

View point

From biodiversity and ecosystem functioning to
the roots of ecological complexity

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Abstract

Biodiversity is monophyletic: life started with a single species. Biodiversity evolved, becoming more and more complex, by a process that went through many patterns of diversification and that is still running. Biodiversity is not teleological, it did not evolve at the present stage to make a proper world for us, or to make ecosystems function; ecosystems functioned also at the dawn of life, when diversity was very low. Ecology and evolution are strictly linked, and both are historical disciplines that involve non-linear systems with a clear chaotic development, with the co-existence of strong constraints (in both form and function) and powerful contingencies (like those that caused the mass extinctions of the past). Historical predictions can only be weak, and can be formulated only when trends are identified (i.e. the attractors of chaotic systems). Modern ecology discarded natural history, setting quantitative goals that forced it to remove quality from its vision of complexity. This attitude led to enormous conceptual advances that are starting to show their limits. The identification of trends, set by constraints/attractors, and of deviations from them, due to contingencies, is an ambitious and practicable goal for mature ecology.

Keywords: Biodiversity; Ecosystem functioning; Chaos; Natural history; Species

Without deviation from the norm, “progress” is not possible.

–Frank Zappa

1. Some ecological questions

After the 1992 Rio de Janeiro Convention about the state of the planet, biodiversity was considered important for the services it provides to man: we need all these species for our well-being (Costanza et al., 1997; Luck et al., 2003). Then, a less anthropocentric position stated that biodiversity is necessary for

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ecosystem functioning (see [Naeem and Wright, 2003](#), for a review). In both cases, however, ecologists resisted giving “equal rights” to all species, considering some as being more important than others ([Ghilarov, 2000](#)). This means that we can even do without some species, maybe most species. *What could be the importance of the thousands of nematode species that are waiting to be discovered in the interstices of sediments at the bottom of the sea? Do we really need to know even that they exist?* Species are assigned to ranks of ecological value according to the types and number of linkages that they have within community networks and how they influence overall ecosystem functioning ([Piraino et al., 2002](#)). The attempt to ascertain the ecological importance of biodiversity, furthermore, often led to the statement that taxonomic diversity is not so important for ecosystem functioning. In other words, ecosystems function even at low diversities, so that taxonomic diversity is uncoupled from ecosystem performance ([Naeem and Wright, 2003](#)). Such a position justifies the concept of taxonomic sufficiency to evaluate biodiversity in ecological studies ([Terlizzi et al., 2003](#)): a reliable description of an ecological system can be reached at a low taxonomic definition, i.e. without identification of species diversity and, thus, of the core of biodiversity. [Kolasa and Li \(2003\)](#), however, showed that species richness might have a stabilizing effect on some communities, implying that the situation might be different if one genus is represented either by one or by five species. The meaning of biodiversity calls for deep analysis, since one of the main questions of ecology is simply “*why are there so many species?*” as posed by [Hutchinson’s \(1959\)](#) Homage to Santa Rosalia. *Are these species there to make ecosystems function? Alternatively: are they there for us to take advantage of their services?* These views might be labelled as teleological and anthropocentric ([Mayr, 1961](#)) and call for some exploration of the philosophical foundations of ecology.

2. Ecology and evolutionary biology divorce

Modern ecology started with evolutionary biology. Darwin’s books were more about ecology than about anything else. The followers of Darwin also developed other approaches. Ernst Haeckel, for instance, besides inventing the word ecology, also founded evolution-

ary developmental biology, summing up his ideas in the famous phrase: *ontogeny recapitulates phylogeny*. Neo-Darwinism influenced biological thought in a profound way, involving taxonomy, genetics, biogeography, and palaeontology, but left out both ecology and developmental biology. Both disciplines became pervaded by mechanistic approaches that, in ecology, reached their apex in systems ecology, with the claim that few efficient descriptors were sufficient to understand how ecosystems function: the flows of few essential elements became the modern paradigms of ecology. The naturalistic approach remained alive while giving importance to few relevant species (e.g. keystone species) and forgetting about the others. Population biology ran parallel to ecosystem-oriented ecology, developing, for instance, more the mathematical modelling of life histories than the knowledge of life cycles (see [McIntosh, 1985](#); [Kingsland, 1995](#) for reviews).

After [Peters’ \(1991\)](#) critique for ecology—*Ecology is helpful only if it provides answers to well posed questions*, many ecologists tried to make predictions. This is done, in physics, by using mathematics to connect variables that, interacting with each other while having a given value, will attain other values after a certain period. These connections are modelled by algorithms. If we have the values of the variables at time zero, and we have the right algorithm, we can predict the values of the variables at time one. This is what is done with the logistic equation, to measure the growth of a population. The predictive power of this model, however, is flawed by K , the carrying capacity, which is measured only a posteriori and cannot be calculated in a predictive way. The Lotka-Volterra equations, furthermore, can handle only interactions of couples of species, being almost useless to predict the behaviour of complex systems, and a system with three species is already too complex ([Huisman and Weissing, 2001](#)), falling in the domain of irreducible ignorance ([Faber and Proops, 1993](#)).

3. Philosophy?

Thinking that ecological predictions are possible implies a philosophical position that biologists copied from mathematicians and physicists: if they can do it, we should do it. In some cases, as it happened

for D'Ancona and Volterra, the naturalists went to the mathematicians to receive some insight from them. In other cases, physicists lent to ecology tried to apply their philosophy to the natural sciences (those involving the presence of species). It is undeniable that these approaches have contributed much to advance our understanding of how ecosystems function and these attempts to generalise counterbalanced the plethora of careful descriptions that remained sterile, each one with its limited meaning. It is suggestive, however, that May (1976), who introduced chaos theory in ecology with a paper called “*Simple mathematical models with very complicated dynamics*”, ended up, 12 years later, with a question that has nothing to do with mathematical modelling (May, 1988): *how many species are there on Earth?* Paradoxically, the complex question asked by Hutchinson in 1959 (*why are there so many species?*) became much humbler in scope in 1988: *how many species are there?*

4. Ecology and evolutionary biology: Siamese twins

The separation of ecology and evolutionary biology is causing much harm to both. As remarked above, both became highly mechanistic and lost some of their founding ideas. Reductionism and the quest for mathematisation split natural history into several sub-disciplines, so that they lost contact with each other. The main distinction between ecology and evolutionary biology is the perception of time. Ecological time runs much faster than evolutionary time, but both are dials of the same clock: they measure the history of life. Evolutionary biologists have discussed much about the differences between their science and other approaches to the study of nature, such as physics. Physics is not historical, whereas biology is (e.g. Mayr, 1961, 1988). If we study history, the core question is: *can we hope to predict history (i.e. the future)?* If the expression of life is governed by the rules that govern other types of history (like human history), it is vital for us to understand if we are asking answerable questions. When physicists devoted their efforts to obtain perpetual motion, they were simply wasting their time. Once it became clear that it was fundamentally impossible, they turned their attention to other issues.

Most efforts at predicting ecological situations are in vain, especially in the medium–long term. Contrary to predictive ecology, predictive evolutionary biology is not so popular: nobody dares predict evolution, if not in a science fiction fashion (or with genetic engineering, but this is another story). Fisheries ecologists dedicated serious and tremendous efforts to model our impact on fish populations, so as to provide advice for wise management of these resources, but the results they have obtained are not so valuable. Sometimes their predictions work, but many times they fail. The result is that large predatory fishes are disappearing (Myers and Worm, 2003), in spite of our expert planning. *Do management models fail because the analysis is not perfect yet, or do they fail because they ask the impossible (and the right predictions occur just by chance)?* Answering this question is crucial to decide how to invest research efforts and where to go with our work.

5. Predicting the weather (and more)

Meteorologists have justified, with chaos theory, their failure in predicting the weather over the medium–long term. We invest large amounts of money to measure the weather and have very powerful algorithms to analyse the data from satellites and land stations. We also have very long time series that witness the trends of the weather. We know the history of our meteorological conditions. Climate, at a global scale and over relatively short time scales (e.g. decades) is rather predictable. We know that winters are colder than summers and that tropical areas are warmer than temperate ones. We have identified trends, and limits of variation determined by the attractor of climate, but all our knowledge based on past climate history cannot lead us to predict deviations from its norms. (Un)fortunately, deviations from norms occur all the time. The summer of 2002 was extremely rainy, and there were floods all over Europe, whereas the summer of 2003 was extremely hot and more than 20,000 people died in France and Italy. Both events arrived with no warning from meteorologists, and nobody is daring to predict the weather of the summer of 2004. The weather (and its long-term expression: climate), furthermore, is not the only determinant of ecological systems: food and nutrient

availability, predation, competition, mutualism, disturbance, and landscape structure, among others, contribute to determine the structure and function of communities and ecosystems, creating the most complex scenario of the known universe. If the weather (and climate) cannot be predicted with precision over the medium and long term, and if the weather is only one of the variables affecting the performance of ecosystems, most with unpredictable behaviour, it is obvious that we cannot predict ecological phenomena (with precision). We can predict that frost will kill plants, but this is a physiological prediction, and it does not help much in ecology, since we cannot predict the occurrence of frost in proper advance and precision.

6. Initial conditions

Chaos theory has an important concept to offer to ecology: an apparently irrelevant factor, or an apparently irrelevant change in a relevant factor, can have an important impact on the history of a complex system (i.e. a system regulated by many factors) making it behave in a non-linear fashion (Boero, 1994, 1996). After a fisheries collapse in spite of no change in fishing effort, for instance, we may discover that a jellyfish bloom depleted the larval supply, or that an extremely cold winter impaired recruitment, or that the currents changed and the fish changed their migrating route. After the event, we may find the reasons for the failure of our prediction. The predictions should work if the initial conditions do not change. Furthermore, we measure the conditions of the factors that we retain as significant, and disregard all other possible influences “for ease of analysis”. The problem is that the initial conditions do not remain stable, and the irrelevant factors or variations can become relevant. Cushing et al. (2003) proposed a “controlled ecosystem” whose complex dynamics can be measured accurately but, as remarked by Sole and Alonso (2003), theirs is a “rather specific system”, disregarding many other factors. Equation-based predictive ecology is probably like perpetual motion: it is simply impossible. There is a mathematical demonstration for this, just as there are laws of thermodynamics to demonstrate the impossibility of perpetual motion. Huisman and Weissing (2001), among others, demonstrated, with the argu-

ments of chaos theory, that multispecies competition is *fundamentally* unpredictable!

7. Attractors and weak predictions

Chaos theory has another face of this hopeless medal: the attractors (Boero, 1996). With attractor identification we can confidently say that next winter will be cold and next summer will be hot, that the monsoon will take place in the rainy season and that then it will be followed by a dry season. The “history” of the weather fluctuates around a given set of possibilities, and thus is “attracted” by a given set of conditions, in this case by the rotation of the Earth around the sun and the inclination of its axis. Therefore, we can predict the weather, but only in a weak general fashion. Nevertheless, we can detect irregularities and start to worry if, for instance, the climate attractor seems to have changed. The first thing we do is to look at the records, to see if in the past there were similar situations and at what rate they occurred. The world changes all the time. We know this from palaeoecology and evolutionary biology (Meyers and Bull, 2002). Now the question is: *is it changing at a faster pace than in the past?* Furthermore: *is it changing because of us?* And: *what can be the consequences of this change if the trends are maintained?* We can answer these questions; we can try to reconstruct the attractor of climate and see if it changed in a significant way. At this point, we can predict that if temperature is rising, there will be a widening in the distribution of tropical species towards temperate areas, and there will be a shrinking in the distribution of cold-weather species. These observations will reinforce the perception of climatic change, since the biological effects are starting to become apparent. For example, out of 90 exotic fish species that entered the Mediterranean Sea in recent years, only three are boreal, all the others are of tropical affinity (Golani et al., 2002). We can predict that if temperature remains higher than in the past, the newcomers will become more and more abundant and further new species from warm climes will arrive. Can we construct algorithms which generate this prediction? Yes, we can do this with algorithms, but their precision will be misleading. The prediction is inevitably weak. Anyway, having identified an attractor (temperature

conditions) and having identified its change (global warming) and the putative causes (human activities?) and the effects (increase of tropical species in temperate areas) of this change can still be extremely useful, fitting the requirements set up by Peters (1991). At this point, after having identified a relevant trend, we can identify its important components and analyse them one by one with a reductionist approach. We can split our impact into many possible sub-impacts in order to analyse what we are doing to raise the temperature of the planet. This is a very difficult thing to achieve, though. The memory of failures is very short. When Mount St. Helen erupted, in 1980, climatologists predicted a sharp decrease in temperatures in the northern hemisphere, leading to some sort of ice age. Nothing happened, and this catastrophic prediction was swept under the carpet of oblivion.

8. Regularities versus irregularities

We like regularities. Our perception of beauty is linked to regularity. Perfection is simply the absence of faults, and faults are irregularities. This is why we like equilibria so much. When we analyse a situation we look for regularities, recurring events, something that allows us to “predict”, laws, norms (Ghilarov, 2001; Turchin, 2001; Colyvan and Ginzburg, 2003).

Therefore, it is human that ecologists look for regularities, and find them. The mistake is to think that, since there are predictable regularities, the world is regular and predictable (Boero, 1994, 1996; Hansson, 2003). In spite of recurrent regularities, changes occur all the time (Faber and Proops, 1993). The attractor of the weather, for instance, buffers the changes in climate that we might induce with our action but, sometimes, the attractor might be disrupted allowing the system to behave in a different way.

Sometimes the change is induced by a single event that took place over a short time and that influenced the history of the system (Boero, 2001a). The Mediterranean, in recent years, was covered with *Veleva veleva*, a floating hydroid that feeds on the eggs and larvae of fish. This event passed unnoticed by fisheries ecologists, but it may have caused an increase in larval mortality, depressing the recruitment of some fish species. If the yield of fisheries turns out to be lower than in preceding years, no fishery biologist

will consider predation on early developmental stages by *Veleva*. Such events are not included in their models. The explanation is very simple: jellyfish blooms are well-known for their erratic occurrence (CIESM, 2001) and thus their inclusion in any model might severely reduce its predictive power.

9. Contingency versus constraint

History is ruled by contingency, this fits well with chaos theory: a clear contingency like the fall of an asteroid on the planet can lead to a dramatic change in biodiversity (the extinction of dinosaurs). This aspect of biodiversity history, however, is also ruled by constraint (the attractor of chaos theory). The animals that almost disappeared (reptiles) were replaced by animals that have the same basic body plan (birds and mammals): vertebrates with four limbs. The answer to the ecological contingency was constrained by morpho-functional limits. Thermodynamics pose an even more rigid constraint to the functioning of ecosystems, providing a set of rules (ecological laws?) that must be respected by all ecosystems. In other words, we can predict that the answer to any environmental problem will have to remain within some limits, dictated by thermodynamics and physiology, but we cannot go much further than that: we cannot predict what new species will “solve” the problem, what will be the expression of biodiversity in the future.

10. The history of life: that's why there are so many species!

We know that all living beings derive from a common ancestor; the coding of living matter by DNA is an irrefutable proof of common descent. Life is monophyletic, which means that its origin was single and that, in the beginning, there was a single population of similar individuals, belonging to the first species. This first species made up a low-diversity community that inhabited the first ecosystem. Given that space was not limiting yet, it is probable that the first selective force for evolutionary change was intraspecific competition for resources. Stochastic mutations provided a pool of new adaptive potentials, and individuals started to spread. Then speciation events started.

The answer to Hutchinson question: “*why are there so many species?*” might be: the first species expanded and reached new types of habitats, where different environmental pressures channelled it into new genetic and adaptive domains, leading to allopatric speciation; then these first species encountered each other and the resulting interactions started a Red Queen process (Van Valen, 1973); an arms race (Vermeij, 1993) that caused further change. As a chain reaction, life started to become diverse and its diversity sparked new diversity. In spite of mass extinctions, present diversity is higher than past diversity (at least from what we can infer from palaeontology, see Jackson et al., 2001). Biodiversity is not teleological; it is tautological. Species are many because being many makes them increase. If there is a mass extinction (e.g. Benton and Twitchett, 2003), this is just a further impulse to diversification. At least this is the attractor of the history of life until now, and chances are good that it will continue this way even after the extinction of *Homo sapiens* and of the species that are strictly linked to his activities.

11. After island biogeography

One of the founders of island biogeography (MacArthur and Wilson, 1963), McArthur, aimed at putting ecology outside history (Kingsland, 1995), outside the variations of individuals and populations that might have an influence on ecosystem functioning, in an attempt to look for general rules that might be expressed in mathematical terms. The other founder of the theory, Wilson, based his later career on biodiversity and sociobiology, so focusing exactly on what McArthur probably considered noise, and he used almost no mathematics. Stemming from the same intuition, two or more routes can be taken. They can become separated but, having a common descent, they are intertwined. The reductionistic approach focuses on some aspects but, eventually, things are to be put together, even more deeply than consilience (Wilson, 1998) can envisage (e.g. Ford and Ishii, 2001).

12. Popper: universal versus existential statements

Popperian logic asks scientists to produce hypotheses of universal value. If a given hypothesis (the

favourite example is “*all crows are black*”) is proven false (by the finding of a white crow), then it is to be rejected. What is not completely clear is that it is just the universality of the statement to be rejected. In spite of the albino crow, however, the rule about the colour of crows holds for the greatest majority of crows, and if we discard “*all crows are black*” there is no other law on the colour of crows that has universal value. This suggests that universal laws do not belong to the ecological realm (Wilson, 2003), that we will always find exceptions, and that ad hoc explanations (albinism in crows) are not a curse to our science, they are a blessing. If we look at laws, we end up with physics, but ecology is much more than physics (Pickett et al., 1994), even if it obeys its laws, just as literature is much more than grammar, even if it obeys grammar’s laws. The models of community development are three (by now) (Connell and Slatyer, 1977) and each time one is proven right (verified), the other two are falsified (in their generality). Evolution is both gradual and saltational. Populations can develop according to the logistic curve, but they can also go through sudden flushes and crashes (Carson, 1990). Furthermore, these models are not mutually exclusive and the same result can be reached by a blend of causes, what Mayr (1988) called multiple causality.

13. Emergent properties

Most ecology textbooks start saying that ecology is the science of interactions, and that it has emergent properties, i.e. the whole is much more than the sum of its parts. In subsequent pages, however, ecological systems are usually split into parts, and there is no synthesis. Ecosystem functioning, for instance, is just ecosystem metabolism (i.e. biogeochemistry) (see Naeem and Wright, 2003, for a definition) and does not consider supply-side ecology (Roughgarden et al., 1988; Frascchetti et al., 2003), as if reproduction (i.e. propagule supply) were not part of the functioning of a system based on living beings. Reductionistic ecology is an oxymoron that goes against the essence of ecology but, paradoxically, it is the most practised approach to ecology. Loehle (2004) provides a timely account on complexity and on its reduction for modelling purposes; it is suggestive that his essay is concluded with this sentence: “In the complex field

of metapopulation dynamics, over-simplified assumptions have led to conclusions that are extreme or even false” (p. 4).

14. Where to go now?

What is the other route, then? We need a new natural history (Dayton and Sala, 2001), because the concept of natural history gives justice to the historical nature of the life sciences. Natural history formed the basis of Darwin’s intuitions and is a very powerful tool. It has been labelled as descriptive, a science of inferior rank if compared to experimental science. We must not forget about the comparative method, a very important tool in historical sciences (Harvey and Pagel, 1991), where experiments are often a ridiculous attempt to imitate natural conditions. This does not mean that all experiments are bad, but sometimes they are performed just when/where they are possible, or only at manageable spatial and temporal scales which often do not match the scales relevant for the process investigated (Knowlton, 1992; Petraitis and Latham, 1999). The removal of limpets from intertidal rocky shores is an easy task, whereas the removal of jellyfish from the water column is a hopeless enterprise. With this attitude, we might end up answering questions regarding phenomena that have a limited bearing on ecosystem function (*what is the impact of limpet grazing on algal mats?*) and leave probably more important questions unanswered (*what is the impact of jellyfish predation on fish recruitment?*).

It is imperative to perform experiments when they are feasible, and it is imperative to look for comparative evidence when experiments are almost impossible (Petraitis and Latham, 1999; Balmford et al., 2003). We have to understand episodic events (Boero, 1996) and stop looking just for regularities (Hansson, 2003) or to the first cause we identify (forgetting about multiple causality). The study on zooplankton grazing, for instance, is very focused on crustaceans, but a salp bloom might graze in a week what a multispecies copepod assemblage grazes in a whole season (Bone, 1998). Almost nobody studies thaliacean blooms because they are irregular in occurrence, they last a few days and a project on them has a high probability of failure due to lack of material. Plankton dynamics, furthermore, are surely driven by biogeochemical cy-

cles, so that nutrient availability will condition the production of phytoplankton and, from this, the functioning of the rest of the planktonic trophic network. Biogeochemical cycles, however, are only one face of the coin, and the role of life cycles is of no lesser importance (Boero et al., 1996; Marcus and Boero, 1998; Pati et al., 1999). The quality of plankton (i.e. its species composition), in fact, depends not only on nutrient availability but also on the propagule supply of the various species. This, in its turn, will lead to success of a given species according to a very wide set of processes (Fraschetti et al., 2003). Considering all these processes and patterns in ecosystem functioning requires a thorough knowledge of natural history. An increase in the number of interacting variables decreases the possibility of predicting the future behaviour of a system.

Ecologists with a mathematical attitude must continue to produce their models, those who like to perform experiments must go on with their manipulations, but a new scientific respect is to be given to observational ecology, putting it into a theoretical framework that is liberated from the obligation of being predictive in an equation-based sense. Observations might serve to produce better models, and to test them, providing relevant case histories to modellers. Palaeontologists cannot perform experiments, but they have provided a huge amount of insight to evolutionary theory. The same approach should be taken in ecology (Lee, 1997), with the abatement of the compartmentalisations that make of ecology an immature science.

15. The maturity of ecology

Young people dare, mature people are careful. Ecologists, in early years, dared to predict future history and, as often happens to daring people, crashed against the wall of fundamental unpredictability. Ecologists must continue to be daring, but be conscious of their limits. After all, claiming to understand biocomplexity with a set of formulas is not as daring (in terms of effort) as saying that we must answer questions such as “*How many species are there on Earth?*” by thoroughly exploring the life of our planet. Astrobiologists, whatever they are (Chaisson, 2003), dare to ask for enormous resources to explore the universe to find some life, whilst ecologists do not dare to ask for far

fewer resources to explore thoroughly the diversity of the planet we live in. A sign of maturity is also finding a proper goal and to dare to fight for it, having the strength to change direction if the former goal (e.g. predict history, with precision) is impossible to reach.

The quest for ecological quantification and experiment-based hypothesis testing, stemming from the failure of natural history to provide deep insight into the functioning of ecological systems, led ecologists to forget about what natural history was studying: the qualities of ecological systems (Dayton, 2003). It is time to reconcile quantity with quality. We must solve the paradox, for instance, that in the age of biodiversity, we suddenly realise that expertise in species identification is vanishing (Boero, 2001b).

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References

- Balmford, A., Green, R., Jenkins, M., 2003. Measuring the changing state of nature. *Trends Ecol. E* 18, 326–330.
- Benton, M., Twitchett, R., 2003. How to kill (almost) all life: the end-Permian extinction event. *Trends Ecol. E* 18, 358–365.
- Boero, F., 1994. Fluctuations and variations in coastal marine environments. *P.S.Z.N.I: Mar. Ecol.* 15, 3–25.
- Boero, F., 1996. Episodic events: their relevance in ecology and evolution. *P.S.Z.N.I: Mar. Ecol.* 17, 237–250.
- Boero, F., 2001a. Adriatic ecological history: a link between jellyfish outbreaks, red tides, mass mortalities, overfishing, mucilages, and thaliacean plankton? In: *Gelatinous Zooplankton Outbreaks: Theory and Practice*, vol. 14. CIESM Workshop Series, Monaco, pp. 55–57.
- Boero, F., 2001b. Light after dark: the partnership for enhancing expertise in taxonomy. *Trends Ecol. E* 16, 266.
- Boero, F., Belmonte, G., Fanelli, G., Piraino, S., Rubino, F., 1996. The continuity of living matter and the discontinuities of its constituents: do plankton and benthos really exist? *Trends Ecol. E* 11, 177–180.
- Bone, Q. (Ed.), 1998. *The Biology of Pelagic Tunicates*. Oxford University Press, Oxford, 362 pp.
- Carson, H.L., 1990. Increased genetic variance after a population bottleneck. *Trends Ecol. E* 5, 228–231.
- Chaisson, E.J., 2003. A unifying concept for astrobiology. *Int. J. Astrobiol.* 2, 91–101.
- CIESM, 2001. *Gelatinous Plankton Outbreaks: Theory and Practice*, vol. 14. CIESM Workshop Series, Monaco, 112 pp., <http://www.ciesm.org/publications/Naples01.pdf>.
- Colyvan, M., Ginzburg, L., 2003. Laws of nature and laws of ecology. *Oikos* 101, 649–653.
- Connell, J., Slatyer, H., 1977. Mechanisms of successions in natural communities and their role in community stability and organization. *Am. Nat.* 111, 1119–1144.
- Costanza, R., D'Arge, R., deGroot, R., Farber, S., Grasso, M., Hanron, B., Limburg, K., Naeem, S., O'Neill, R., Paruelo, J., Saskin, R., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260.
- Cushing, J.M., Costantino R., Dennis B., Desharnais R., Henson S., 2003. *Chaos in Ecology: Experimental Non Linear Dynamics*. Academic Press, San Diego, 225 pp.
- Dayton, P., 2003. The importance of the natural sciences to conservation. *Am. Nat.* 162, 1–13.
- Dayton, P., Sala, E., 2001. Natural history: the sense of wonder, creativity and progress in ecology. *Sci. Mar.* 65 (Suppl. 2), 199–206.
- Faber, M., Proops, J., 1993. *Evolution, Time, Production and the Environment*. Springer Verlag, Berlin, 288 pp.
- Ford, D., Ishii, H., 2001. The method of synthesis in ecology. *Oikos* 93, 153–160.
- Fraschetti, S., Giangrande, A., Terlizzi, A., Boero, F., 2003. Pre- and post-settlement events in benthic community dynamics. *Oceanol. Acta* 25, 285–295.
- Ghilarov, A., 2000. Ecosystem functioning and intrinsic value of biodiversity. *Oikos* 90, 408–412.
- Ghilarov, A., 2001. The changing place of theory in 20th century ecology: from universal laws to array of methodologies. *Oikos* 92, 357–362.
- Golani, D., Orsi Relini, L., Massuti, E., Guignard, J.P., 2002. Fishes. In: Briand, F. (Ed.), *CIESM Atlas of Exotic Species in the Mediterranean*, vol. 1. CIESM Publishers, Monaco, 256 pp.
- Hansson, L., 2003. Why ecology fails at application: should we consider variability more than regularity? *Oikos* 100, 624–627.
- Harvey, P., Pagel, M., 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford, 239 pp.
- Huisman, J., Weissing, F., 2001. Fundamental unpredictability in multispecies competition. *Am. Nat.* 157, 488–494.
- Hutchinson, G.E., 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* 93, 145–159.

- Jackson, J.B., Lidgard, S., McKinney, F. (Eds.), 2001. *Evolutionary Patterns. Growth, Form and Tempo in the Fossil Record*. University of Chicago Press, Chicago, 399 pp.
- Kingsland, S.E., 1995. *Modeling Nature: Episodes in the History of Population Ecology*, second ed. University of Chicago Press, Chicago, 316 pp.
- Knowlton, N., 1992. Threshold and multiple stable states in coral reef community dynamics. *Am. Zool.* 32, 674–682.
- Kolasa, J., Li, B.-L., 2003. Removing the confounding effect of habitat specialization reveals the stabilizing contribution of diversity to species variability. *Proc. R. Soc. Lond. B* 270 (Suppl.), 198–201.
- Lee, M.S.Y., 1997. Documenting present and past biodiversity: conservation biology meets palaeontology. *Trends Ecol. E* 12, 132–133.
- Loehle, C., 2004. Challenges of ecological complexity. *Ecol. Complexity* 1, 3–6.
- Luck, G.W., Daily, G.C., Ehrlich, P.R., 2003. Population diversity and ecosystem services. *Trends Ecol. E* 18, 331–336.
- Marcus, N., Boero, F., 1998. The importance of benthic–pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. *Limnol. Oceanogr.* 43, 763–768.
- May, R.M., 1976. Simple mathematical models with very complicated dynamics. *Nature* 261, 459–467.
- May, R.M., 1988. How many species are there on Earth? *Science* 241, 1441–1449.
- Mayr, E., 1961. Cause and effect in Biology. *Science* 134, 1501–1506.
- Mayr, E., 1988. Is biology an autonomous science? In: Mayr, E. (Ed.), *Towards a New Philosophy of Biology*. The Belknap Press of Harvard University Press, Cambridge, pp. 8–23.
- MacArthur, R.H., Wilson, E.O., 1963. An equilibrium theory of insular zoogeography. *Evolution* 17, 373–387.
- McIntosh, R.P., 1985. *The Background of Ecology*. Cambridge University Press, Cambridge, 400 pp.
- Meyers, L.A., Bull, J., 2002. Fighting change with change: adaptive variation in an uncertain world. *Trends Ecol. E* 17, 551–557.
- Myers, R., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.
- Naeem, S., Wright, J., 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecol. Lett.* 6, 567–579.
- Pati, A.C., Belmonte, G., Ceccherelli, V.U., Boero, F., 1999. The inactive temporary component: an unexplored fraction of meiobenthos. *Mar. Biol.* 134, 419–427.
- Peters, R.H., 1991. *A Critique for Ecology*. Cambridge University Press, Cambridge, 366 pp.
- Petratis, P.S., Latham, R.E., 1999. The importance of scale in testing the origins of alternative community states. *Ecology* 80, 429–442.
- Pickett, T., Kolasa, J., Jones, C., 1994. *Ecological Understanding. The Nature of Theory and the Theory of Nature*. Academic Press, San Diego, 206 pp.
- Piraino, S., Fanelli, G., Boero, F., 2002. Variability of species' roles in marine communities: change of paradigms for conservation priorities. *Mar. Biol.* 140, 1067–1074.
- Roughgarden, J., Gaines, S.D., Possingham, H., 1988. Recruitment dynamics in complex life cycles. *Science* 241, 1460–1466.
- Sole, R.V., Alonso, D., 2003. Chaos in a bottle. *Trends Ecol. E* 18, 556–557.
- Terlizzi, A., Bevilacqua, S., Fraschetti, S., Boero, F., 2003. Taxonomic sufficiency and the increasing insufficiency of taxonomic expertise. *Mar. Poll. Bull.* 46, 556–561.
- Turchin, P., 2001. Does population ecology have general laws? *Oikos* 94, 17–26.
- Van Valen, L., 1973. A new evolutionary law. *Evol. Theory* 1, 1–30.
- Vermeij, G., 1993. *Evolution and Escalation: an Ecological History of Life*. Princeton University Press, Princeton, 544 pp.
- Wilson, E.O., 1998. *Consilience: the Unity of Knowledge*. Knopf A., New York, 332 pp.
- Wilson, J.B., 2003. The deductive method in community ecology. *Oikos* 101, 216–218.