem diversity and complexity.

Keywords: ecological networks, metapopulations, functional response, food webs, biodiversity, ecological stability, history of ecology

Introduction
Biological interactions among organisms are a central theme of ecology. They play a fundamental role in governing the dynamics in space and time of populations and communities. Understanding the mechanisms underlying these dynamics and describing them in a quantitative way was the focus of two great Italian scientists, Vito Volterra and Umberto D’Ancona (Figure 1). This review paper will be a sort of ride through the history of ecology governed by my personal taste and research experience, which is chiefly theoretical. However, I want to convey the message that good models of complex ecological interactions always derive from a cooperation between theoretical exploration and field and lab work.

This cooperation is indeed apparent in the relationship that linked Vito Volterra and Umberto D’Ancona (Scudo 1971). Vito Volterra was already a famous mathematician with a prominent role in past century’s Italy (he was a senator of the kingdom since 1906) when he met a young zoologist, Umberto D’Ancona, who was courting his daughter Luisa. D’Ancona was intrigued by the fluctuations of landings in Trieste’s fish market. If fish were divided into predators and prey they showed coupled oscillations which were in a way similar to the oscillations of the mechanical systems studied by Volterra (D’Ancona 1926). Volterra analysed the problem with the full strength of his mathematical ability. In 1926, he published the monograph ‘Variazioni e fluttuazioni del numero d’individui in specie animali conviventi’ in the Memorie dell’Accademia dei Lincei (Volterra 1926a) and the article ‘Fluctuations in the abundance of a species considered mathematically’ in the journal Nature.

*Correspondence: M. Gatto, Dipartimento di Elettronica e Informazione, Politecnico di Milano, Via Ponzio 34/5, 20133 Milano, Italy. Email: marino.gatto@polimi.it

1Dedicated to the memory of Franco Scudo (1935–1998).

ISSN 1125-0003 print/ISSN 1748-5851 online © 2009 Unione Zoologica Italiana
DOI: 10.1080/11250000802364657
(Volterra 1926b). In 1927 there appeared a second edition of the monograph (Volterra 1927), much enlarged and updated. It was published with the Regio Comitato Talassografico Italiano (Royal Committee for Sea Studies). The new monograph considered not only predator–prey dynamics, but also various ecological interactions in communities with any number of species. After Volterra’s death in 1940, Umberto D’Ancona published the book ‘La lotta per l’esistenza – The struggle for existence’ (D’Ancona 1942) which was deeply inspired by Volterra’s work and was a brave homage to a scientist who had refused to take a mandatory oath of loyalty to the Fascist regime.

Standing on the shoulders of the two great forefathers, I will try to outline the evolution of this research area, focusing on the inherent complexity of the biological structures studied by ecologists and on the web of interactions that characterize them. Although ecosystems consist of very complicated networks, one can make a rough distinction between two network categories: spatial networks, in which local populations are connected by dispersal, and food webs, in which different species are connected by ecological interactions. Of course, a realistic description of the functioning and temporal dynamics of terrestrial and marine ecosystems should include both the spatial and the trophic structure. Having this target in mind, I will first discuss the role of spatial inhomogeneity in prey–predator interactions and the importance of nonlinearity in predators’ functional response for population dynamics. Then I will consider food chains, the role of top predators and the problem of bottom-up vs. top-down control.

Finally I will review what we know about the structure of ecological networks and discuss the ultimate problem: linking stability, complexity, diversity and productivity. I will put all the problems in a historical perspective evidencing the connection between the most recent developments and the work of the pioneers.

**Sustained oscillations of prey and predators**

The problem of coupled oscillations in predator–prey dynamics is certainly one of the most fascinating in ecology. The most famous data displaying this kind of dynamics are probably those coming from the records of the Hudson Bay Company for the lynx and the snow hare (Elton 1927). Actually, Volterra was not alone in his quest for an explanation of coupled oscillations. In 1924 Alfred J. Lotka, a Ukrainian statistician and demographer, the son of American expatriate missionaries who had returned to the USA, had already published the monograph ‘Elements of physical biology’ (Lotka 1924) in which he had proposed the following couple of differential equations for describing the predator–prey interaction

\[
\frac{dx}{dt} = rx - pXY \\
\frac{dy}{dt} = epXY - my
\]

(1)

\(x\) and \(y\) are the prey density and the predator density, respectively; \(r\) is the Malthusian rate of increase of the prey; \(m\) the mortality rate of the predator; \(p\) the
predation rate; \( e \) the coefficient of conversion from prey to predator numbers or biomass.

Volterra, who in 1926 was not aware of Lotka’s work (see Kingsland 1995 for an interesting historical perspective on the development of population ecology), wrote the same system of equations in his own monograph. These two equations are the simplest example of a general class of equations which are now termed Lotka–Volterra equations. According to Lotka and Volterra this couple of equations could nicely explain the oscillations of a prey and its predator. However, despite the mysticism surrounding these two equations, we now know that both Lotka and Volterra were wrong. In fact their system was predicated on a very unrealistic assumption, that the prey can grow in a Malthusian fashion if uncontrolled by predators. Thus, the resulting system is not dissipative, a condition which is physically and biologically impossible on our earth. Nondissipative systems are not constrained by energy limitation and the second principle of thermodynamics. They display an infinity of oscillations (see Figure 2a) whose amplitude depends on initial conditions (like planets orbiting around the sun). If a bit of realism is introduced into Lotka–Volterra equations, by assuming a carrying capacity for the prey, e.g. via logistic growth, the resulting dissipative system no longer exhibits sustained oscillations (Figure 2b). Predator and prey converge towards an equilibrium in the long term, with or without damped oscillations, in any case without ever perpetuating oscillations.

The role of space and nonlinearity in trophic interactions

What, then, are the factors that cause some real ecological systems to oscillate, at least for a reasonably long time, in a sustained way? There are several possible mechanisms. I will describe the two I consider most important: the spatial structure of populations and the nonlinearity of trophic interactions. Let me introduce the first by illustrating the experiments of another giant of modern ecology, Georgyi Frantsevitch Gause (Figure 3), who was directly inspired by Volterra’s work. Gause, a microbiologist, worked with very simple organisms, protozoa, because they can be easily grown in cultures and their life cycle is short compared to a scientist’s lifetime. Gause is best known for his work on competition, but his work on predation is also illuminating. When Gause (1934) put *Paramecium caudatum* (the prey) and *Didinium nasutum* (the predator) in the same test tube, the predators ingested all the prey and then starved to death (Figure 3). Why does this not occur in nature? Gause thought that the key point was that the artificial environment (the tube) was homogeneous, limited and closed. To get around this problem, he performed another experiment: every few days he artificially introduced immigrations from outside, a very simple way of connecting the habitat of the tube to an external environment. So, he was able to produce sustained oscillations for the predator–prey interaction (Figure 3).

However, Gause’s way of introducing spatial inhomogeneity is really artificial, a sort of trick. We would like to have a system mimicking nature that oscillates without any intervention of the experimenter. More than 20 years after Gause’s experiments with protozoa, Carl Barton Huffaker (1958) used mites to run a beautifully conceived experiment (see Figure 4). *Eotetranychus sexmaculatus* is a herbivore while *Typhlodromus occidentalis* is a predator. The environment consisted of a tray of oranges (food for the herbivore) connected by bridges. Spatial

---

**Figure 2.** The orbits of Lotka–Volterra prey–predator model with (A) Malthusian prey, and (B) logistic prey.
inhomogeneity and the movements of prey and predators created the conditions for observing sustained oscillations at the global level (instead, the dynamics on each orange was kind of irregular).

It was only in 1969, in a paper that remained unnoticed for a decade, that Richard Levins made the strong remark that, in natural conditions, too, many populations have a patchy, inhomogeneous, insular structure and that their persistence at the global level is guaranteed by a balance between local extinctions and immigrations from other, still occupied patches. Levins (1969) termed these spatially structured entities metapopulations (populations of populations). He basically dealt with single species metapopulations, but of course there can be multispecies metapopulations with different ecological interactions. Huffaker’s system was in fact the first prey–predator metapopulation studied in the laboratory, as far as we know.

On the basis of experimental evidence, we can then say that spatial structure plays a fundamental role in determining the dynamics and the persistence or extinction of populations. What are then the consequences of incorporating space into simple predation models? Do we really obtain the oscillations we are looking for? The answer is positive. The example I choose to prove this assertion is the celebrated Nicholson–Bailey model for host–parasitoid interaction (Nicholson and Bailey 1935). It is the basic model for parasitism exactly as the Lotka–Volterra model is the basic model for predation. Generations are discrete in time. The host, if it were not parasitized, would grow exponentially, because Nicholson and Bailey assumed it is Malthusian like the prey in the Lotka–Volterra system (1). The Nicholson–Bailey model predicts the results obtained by Gause with the protozoa. The parasitized host will become extinct and then the parasitoid will become extinct too in the next generation (Figure 5a). However, if we incorporate space in the Nicholson–Bailey model using the metapopulation structure advocated by Levins, we discover that the system is not doomed to extinction, but is persistent, although it oscillates. This was demonstrated by Hassell et al. (1991). Local populations of hosts or parasites that become extinct can be rescued by the immigration from other, still occupied

Figure 3. A, Georgyi Frantsevitch Gause; B, The results of his experiments with Paramecium caudatum and Didinium nasutum.
patches of habitat. This produces fluctuations in space and time (see Figure 5b) similarly to Huffaker’s experiment.

Nonlinear trophic interactions is another causal pathway that can determine permanent oscillations. It was Buzz Holling (1959) who first described the
nonlinear mechanism underlying a predator’s functional response (defined as the amount of prey found and ingested by a predator in the unit time). Initially, he used the finger of his secretary Miss Patricia Baic as predator and discs of sand paper as prey (Figure 6a). He experimentally obtained an increasing and saturating function of the prey density, the so-called disc equation. This function is a hyperbola and is to be contrasted with the Lotka–Volterra assumption that the response is linear (in Equation 1 the functional response is simply \( px \)). Linearity implies that the predator’s hunger is actually infinite, because a Lotka–Volterra predator could ingest any amount of prey in the unit time, of course provided that the prey is available. Apart from Miss Baic, Holling’s ‘disc equation’ effectively describes the behaviour of many real predators from ladybirds to wolves (e.g. Figure 6b).

The saturation of Holling’s functional response has a destabilizing effect, because the larger the density of prey the lower the risk of predation, hence the mortality rate, for each prey. As a result, the Lotka–Volterra model modified by including a Holling-type functional response for the predator produces the oscillations we were looking for. Even if we assume that the prey grows logistically so that the system is dissipative, none the less there exist sustained oscillations to which the prey and the predators are attracted in the long run (Figure 6c). Rosenzweig and MacArthur (1963) are considered the first scientists who pointed out this result in a famous article which appeared in the American Naturalist. However, if we dig out the literature, we find out that the first who understood that key point was another very illustrious scientist, no less than the father of modern probability theory, Andrei Nikolaevich Kolmogorov. Kolmogorov’s paper (1936) is written in Italian for an Italian journal: the reason is very simple, he was a friend of Vito Volterra’s! This flourishing of studies in the period preceding World War II prompted Scudo and Ziegler (1978) to term these years as the ‘golden age of theoretical ecology’.

The oscillations deriving from Holling’s functional response have important consequences for the chain of interactions underlying the ecosystems’ functioning. For instance, it can imply the violation of competitive exclusion, as predicted by theory and anticipated by a very nice set of experiments conducted by Utida in the 1950s (Utida 1957). Also, Holling’s functional response can imply chaotic, yet deterministic, fluctuations in tritrophic food chains (Hastings and Powell 1991). But the predators’ saturation implied by the functional response can have important effects on spatial patterns too. Nathan and Casagrandi (2004) have

Figure 6. Holling’s functional responses of two predators: (A) Miss Patricia Baic’s finger searching sandpaper discs (reprinted from Holling 1959, courtesy of Dr. Robb Bennett, Entomological Society of Canada), (B) larvae of the damselfly Ischnura elegans preying on Daphnia (left: 20°C, right: 27.5°C; after Thompson 1978). Panel (C) shows the permanent oscillations of a Lotka–Volterra model with logistic prey and predator’s functional response: prey (solid line) and predator (dashed line) numbers.
shown how a prey–predator model incorporating seed dispersal and Holling-type predation can nicely explain the different seedling patterns of tree vegetation we can observe: the density of recruits that survive predation can either peak at some distance away from the seed source (the so-called Janzen–Connell pattern) or decline monotonically with distance (the so-called Hubbell–McCanny pattern).

The trophic structure of ecosystems: Top-down vs. bottom-up control

Previously, I wrote that the second edition of Volterra’s ‘Variazioni e fluttuazioni del numero d’individui in specie animali conviventi’ (1927) considered any number of species and different kinds of ecological interactions. In fact, the real challenge for ecologists is to understand not only the functioning of food chains, but the functioning of a whole ecosystem. Of course this is not an easy task, if not else because defining and recognizing ecosystems in nature can be quite difficult. Arthur George Tansley (1935), who first clearly defined the concept of ecosystem, wrote ‘These ecosystems, as we may call them, are of the most various kinds and sizes. ... Actually the systems we isolate mentally are not only included as parts of larger ones, but they also overlap, interlock and interact with one another’. The task of the ecosystem ecologist is indeed daunting! An account of the scientific challenges posed by the study of ecosystems can be found in Simon Levin’s book (1999) devoted to the complexity of life on our planet.

The trophic structure of ecological communities and ecosystems was first outlined by Charles Elton (1927). Elton’s pyramids can explain some basic, yet very important, properties of ecological communities, in particular the flow of energy between different trophic levels. Even if we consider just the flow of energy, a first question arises: what controls this flow in the food chain? The first biologist who clearly posed the problem was an Italian, Lorenzo Camerano (1880). According to Camerano, naturalists are divided in two categories. The first category reasons: ‘Birds feed to a great extent on insects; so if we increase the numbers of birds, the number of insects will decrease’. This is what we now call top-down regulation. The second category has a ‘bottom-up’ perspective: ‘the number of birds is high particularly in those places where insects are very abundant. The number of insects in a region depends essentially on the amount of food found in it. In general, birds have only a small role in destroying insects that might damage crops.’

In 1960, Hairston, Smith and Slobodkin in a very short, crystalline and beautiful paper (Hairston et al. 1960) made their point on top-down vs. bottom-up very clearly: ‘In summary, then, our general conclusions are: (1) Populations of producers, carnivores, and decomposers are limited by their respective resources in the classical density-dependent fashion. (2) Interspecific competition must necessarily exist among the members of each of these trophic levels. (3) Herbivores are seldom food-limited, appear most often to be predator-limited, and therefore are not likely to compete for common resources.’ So, herbivores would be top-down controlled, the other trophic levels bottom-up. The so-called HSS (Hairston Smith Slobodkin) theory has been debated, criticized, ameliorated, but it is still the reference theory for any study on bottom-up vs. top-down. I do not know whether Robert Paine (1966) was deeply influenced by the HSS theory when he ran his wonderful experiments on intertidal communities. No reference to HSS theory is explicitly found in his 1966 paper, but reference is made to other similar work. Certainly, Paine strongly made the point that top-down control of carnivores is fundamental to maintaining biodiversity: when he eliminated the top predator at Mukkaw Bay, the starfish Pisaster ochraceus, the species diversity of the community collapsed dramatically, from 15 to 8 species. Subsequent collaboration between Bob Paine and Simon Levin (1974) clarified that biodiversity was also maintained by disturbance localized in space and time. In a way, they incorporated the idea that external disturbance plays a role in population regulation, a concept that was strongly, if not excessively, advocated by Andrewartha and Birch (1954).

Top-down effects are very clear in freshwater. Biomanipulation of small water bodies has proved that point beyond any doubt: water is clearer where predatory fish have been removed. As for oceans, biomanipulation is much more difficult. Sometimes, unpleasant events, like the collapse of a fishery (Scheffer et al. 2005), can assist the ecologist in understanding how the marine trophic chain works. In the Scotian Shelf the top-down effect was made rather clear by the crash of the cod population which occurred in the late 1980s and early 1990s. Frank et al. (2005) have shown how the effects of the decline of Gadus morhua and other large predators cascade down the food web, through small fish, crab and shrimp (all increasing), zooplankton (decreasing) and phytoplankton (increasing) to the level of nutrients (decreasing nitrate concentration). Myers et al. (2007) have used meta-analysis to investigate several data sets collected in the Atlantic Ocean and
have pointed out the cascading effects of the decline of great sharks, due to overfishing in the past 35 years. The community restructuring has cascaded downward from the cownose ray, whose enhanced predation on its bay scallop prey was sufficient to terminate a century-long scallop fishery.

In other cases, more pleasant events, like the establishment of marine protected areas, can clarify the role of predation. Paolo Guidetti (2006), studying the protected area of Torre Guaceto (Italy), has demonstrated wonderfully how the sea bream exerts an important influence in Apulian rocky reefs. The bream controls the density of sea urchins, which feed on erect macroalgae. Without the sea bream, the sea urchins overgraze macroalgae thus creating barrens (i.e. bare rocks with encrusting algae).

A final remark on the top-down versus bottom-up control deserves mention. The traditional food-web scheme is one in which the top level consists of large predators. However, it must be remembered that at the top of the chain we can find parasites or hyperparasites or viruses. This has been often neglected in the past. It is now widely accepted that many populations are regulated by disease and parasitism (Anderson and May 1978). Parasite ecology has thus become an important topic and is dealt with in a growing literature which examines the peculiarity of host–parasite interactions. For instance, Gatto and De Leo (1998) showed that communities of macroparasites can coexist at equilibrium thus violating the competitive exclusion principle. This is an important departure from predation theory. As I said above, in prey–predator systems time oscillations are necessary to obtain coexistence between species competing for the same prey.

Biodiversity, ecosystem functioning and ecological networks

The problem of top-down vs. bottom-up control is only one of the many questions we can ask about ecosystem functioning. The description of an ecosystem structure as a chain of trophic levels is obviously simplistic. In reality ecosystems consist of very complicated networks. Therefore, this final section is devoted to the more general problem of the relationships between the complexity of ecological networks, ecological diversity, and the functioning of ecosystems.

Very approximately, one can distinguish two kinds of networks that characterize the structure of ecosystems: spatial networks, in which local populations are connected by dispersal, and food webs, in which different species are connected by ecological interactions. Of course, a realistic description of the functioning of terrestrial and marine ecosystems should include both the spatial and the trophic structure. However, up to now this has never been seriously attempted at least to my knowledge.

The spatial or trophic structure is often summarized by a graph with nodes and arcs. In spatial networks nodes represent local populations and arcs represent dispersal corridors between populations. It must be remarked that spatial proximity must be measured with the proper metric (distance along the graph), which is not a Euclidean metric usually. In food webs each node is a species or a functional group and each arc represents an ecological interaction. The network of trophic interactions can be very complicated. The Ythan estuary food web (Figure 7) is one of the most complex ever described. It comprises more than 150 species. The flounder is the species with the largest number of trophic connections.

Biodiversity is now imperiled by several factors. The joint action of habitat fragmentation and alteration, climate change, pollution and overharvesting is bringing a lot of species to extinction. Understanding whether there is a connection between biodiversity (e.g. measured in the simplest way, as number of species) and functioning is very important. It is generally accepted that ecosystems are fortunately redundant to a certain degree. Ecosystem functioning is a less than linear function of biodiversity.

But how can one measure ecosystem functioning? Productivity is certainly a good indicator of ecosystem health. There is a high likelihood that ecosystems display an increasing, saturating relationship between species number and productivity. This has been shown, for example, by the painstaking and very well conceived work of Dave Tilman (Tilman et al. 2001) in North American grasslands.

However, there is a second concept describing ecosystem functioning which is more complicated and much more debated. It is the concept of stability. The traditional viewpoint put forth by Charles Elton and Eugene Odum was that the more diverse an ecosystem, the more stable. Actually, Elton (1958) gave a precise meaning to stability, when he stated ‘Simple communities were more easily upset than richer ones; that is, more subject to destructive oscillations in populations, and more vulnerable to invasions.’ This viewpoint was somehow challenged by Robert May’s (1973) theoretical work. He found that the larger is the number of species in a model community the less likely is its stability. This is summarized by his famous
inequality: a community with \( S \) species and a given connectance \( C \) and interaction strength \( i \) is stable if

\[
SC < i^{-2}
\]

This started a long debate on the relationship between diversity and stability which is still going on. To understand the terms of the question we should first remember that Bob May’s condition is derived under the following assumptions: (1) food webs are randomly assembled, (2) connectance and interaction strength are independent of species number, (3) stability is defined as equilibrium stability in Lotka–Volterra systems (à la Lyapunov, such as in mechanics). Clearly, these assumptions are crucial (McCann 2000). So let me discuss them.

First of all, is it significant to consider randomly assembled food webs? It is difficult to think that ecological networks are completely random, if not else because biological evolution is the result not only of case, but also of natural selection. But if they are not, how far are they from randomness? The modern network theory (for a review see Boccaletti et al. 2006), mainly developed by theoretical physicists in the past decade, can help us understand the question more deeply. The theory has been shown to be useful for describing very different problems, from social networks to the diffusion of viruses in the world-wide web.

To briefly introduce the basic concepts of the theory, let me first define some parameters that are currently used in the study of networks (see Figure 8, which displays a simple example). The network is described by a graph with \( S \) nodes connected by \( L \) arcs (or links). In ecological terms each node may represent a patch of a metapopulation or a species in a food web. The arc can indicate spatial proximity (measured in the proper metric) or a trophic link. Here below I list some of the most important parameters defining the characteristics of a network.

- The density of links (\( L/S \)) which is sometimes called the complexity of the network.
- The connectance \( C = L/S(S-1) \) which is the number of links divided by the maximum possible number of links (if the graph were completely...
connected); it is thus the average fraction of nodes linked to one node.

- The characteristic distance $D$ of the network which is the average of the distances between all nodes. The distance between two nodes is defined as the minimum number of links connecting them.

- The clustering of the network which characterizes the fact that the network is organized in clusters (smaller communities inside a bigger community). Clustering, also known as transitivity, is a typical property of social networks, where two individuals with a common friend are likely to be friends. One way to define a clustering coefficient $CL$ is thus the average fraction of node pairs one link away from a node (i.e. ‘friends’ to that node) that are also linked to each other (i.e. ‘friends’ between themselves).

A more sophisticated concept that is very useful in studying networks is the distribution of links. There are networks of a given density of links in which all the nodes have more or less the same number of links. In some cases, the number of links of each node (called the degree of the node) is distributed as a Poisson. The road networks are of this kind. But airline routing maps are radically different. There are a few hubs with a lot of connections. Most airports are small with just a few links to major hubs. Often the distribution turns out to be the so-called scale-free distribution: if we put on a logarithmic scale both the node degree and the fraction of nodes with a given degree, we obtain a straight line. If you zoom on a straight line, you still see a straight line (that’s why there is scale invariance).

Erdős and Rényi (1959) were the first who studied completely random graphs, in which two of the $S$ nodes are connected at random with a certain probability. Completely random networks with a given density of links have certain typical properties. First, clustering and connectance coincide. Second, the characteristic distance between two nodes increases less than linearly with the number of nodes, in a logarithmic fashion (while in regular lattices or grids it would increase linearly). Third, the distribution of links is Poisson.

However, it is difficult to think that the networks we see, be they the internet or the network of coauthors in scientific literature, are completely random, if not else because they build up and evolve according to some basic non-random mechanisms. Thus the literature of networks has defined two other very famous categories of networks. The first category is that of small-world networks (Milgram 1967). They are derived from regular lattices in which shortcuts between two nodes are randomly introduced. As a result, they have a characteristic distance that increases logarithmically with the number of nodes, like in completely random networks. However, they have large clustering compared to random networks, due to shortcuts. The distribution of links, instead, is approximately Poisson as in random networks. The second category is that of scale-free networks, which of course have a scale-free distribution of links. They are the result of a dynamic process (the so-called rich-get-richer process) in which at each time step nodes with a high number of links obtain new links with a higher probability than nodes that have few links. The World Wide Web is the most celebrated example of this kind of networks.

Now, the great question is: what kind of networks are food webs? First of all, are they completely random or small-world? The answer seems to be ‘neither’. The analysis of 16 food webs (Dunne et al. 2002) shows that the characteristic distance increases less than linearly, but the clustering is not too large and the distribution of links is never Poisson. On the other hand, from an empirical viewpoint it looks like small networks, of any kind, have smaller clustering than big networks (see again Dunne et al. 2002). So, it might be possible that, if we could study much larger food webs with thousands of species, the clustering would be higher. Of course, that would require a big experimental effort.

The second question is: are food webs scale-free? Or do they have a characteristic scale? Again the answer is: it depends. Montoya et al. (2006) have studied the problem and found out that the distribution is rarely scale-free (see Figure 9). Dunne et al.’s (2002) previously cited analysis of 16 food webs did not provide a significant straight line of the log-log plot. We can thus conclude that ecological networks defy any predefined model, but surely they are not totally random as Bob May had assumed.

Another problem that is worth being discussed is the definition of stability. Equilibrium stability, which was May’s original assumption, is the simplest definition of stability. It is very much based on the idea that, without man’s action, the species would be in a beautiful natural equilibrium. But this is not true! Previously, we have discussed how simple and realistic biological mechanisms can create natural oscillations and local extinctions! It was again Buzz Holling (1973) who made clear that there are several different concepts of stability for ecologists: general stability, resilience, structural stability, multiplicity of attractors. I’m glad to see that in their recent article Ives and Carpenter (2007) have listed also the criterion of stability to invasions, which was one of
the stability concepts cited by Elton in 1958 (although Ives and Carpenter do not cite Elton 1958 in their references).

Elton's second criterion (destructive oscillations) is very much related to how wide oscillations are if compared to the average abundances or biomasses in the ecosystem. Thus Tilman used the coefficient of variation (ratio of standard deviation to mean) of population abundances as an index of stability for his experimental grassland plots (Tilman et al. 2006). Very interestingly, he found out that the increase of the number of species can imply a decrease of stability for each single population, but an increase in stability (i.e. a smaller coefficient of variation) for the standing biomass of the whole ecosystem. Also, Lisandro Benedetti-Cecchi (2000), coupling field experiments on intertidal assemblages of northwest Mediterranean rocky shores with simulation modelling, showed that food-web models that embody variance in trophic interactions have increased capacity to explain the spatial and temporal variability of consumers and resources documented in empirical studies.

In their recent review Ives and Carpenter (2007) say 'Rather than search for generalities in patterns of diversity–stability relationships, we recommend investigating mechanisms. A given diversity-stability relationship may be driven by multiple mechanisms, and the same mechanisms may evoke different diversity–stability relationships depending on the definitions of diversity and stability.' I do agree. And to point out that this kind of research is possible, let me finally cite a work which is a good example of finding general ecological mechanisms in food webs. Rooney et al. (2006) have pointed out that many aquatic and terrestrial ecosystems are characterized by the presence of two highly asymmetrical energy channels: detritus and phytoplankton for aquatic ecosystems, bacteria and fungi for the terrestrial ones. As we move up the food chain towards the top predator the channels become more and more intertwined, as has been proved by measuring the proportion of phytoplankton- or bacteria-derived carbon in each trophic level.

The two channels in the food webs investigated have very different features: the pelagic (marine ecosystem) and bacterial (soil ecosystem) channels are fast and have strong interactions and large primary production; the benthic and fungal channels are slow and have weak interactions and small primary production. It is this asymmetry that guarantees stability. To prove this point, Rooney and colleagues have constructed a model ecosystem with a top predator and two food chains rooted in the predator. Then they have studied how the stability of the system (in terms of its dominant eigenvalue) varies with the parameters describing the symmetry of the characteristics of the two food chains. It turns out that increasing asymmetry leads the model to increasing stability. The work of Rooney et al. (2006) is a very interesting example of blending field data with modelling, very much in the spirit of Volterra and D’Ancona.

Conclusions

Eighty years after Vito Volterra and Umberto D’Ancona met and developed a theory of ecological interactions, we can have a look in retrospect and see how much progress the science of ecology has made. From simple laboratory experiments we have now progressed to field data collection at the global level with satellites pouring any sort of previously unbelievable information on terrestrial and marine ecosystems. For instance, the abundance of primary producers is now monitored at a very fine spatial and
temporal scale. It is possible to determine the ecological impact of human activities on the oceans at the global scale (Halpern et al. 2008). Nowadays, supercomputers allow us to run very complicated mathematical models with unprecedented details on the climatological, chemical and ecological mechanisms. The models used by the Intergovernmental Panel on Climate Change (IPCC 2007) to predict the future of our living planet are a very good example of this global ecological modelling.

Yet, the problem of bridging the experience of lab and field ecologists with the dream-world of theoreticians is always present. Theoreticians, in their quest of a general explanation for ecological interactions, are inclined to consider as exceptions some facts that instead field ecologists consider as the most interesting events of natural history.

Ferdinando Boero’s work on gelatinous plankton is a very good example (Boero et al. 2008): the pulses of this type of plankton, often neglected, can explain the cycling diversity of marine plankton. Fortunately, a new brand of ecologists is emerging, not only in America or the UK, but also in Italy. They are well trained in both experimental and theoretical ecology and are increasingly skilful not only in running experiments and collecting data but also in developing the relevant theories. They are indeed the genuine great-grandchildren of Volterra and D’Ancona!

Acknowledgements

The article is dedicated to Franco Scudo, a great friend and scientist who prematurely died in 1998. Franco, a physicist, graduated with a thesis supervised by Umberto D’Ancona. He had a multidisciplinary approach to ecology, evolution, history of science, and mathematical modelling and greatly encouraged me at the beginning of my career as an ecologist. This review was presented in two invited lectures at the 67th meeting of the Italian Zoological Union (UZI), Naples, and the 17th meeting of the Italian Society of Ecology (StIE), Ancona. I thank Ferdinando Boero for convincing me that I had to write this review and for reading and commenting on a first draft of the paper. Also, I am deeply grateful to Renato Casagrandi. I greatly benefited from discussion with him in the past years and from the comments he made on the manuscript.

References


Gause GF. 1934. The struggle for existence. Baltimore: Williams & Wilkins.


Volterra V. 1927. Variazioni e fluttuazioni del numero d’individui in specie animali conviventi. Venezia: Regio Comitato Talassografico Italiano, Mem. CXXXI.