F1000Prime REPORTS

Published: 12 May 2015

From Darwin's *Origin of Species* toward a theory of natural history

Ferdinando Boero

Addresses: DiSTeBA, University of Salento, 73100 Lecce (LE), Italy; CNR-ISMAR, via De Marini 6, 16149 Genova (GE), Italy

Email: boero@unisalento.it

F1000Prime Reports 2015, **7**:49 (doi:10.12703/P7-49)

The electronic version of this article is the complete one and can be found at: http://f1000.com/prime/reports/b/7/49

Abstract

Darwin is the father of evolutionary theory because he identified evolutionary patterns and, with Natural Selection, he ascertained the exquisitely ecological ultimate processes that lead to evolution. The proximate processes of evolution he proposed, however, predated the discovery of genetics, the backbone of modern evolutionary theory. The later discovery of the laws of inheritance by Mendel and the rediscovery of Mendel in the early 20th century led to two reforms of Darwinism: Neo-Darwinism and the Modern Synthesis (and subsequent refinements). If Darwin's evolutionary thought required much refinement, his ecological insight is still very modern. In the first edition of *The Origin of Species*, Darwin did not use either the word "evolution" or the word "ecology". "Ecology" was not coined until after the publication of the *Origin*. Evolution, for him, was the origin of varieties, then species, which he referred to as well-marked varieties, whereas, instead of using ecology, he used "the economy of nature". The *Origin* contains a high proportion of currently accepted ecological principles. Darwin labelled himself a naturalist. His discipline (natural history) was a blend of ecology and evolution in which he investigated both the patterns and the processes that determine the organization of life. Reductionist approaches, however, often keep the two disciplines separated from each other, undermining a full understanding of natural phenomena that might be favored by blending ecology and evolution through the development of a modern Theory of Natural History based on Darwin's vision of the study of life.

Introduction

With *The Origin of Species* [1], universally considered the founding book of the theory of evolution, Darwin recognized a pattern already identified by other scientists. Darwin's most remarkable predecessor was Lamarck, who in the year of Darwin's birth published his *Philosophie zoologique* [2], in which he introduced transformism: present organisms descend from those of the past but are not identical to them.

Darwin's ideas had an enormous impact on modern culture, changing forever our view of the world and our perception of ourselves. More than evolution, the great novelty in *The Origin of Species* was Natural Selection: it is suggestive that the word "evolution" does not appear in the first edition of the *Origin*, the book ending, however, with the word "evolved". The *Origin* contains a myriad of apparently collateral sentences and observations that in many cases contain the seeds of many ecological principles that later were formalized by various authors who were often given the merit of their proposal. These ideas might have been developed with no influence from Darwin, as happened when Darwin and Wallace independently discovered Natural Selection [3] and when many other scientists, in many fields of science, independently reached the same conclusions. However, in some cases, the proponents of these ideas might have read *The Origin of Species* as an evolution book, the ecology in it remaining buried in the back of their minds, as the seed is buried in the soil.

Modern evolutionary theory is based on genetics, a discipline unknown to Darwin, who proposed "alternative" mechanisms for the transmission of characters across generations. For this reason, Darwin's evolutionary thought soon proved inadequate (the so-called eclipse of Darwinism) and had to be reformed at least twice (with Neo-Darwinism and then with the Modern Synthesis). Darwin's ecological thought, however, is as appropriate today as it was 150 years ago and just needs some rephrasing (but his original prose is often much better than the writing of those who followed).

Analyzing the text, I will argue that the *Origin* is a book of both ecology and evolution and that it blends the two disciplines, being the founding book of the Theory of Natural History, as Darwin defined his discipline.

Materials and methods

In his famous film *Rashomon*, Akira Kurosawa showed that an event (here, a book) can be seen and described in many ways, according to the point of view of the witnesses. During the celebration year of the 150th anniversary of the publication of *The Origin of Species* and of the 200th anniversary of Darwin's birthday, in 2009, I reread the first edition of *The Origin of Species* as a book on ecology, instead of a book on evolution, changing my point of view. During the reading, I compared Darwin's writing with current ecological principles, and I found many of them. I ordered them so as to form a conceptual quilt that shows the beginning of modern ecology in an evolutionary framework. Citations from *The Origin of Species* were extracted from searchable versions available on the internet. Paginations vary in different files of the same text; hence, the exact pages of the original printed version (s) are not reported: the readers can find the citations simply by searching any electronic version of the first edition of the *Origin*, such as http://www.gutenberg.org/files/1228/1228-h/1228-h.htm. Reznick [4] wrote a useful guide to a modern reading of the *Origin*.

Results

After a general analysis of the first edition of the *Origin*, the rest of the results lists the main ecological ideas sketched in the book. The order is usually that of appearance in the book but, for ease of comparison, the treatments of plot experiments, coming from different chapters, are merged.

Proximate (i.e. genetic) vs ultimate (i.e. ecological) evolutionary processes

Darwin described a pattern: life has always been changing, and still is. Today's life is different from the life of some million years ago or even of some centuries ago. Furthermore, Darwin proposed Natural Selection as the ultimate process of evolution, i.e. the success of individuals in getting resources by interacting with the environment ("the elements", in Darwin's words) and especially by competing ("struggling") with other individuals for resource acquisition. Nature selects suitable characters from the array of traits that are expressed by a species (variability), and only the features that pass the examination of the great scrutinizer survive. Darwin also recognized that advantages in the obtainment of resources must be followed by reproductive success, hence sexual selection (with the exception of uniparental species).

Darwin provided ample ecological explanations for the survival of the fittest and framed his reasoning within the concepts of what he called the "economy of nature", a discipline that shortly thereafter would have been called ecology by the zoologist Ernst Haeckel.

Darwin also provided proximate explanations about the origin of natural variability, but the work of Mendel was unknown to him: Darwin's ideas about this issue were not based on genetics and were soon proved wrong, his Theory of Natural Selection requiring much adjustment.

Darwin reformed

When Weismann proposed the theory of the germ plasm, postulating the separation of the germ from the somatic line, Lamarckian explanations of the proximate mechanisms of evolution were rejected: acquired modifications in the somatic line cannot be transmitted to the offspring. The germ line is devoted to passing information from one generation to the next and is separated from the somatic line. The germ line does not acquire new features that the soma might gain during the life of an individual. Buss [5] showed that this separation is not a universal feature of animals and that there are exceptions that falsify the universality of Weismann's theory that, however, led to the first reform of Darwinian ideas, the so-called Neo-Darwinism. The pattern (evolution) remained valid, but the proximate processes leading to it were modified. A semi-proximate, non-genetic explanation of evolutionary processes was developed by Ernst Haeckel, who used comparative embryology to propose the famous "biogenetic law": "ontogeny recapitulates phylogeny". These views of development, though, were narrowed by the reductionistic approaches of Wilhelm Roux, who proposed developmental mechanics (*Entwicklungsmechanik*), and by Hans Driesch. They went to the cellular roots of development and did not consider Darwinian evolution to be a causal agent. A further blow to Darwinian explanations of the evolutionary process came from the rediscovery of Mendel's laws, with the onset of genetics as a named scientific discipline. Thus, at the beginning of the last century, biology became reductionistic, started to divorce from natural history, and budded off many branches (from genetics and embryology to ecology) that went through almost autonomous developments. Evolutionary biology focused mostly on proximate processes, becoming a matter of genes, obeying genetic laws almost in a mathematical way, and Darwin's proposals were forgotten (see Mayr [6] for an extensive review.)

Ecology (Darwin's "economy of nature"), the main inspirer of evolutionary thought, divorced from Darwinian thinking. Elton [7] posed the basis of modern ecology in a seminal book (*Animal Ecology*) that started with these sentences:

"*Ecology is a new name for a very old subject. It simply means scientific natural history. … the word 'natural history' brings up a rather clear vision of parties of naturalists going forth on excursion, prepared to swoop down on any rarity which will serve to swell the local list of species. It is a fact that natural history has fallen into disrepute …*".

Darwin defined himself as a naturalist. In Elton's times, natural history had a bad name and was considered a discipline for non-professional scientists. Knowing animals and plants (i.e. biodiversity) was considered an amateur skill. It is ironic that one of the most "mathematized" ecologists of the second half of last century, Robert May, wrote an article on our ignorance about the number of species inhabiting the planet [8], arguing that one of the most important scientific enterprises should be, in Eltonian terms, just to "swoop down rarities so to swell the world lists of species". Huge projects on the exploration of biodiversity—such as the Global Biodiversity Information Facility, the European Network for Biodiversity Information, the European Register of Marine Species, the Census of Marine Life, the Encyclopaedia of Life, and many others—unfortunately are still based on Elton's negative perception of the study of biodiversity at the species level since, in the era of biodiversity, taxonomy (the science that describes and names species) is in severe distress because of lack of funding and career opportunities, just at a time when ample funding is available for the study of biodiversity [9].

In the Thirties and Forties, the importance of Darwinian thinking was reassessed by a group of biologists who wrote a series of seminal books that together formed the Modern Evolutionary Synthesis [6], assembling two main approaches: palaeontologists, zoogeographers, and systematicians studied evolutionary patterns and some ultimate processes, whereas geneticists considered proximate evolutionary processes. These approaches considered species (and populations) to be discrete entities but disregarded the interactions among species in ecological time.

A Darwinian paradox

The scientific community concentrated on the proximate causes of evolution that Darwin missed, developing new disciplines such as molecular genetics, fostered by the invention of powerful instruments to analyze genetic materials. The ecologists and the embryologists had the possibility of contributing further to the identification of the ultimate causes of evolution but made scant attempts at reconciling their disciplines with evolutionary thinking: they too had powerful instruments to go to the proximate roots of their analysis and could not resist doing so, leading to prodigious progress in the way we understand the nuts and bolts of life. Each approach is pursued by well-trained and competent scientists who, eager to know their topics perfectly, do not have time to look outside their specific field of expertise. This resulted in increasingly refined analyses of proximate and mechanistic causes of evolution in all their facets, from molecules to ecosystems, but the pieces of the puzzle are still mostly disconnected. Only recently, with the proposal of evo-devo, or embryology energized with molecular developmental biology, have we started to consider the solution of major evolutionary problems, such as the origin of eyes [10]. Evo-devo, however, considers the genetic causes of the evolution of both organs and individuals to be ontogenetic products, disregarding the bearing of the environment on evolution. Natural history, Darwin's science, should include all of these visions of evolution, but it is still having a bad name. In very recent years, owing to this bad name, some eminent scholars, such as Ricklefs [11] and Tewksbury *et al*. [12], called attention to the importance of natural history, but their claims are still almost unheard. Ricklefs ([11], p. 423), in particular, ridiculed several "new" ideas in ecology that are clearly untenable in light of natural history.

"*… there is a growing tendency for observation to serve theory rather provide new insight or to test the predictions of theory. This tendency manifests itself in the failure of ideas about the diversity, distribution, and abundance of species to be informed by patterns in nature that are readily apparent*".

This sentence repeats Darwin's contempt for "mere theoretical calculations" as compared with observation. Tewksbury *et al*. ([12], p. 300) denounced a dire present for Natural History:

"*We then present several lines of evidence showing that traditional approaches to and support for natural history in developed economies has declined significantly over the past 40 years*".

The decline of Natural History started much earlier, however, and coincides with the already-mentioned sentence in Elton's *Animal Ecology* [7] about the loss of reputation of Darwin's discipline.

Theoretical biology: Darwin's feathers

Kant [13] used the level of mathematization to measure the maturity of any branch of science. Physics is the most mathematized approach to the study of nature, and philosophers of science often use it as a paradigm of what science is or should be. This sparked so-called physics envy in other disciplines [14]: if physics can produce formulas that become laws explaining how nature works, the other sciences should do the same. This envy was enhanced by labeling mathematized sciences as hard and predictive, whereas low-mathematization sciences were labeled as soft and descriptive.

Darwin used an elegant metaphor to distinguish today's hard and soft sciences when he imagined how land, once tilled by Native Americans, had, through centuries of ecological succession, returned to its original state:

"Throw up a handful of feathers, and all must fall to the ground according to definite laws. But how simple is this problem compared to the action and reaction of the innumerable plants and animals which have determined, in the course of centuries, the proportional numbers and kinds of trees now growing on the old Indian ruins".

For Darwin, such problems as the behaviour of feathers falling to the ground can be tackled with a mathematical and predictive approach (the definite laws are those of universal gravitation), but scientists can perform predictions because of the simplicity of the studied objects ("how simple is this problem"). Nowadays, we know, with both quantum physics and the indetermination principle, that even these laws are not universal; in spite of this, they can be used operationally since they are accurate enough to allow, for instance, the sending of rockets to Mars. Darwin realized that the life sciences are more complex than physics and that they are historical. He thus introduced history in the system, showing that the present is the product of history. "In the course of centuries", however, is not evolutionary time; it is ecological time. And the product of evolution, in this case, is not a species but instead a species assemblage: "the proportional numbers and kinds of trees now growing".

With the handful-of-feathers metaphor, Darwin illustrates the difference between ahistorical and nomothetic disciplines (tackling simple problems) vs historical and idiographic ones (tackling difficult problems) [15].

"I have taken some pains ..."

Darwin made many quantitative experiments to test or even generate his ideas, but he did not care much about mathematizing his science. Attracted by the Malthusian reasoning about population sizes in relation to the resources sustaining them, Darwin used mathematics to search for some evidence about the limits of population growth:

"I have taken some pains to estimate the probable minimum rate of elephant's natural increase ...".

The way he describes the exercise (it caused him *pain*) shows that he did not at all like to use his brain for searching evidence in numbers written on paper. He thus liquidates the issue with:

"... but we have better evidence on this subject than mere theoretical calculations, namely, the numerous recorded cases of the astonishingly rapid increase of various animals in a state of nature, when circumstances have been favourable to them for two or three following seasons".

With this sentence, Darwin scorned the future theoreticians who will have built, with "mere theoretical calculations", artificial replicas of reality without considering the possibility of actually studying the real world. These sentences, and the handful of feathers metaphor, reveal that Darwin considered the hard-to-be sciences to be the sciences of simplicity, tackling easy problems, whereas the soft-to-be sciences are the difficult ones. Apparently, he was convinced that the methods of physics in depicting the world ("with mere theoretical calculations") are not conducive to really understanding nature at high levels of complexity and that direct examination of natural facts leads to better understanding.

This position was not embraced by Darwin followers, who in general became strongly affected by physics envy [14] and considered natural history to be a non-scientific discipline. Some physicists, however, feel the urge of merging the so-called Newtonian worldview with the Darwinian one [16], even though this reconciliation is hindered by the historical nature of ecology and evolution: the weight of contingent drivers in shaping the "history" of eco-evolutionary domains makes them intractable with the tools of ahistorical disciplines, where constraints (i.e. laws) dominate.

The theory of ecology

Theoretical ecology is usually conceived as a highly mathematized discipline, in which relationships among the different actors are accounted for in models that might even lead to predictions. Everything started with fisheries, when the zoologist Umberto D'Ancona gave his data to the mathematician Vito Volterra, who elaborated the famous equations, independently produced also by Lotka [17]. Physics envy led ecologists to search for laws that might allow one to predict the future in a deterministic way. One of the greatest theoretical ecologists of modern times, Robert May, published a seminal paper entitled "Simple mathematical models with very complicated dynamics" [18], but later he asked the already-mentioned question that indeed might have horrified Elton: How many species are there on Earth? [8]. A model is relevant if it considers the relevant variables, and species are the most relevant variables when nature is considered. Not knowing the species, doing what Elton ridiculed, can lead to beautiful exercises that are divorced from reality (in Darwin's words, "mere theoretical calculations").

Ecological theory was developed with computers, with mathematical models and simulations, or in experimental settings [19], sometimes in bottles (like those of [20]), sometimes in micro- and mesocosms, or in the field, but only where conditions are conducive to manipulation (e.g. the intertidal or prairie grasses systems). The number of variables (especially species) was kept to a minimum since the calculations and the manipulations are difficult when the interactors and the interactions are many (as happens in the real world).

It is suggestive that Loreau [21], in a review aimed at founding a new synthetic theory of ecology, points out that the two main experiments aimed at linking biodiversity with ecosystem functioning dealt with 16 and 32 species, respectively. From various estimates, biodiversity is made of more than 10 million species! Obviously, these millions of species do not occur all in one place, but it is nonetheless suggestive that low-diversity communities are taken as a paradigm for the relationship between biodiversity and ecosystem functioning. Boero and Fresi [22], for instance, reported 90 species of hydroids on a vertical rocky cliff in the Mediterranean Sea, the whole biota of that single spot probably comprising several hundred species of macroscopic organisms. Similar numbers are reported by Terlizzi *et al.* [23], who found 133 mollusc species at a single site.

Evidently, our planet is inhabited by many more species than hard theoretical ecology can handle. This must be taken into account if we want to understand what is happening out there (and not only what is happening in a computer or in limited experiments).

The entangled bank

A theory is based on the concepts that form its pillars. Community, or biocenosis, is surely a key ecological concept. The credit for coining it is given to Möbius [24], who developed it by describing an oyster bank. In *The Origin of Species*, however, Darwin describes rather clearly a biological community, using the tangled bank as a metaphor:

"*When we look at the plants and bushes clothing an entangled bank, we are tempted to attribute their proportional numbers and kinds to what we call chance. But how false a view is this! What a struggle between the several kinds of trees … what war between insect and insect … between insects, snails, and other animals with birds and beasts of prey … all striving to increase, all feeding on each other or on the trees and their seeds and seedlings …*".

The entangled bank is not a product of chance; it is a well-defined entity deriving from the interactions among all the actors that play a role in it. Communities interact with the physical factors, so as to form ecosystems. In fact, later in the book, Darwin introduces the physical factors, envisaging what was later called an ecosystem:

"*Nearly all (species) either prey on or serve as prey for others; in short, … each organic being is either directly or indirectly related … to other organic beings … the inhabitants of any country by no means exclusively depend on insensibly changing physical conditions, but in large part on the presence of other species, on which it depends, or by which it is destroyed, or with which it comes into competition*".

"Exclusively" means that a community depends on physical conditions, but not only. In certain parts of the *Origin*, Darwin disregarded physical conditions and stressed biotic interactions, namely competition and predation, whereas in other parts he recognised the importance of both biotic and abiotic drivers.

Darwin as a naturalist (or natural historian?)

The sentence above, furthermore, depicts a food web, with the subtle trophic interactions that link species. Darwin labeled himself a naturalist, as indicated by the title of the book describing his voyage with the *Beagle*. Natural history is the discipline of naturalists who indeed might have been less equivocally identified as natural historians. Historians, in fact, study human history, whereas naturalists study the history of nature. It is crucial, at this point, to appreciate the difference between historical and ahistorical sciences, as explained by Mayr [25]. With chaos theory, mathematicians formalised this difference, providing evidence for the inherent unpredictability of complex systems. In this framework, in fact, a complex system should be very sensitive to slight changes in the initial conditions that determine its future behaviour. Chaos theory provides a very useful concept that buffers the hopeless task in of predicting the future: the attractor. These complex systems, in fact, can have recurrent states, as if something were attracting them into a definite orbit but allowing ample "freedom" in its development. Chaos theory was instrumental in justifying failures in predicting the weather over the medium to long term: the attractor defines the alternation of seasons, but the historical nature of the weather makes precise predictions inherently impossible. The attractor might be equalled to the definite laws of physics; it is a constraint that forces the system to behave in a certain way. Once laws are detected and formalised into a formula, it is possible, knowing the initial conditions, to predict the outcome of the behaviour of the system. The identification of constraints is very important, and some laws of ecology (or, better, of physiology) have been singled out, such as Liebig's law of the minimum. All the "laws" of ecology, however, do not act in isolation from each other, and their interactions, plus the changes in conditions due, for instance, to adaptation or to climate change, can modify the scenario in such a way that the laws are often broken or modified. These diversions from the expected outcome of the interactions among the components of the systems are often called contingencies and their effects cannot be predicted. They change the conditions that are taken into account by the "laws" and are conducive to some resistance by the domain of the attractor(s), eventually breaking the constraints and pushing the system into the domains of different attractors. In the absence of contingencies, the attractors have total influence over the behaviour of a system which then behaves in a completely predictable fashion. Without contingencies, the future is similar to the past and events occur over and over again or change according to a definite path that can be inferred by the application of the laws. This is obviously a system devoid of history. History, in fact, is the deviation from the norm, is the contingency that pushes the system into a different orbit, sparking new conditions that will lead to unexpected outcomes. We can predict the orbits of the planets, and the behaviour of electrons and molecules, because these systems occur at scales that are either too large or too small for our scale of perception. But when we pass to the scale of living beings and consider systems assimilable to Darwin's entangled bank, history takes its toll. The laws continue to act, but since they are too many and have only limited application, contingencies can be more powerful than the laws. The disentangling of such an entangled scenario seemed hopeless to Darwin, if not in the light of competition:

"*Yet unless it* (i.e. competition) *be thoroughly engrained in the mind, I am convinced that the whole economy of nature, with every fact on distribution, rarity, abundance, extinction and variation, will be dimly seen or quite misunderstood*".

Darwin, in this way, was very humble and accepted the inherent unpredictability (but not the vision or the understanding) of the entangled bank. It is suggestive that, 149 years after *The Origin of Species*, Doak *et al.* [26] realised that the approaches to ecology require more humility and that it is impossible to avoid "surprises" (i.e. facts or events that were not predicted by analysing the past and applying the rules that apparently determined its course). With the entangled bank, Darwin describes the origin of a community, but he does not dare to predict its future behaviour!

Fitness

Darwin also introduced the concept of fitness, even if he did not use this word:

"*I use the term Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including not only the life of the individual, but success in leaving progeny*".

The solution of contingent problems, linked to the survival of the individuals, is useless if they are unable to reproduce, and the two pressures, one for mere survival and one for reproduction, act in synergy and fuel each other. Hence:

"*A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase*".

This concept, deriving from the ideas of Malthus, is expressed several times in the *Origin*:

"*All plants and animals are tending to increase at a geometrical ratio*".

But Darwin is aware that this race toward numerical increase cannot go on forever. It is suggestive that many experimental manipulations aimed at understanding ecological phenomena do not care much about the reproduction of the investigated individuals, the experiments being of short duration!

Carrying capacity

In the logistic curve, r represents the rate of numerical increase of the population, whereas K represents the carrying capacity. The link of the two variables is vivid in Darwin's prose:

"*Although some species may be now increasing, more or less rapidly, in numbers, all cannot do so, for the world would not hold them*".

And Darwin applied these concepts to human populations, predicting a stop to our growth because of impairment of the environmental systems sustaining us:

"Even slow-breeding man has doubled in twenty-five years, and at this rate, in a few thousand years, there would literally not be standing room for his progeny".

r and K strategies

Building on the logistic curve, Pianka [27] distinguished two main patterns in the way populations develop with time: r and K strategies are reported in all ecology textbooks. The concept, however, is well expressed in the *Origin*:

"If an animal can in any way protect its own eggs or young, a small number may be produced, and yet the average stock be fully kept up; but if many eggs or young are destroyed, many must be produced, or the species will become extinct".

Experimental plots 1: predation

The way Darwin developed his ideas was based mostly on observation and logical speculation, but his life in the country became conducive to the use of experimental plots. In chapter III of the *Origin*, he wrote:

"… on a piece of ground … dug and cleared … I marked all seedlings … as they came up, and out of the 357 no less than 295 were destroyed, chiefly by slugs and insects".

The measure of the pressure of grazers on plants led to a general statement that based the structure of communities on biotic interactions:

"… it is not the obtaining of food, but the serving as prey to other animals which determines the average numbers of a species".

Insects and snails, the natural "enemies" of plants, are not alone in exerting a predatory pressure on plants:

"… a multitude of seedlings and little trees which had been perpetually browsed down by the cattle".

In this part of his argument, Darwin specifically denied the importance of abiotic factors (i.e. nutrients for plants) in conditioning the structure of plant communities ("it is not the obtaining of food") and focuses on predation.

Experimental plots 2: biodiversity and ecosystem functioning

Later in the book, in chapter IV, however, Darwin introduced the concept that a greater diversity of life forms (now known as biodiversity) is conducive to a greater production (an often-used proxy for ecosystem functioning):

"… if a plot of ground be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised. The same has been found to hold good when first one variety and then several mixed varieties of wheat have been sown on equal spaces of ground".

So not only species of different genera but also mixed varieties of the same species lead to greater yield. These statements cover both intraspecific and interspecific diversity and are a clear and concise expression of the link between biodiversity and ecosystem functioning. Measuring biodiversity by the number of plant species (or varieties), and ecosystem functioning by their production, is still a much-used way of studying biodiversity and ecosystem functioning (see Loreau [21] for a review).

The use of experimental plots, thus, led to two explanations for the diversity of life, one linked to the pressure of predation and one linked to the pressure of competition. The two examples are in different parts of the book and are linked so as to form a coherent picture through the concept of economy of nature:

"So in the general economy of any land, the more widely and perfectly the animals and plants are diversified for different habits of life, so will a greater number of individuals be capable of there supporting themselves".

This statement suggests that evolution led to a great diversification in the way species take advantage of the possibilities for growth offered by any environment and that these differences make competition less harsh, allowing the coexistence of a great number of species.

The struggle with the elements

Darwin was convinced that the struggle for existence was a matter of biotic interactions among species and among the individuals of the same species. He was aware that climate is important in determining the distribution and abundance of organisms, but he considered it a mediator between the organisms and the way they interact with each other to obtain resources (food):

"… climate chiefly acts in reducing food, it brings on … struggle between the individuals, whether of the same or of distinct species, which subsist on the same kind of food …".

The influence of climate on the distribution of species along latitudinal gradients was obvious to Darwin:

"… *when we travel from south to north… species gradually getting rarer … and finally disappearing …* but he discarded the direct influence of climate: … *but this is a very false view …* and privileged species interactions instead: … *each species constantly suffering enormous destruction … from enemies* (i.e. predation) *or from competition …*".

However, the evidence of the influence of abiotic factors becomes overwhelming in what we would call extreme environments:

"*When we reach the Arctic regions, or snow-capped summits, or absolute deserts, the struggle for life is almost exclusively with the elements*".

This sentence implies that Darwin recognized two types of "struggle": the struggle of species with each other and the struggle of each species with the "elements". It is clear, however, that Darwin tended to minimize the importance of physical factors, privileging competition and predation as the main ecological drivers; this view was shared by some ecological schools (especially Anglo-Saxon ones), and at a certain point of the history of ecology, some recognised that abiotic factors had a role in determining community organization [28]. Continental-European ecologists, on the other hand, focused on specific abiotic factors to explain the distribution of organisms. Pérès and Picard [29], for instance, proposed light as the main driver of the distribution of marine benthic species, whereas Riedl [30] enhanced the role of water movement.

The place of species in the economy of nature

Hutchinson [31] is credited with the modern definitions of one of the main concepts of ecological theory: the ecological niche. The concept, however, is present in *The Origin of Species*:

"*… the dependency of one organic being on another lies generally between beings remote in the scale of nature … the struggle will be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers … competition should be most severe between allied forms, which fill nearly the same place in the economy of nature*".

The last sentence states that the harsher form of competition is the intraspecific one, since "allied forms fill nearly the same place in the economy of nature", which in modern terms means that they occupy the same ecological niche. Interspecific competition is also taken into consideration, by using the same line of reasoning:

"*For it should be remembered that the competition will generally be most severe between those forms which are most nearly related to each other in habits, constitution, and structure*".

Parasitism, mutualism, trophic cascades, predation, and competition

The country life that Darwin led for the greatest part of his existence allowed him to be in strict contact with nature and to realize the subtle interactions that can be appreciated only by hunters or cattle raisers. Hence, he reported the impact of vermin (i.e. parasitic worms or insects) in conditioning the stocks of vertebrates:

"*There seems to be little doubt that the stock of partridges, grouse, and hares on any large estate depends chiefly on the destruction of vermin …*".

Besides some outstanding examples [32,33], parasitism is rarely considered ecologically important and its bearing on the structure and function of communities is as ignored as is the importance of physical factors. Darwin also recognized the importance of mutualism, with enthomophilous pollination as an outstanding example:

"*Humble bees are highly beneficial to the fertilisation of our clovers …*".

The importance of these phenomena becomes evident when the pollinators are destroyed by predators:

"*… the number of humble bees depends on the number of field-mice, which destroy their combs and nests …*".

But the predators of humble bees are in turn preyed upon by cats:

"*… the number of mice is largely dependent on the number of cats …*".

And then the circle is closed:

"*… the presence of a feline animal might determine … the frequency of certain flowers*".

Darwin even makes predictions about possible outcomes of intricate species interactions:

"*Perhaps Paraguay offers the most curious instance of this; for here neither cattle nor horses nor dogs have ever run wild, though they swarm southward and northward in a feral state; and Azara and Rengger have shown that this is caused by the greater number in Paraguay of a certain fly, which lays its eggs* *in the navels of these animals when first born. The increase of these flies, numerous as they are, must be habitually checked by some means, probably by birds. Hence, if certain insectivorous birds (whose numbers are probably regulated by hawks or beasts of prey) were to increase in Paraguay, the flies would decrease—then cattle and horses would become feral, and this would certainly greatly alter (as indeed I have observed in parts of South America) the vegetation: this again would largely affect the insects; and this, as we just have seen in Staffordshire, the insectivorous birds, and so onwards in ever-increasing circles of complexity"*.

These are probably the first examples of trophic cascades, a concept credited to Hairston *et al.* [34], although they did not call it a trophic cascade! Darwin repeated several times that nature is a network of relationships among species:

"Nearly all (species) either prey on or serve as prey for others; in short, … each organic being is either directly or indirectly related … to other organic beings …".

The influence of climate, again, is lessened:

"… the inhabitants of any country by no means exclusively depend on insensibly changing physical conditions …",

but this is probably a reaction to former ideas on the distribution and abundance of animals, since what Darwin opposed is, again, the idea that what we see is "exclusively" determined by the climate. The explanations, then, become probabilistic. The distribution and abundance of a given species are instead determined…

"… in large part on the presence of other species, on which it depends, or by which it is destroyed, or with which it comes into competition".

The importance of life cycles: seeds and dispersal

Considering the vegetation surrounding a pond, Darwin made "several little experiments" and questioned the competence of botanists about the importance of life cycles:

"I do not believe that botanists are aware how charged the mud of ponds is with seeds: I have tried several little experiments …: I took … three table-spoonfuls of mud … on the edge of a little pond. … I kept it … for six months … counting each plant as it grew; the plants were of many kinds, and were altogether 537 … in a breakfast cup!"

In this way, Darwin reported about the hidden diversity of life, stressing the importance of soil seed banks, a topic that would become fashionable only after a very long time [35]. The awareness of the relevance of life cycle patterns and the bearing of dormancy of "seeds" of any kind is extended to animals:

"The same agency may have come into play with the eggs of some of the smaller fresh-water animals".

It took more than a century to appreciate the ecological role of resting stages in seasonal environments such as coastal marine ones [36,37]. Darwin then upgraded to much larger scales the small scale of the pond and the "little experiments" of seed culture, so as to understand the patterns of colonization of distant islands by continental vegetation. First, he carried out some experiments:

"Until I tried … a few experiments, it was not even known how far seeds could resist the injurious action of sea-water. To my surprise I found that out of 87 kinds, 64 germinated after an immersion of 28 days, and a few survived an immersion of 137 days".

And he used the results to match seed survival with the speed of marine currents and the distance of islands from continents, developing, in one shot, source and sink theory [38] and supply side ecology [39]:

"In Johnston's Physical Atlas, *the average rate of … Atlantic currents is 33 miles per diem …; on this average, the seeds of 14/100 plants belonging to one country might be floated across 924 miles of sea to another country; and when stranded, … they would germinate"*.

These considerations about the connections between islands and the continents, allowing for successful colonization, together with the famous discussion about the fauna of the Galapagos Islands, posed a solid basis for the development of the theory of island biogeography [40].

The evolution of biodiversity

In his "Homage to Santa Rosalia", Hutchinson [41] asked why there are so many kinds of animals, posing the basis for the perception of the functional meaning, if any, of the diversity of life. Darwin provided answers to this question in several parts of the *Origin*. Dealing with the diversity of animals and plants, he wrote, as we have already seen:

"So in the general economy of any land, the more widely and perfectly the animals and plants are diversified for different habits of life, so will a greater number of individuals be capable of there supporting themselves".

The resources are in one big compartment, but the way to use them differs in the various species and allows for coexistence if the "habits of life" are different enough. Furthermore, with Natural Selection, Darwin gave a clear explanation of the origin of biodiversity:

"The preservation of favourable variations and the rejection of injourious variations I call Natural Selection".

Hence, the species inhabiting the planet at a given moment are the best response to the Natural Selection of the favourable variations against the injurious ones. He also proposed some trends in the evolution of diversity, so envisaging cladogenesis:

"*Dominant groups tend to become still more dominant* … and proposed that … *the larger genera tend to break down into smaller genera* …".

The more a group is favoured by Natural Selection, the more it becomes diversified. The winning design is modulated so that species can coexist while having a proximate common descent (being referable to the same genus). Hence, Darwin considered genera to be groups of closely related species that are descended from one such successful common ancestor. The diagram in chapter IV depicts the patterns of biodiversity increase and is illustrated with the final sentence of the summary of the same chapter:

"As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications".

This is probably the most suggestive definition of biodiversity: the beautiful ramification of the Tree of Life which fills the crust of the earth!

The Red Queen hypothesis, I presume …

The previous statements describe a pattern, but Darwin also individuated the process leading to continuous change in the features of species.

"No country can be named in which all the native inhabitants are now so perfectly adapted to each other and to the physical conditions under which they live, that none of them could anyhow be improved …".

This sentence recognizes that species must be adapted both to each other and to the physical conditions, acknowledging the importance of both abiotic and biotic factors in determining Natural Selection. The important intuition, however, is that

"… if some of these many species become modified and improved, others will have to be improved in a corresponding degree or they will be exterminated".

Van Valen [42] proposed the same principle as the Red Queen hypothesis. As suggested by Boero *et al*. [43], biodiversity is the result of a chain reaction in which, according to Red Queen processes, each change sparks further changes which in turn cause other changes in an endless process that has no functional meaning if not the survival of the fittest. Early ecosystems "functioned" with very low diversity, and the processes individuated by Darwin led to a steady increase of biodiversity while ecosystems obviously continued to function [44]. Ecosystems, in fact, do function both at low and at high biodiversity; otherwise, they cease to exist. Asking for a functional meaning to the diversity of life is a futile question: biodiversity is tautological (it exists) and not teleological (it does not exist for a purpose)!

Reference points

Pauly [45] warned that our expectations about what is ecologically "good" are biased by our perception of the state of the environment, based on our previous experience. Darwin took a similar stance while discussing the way humans select the organisms they raise, and posed a serious warning about our anthropocentric view of nature:

"Man selects only for his own good; Nature only for that of the being which she tends".

In this way, Darwin described the difference of what is good for us and what is good for Nature, and he continued with:

"… how fleeting are the wishes and efforts of man! how short his time! and consequently how poor will his products be, compared with those accumulated by nature during whole geological periods!"

These statements cast serious doubt on the effective "improvement" of organisms that, for instance, are genetically modified for our own good, disregarding the good of the organisms themselves. Biotechnologies usually do not consider either ecology or evolution, yet the organisms they create can be powerful evolutionary drivers with a bearing on the functioning of ecosystems. They can play this role because of the changes they induce in other species they are in contact with, triggering the Red Queen processes proposed by Darwin. In performing evaluations of the use of genetically modified species, one might ask: what is a "good" functioning of an ecosystem? What are the features that allow us to label a species as "bad"?

Conservation biology is often very "conservative" and labels as "bad" most changes in the composition of communities. Darwin warned about judging what is good (or bad) for us and what is good (or bad) for nature. The ecosystem approach, envisaging man as a part of Nature, is an attempt at reconciling our expectations with the natural trends of any kind of environment or organism.

Conclusions

Ecology and evolution: natural history!

In his research protocol, Darwin knew very well the difference between ecology and evolution, even if he used neither term in the first edition of the *Origin*. He used "economy of nature" to label what today we call ecology, whereas "evolution" was obviously the process that led to the origin of varieties, then species. Darwin practiced both disciplines, but he did not call himself either an evolutionist or an economist of nature. He instead used the term "naturalist" to label himself as a practitioner of both ecology and evolution under a single synthetic view. As already mentioned, it is remarkable that ecology did not contribute much to the Modern Synthesis of the first half of the last century, an approach dominated by genetics, systematics, and palaeontology. The Modern Synthesis thus disregarded one of the main drivers of Darwinian thinking: the economy of nature, the motor of Natural Selection and thus of evolution. Reductionistic evolutionary biology focused on the proximate causes of evolution (genetics) and on the patterns of life diversification (systematics and palaeontology), disregarding the ultimate causes, linked mainly to ecological processes, the intertwining of the action of both physical and biotic factors in determining evolutionary change, so well explored in the *Origin*.

Several authors [21,46] are formulating synthetic approaches either to biodiversity and ecosystem functioning or to community ecology, calling for a timely fusion between ecology and evolution. These "novel" views are reviving Darwinian natural history in a second synthesis that finally is putting evolution into ecology and vice versa, as invoked by Ricklefs [11] and Tewksbury *et al.* [12] among others. In this effort to place all disciplines into an evolutionary framework, evo-devo represents the other side of the coin of the "missing synthesis", with a timely return of developmental biology to the Darwinian paradigm (e.g. Gehring and Seimyia [10]). The basic sciences that led Darwin to write the *Origin*, in fact, are both ecology and developmental biology, and both were marginal to the elaboration of the "modern synthesis".

Back to Darwin … into the future

Darwin's research protocol was totally free from prejudice, considering both patterns and processes, practicing both inductive and deductive reasoning, using both the experimental and the comparative method. In some parts of the *Origin*, Darwin privileged some evolutionary drivers (his favorites were intra- and interspecific biotic interactions) but, in other parts, he recognised that other drivers (above all, physical factors) were also important. The only falsifications ensuing from his observations, experiments, and reasoning were about the universality of some of the mechanisms he proposed, each being valid under some circumstances and invalid under others, all being driven by Natural Selection and having evolution as the only universal result. Natural Selection is a "law" of nature, but it is explanatory and not predictive, and we can see its effects only *a posteriori*: it explains what happened but does not predict what will happen.

This constructive attitude, ridiculed for some time by the Popperian paradigm that called for universal statements only and rejected existential ones, demonstrated that in the sciences of complexity (and nothing is more complex than life in the known universe) there are very few universal phenomena (one is evolution driven by Natural Selection) whereas existential ones are the rule. Species evolve due to both biotic and abiotic interactions, and there is not just one way in which evolution takes place. Experimental protocols are very useful but, under some circumstances, the only way to tackle problems is through comparative analysis. There is no logical supremacy of an approach over the others, and all approaches concur to tackle the problem of life from all its facets, as argued by Cleland [15].

Multicultural biology

Darwin obviously practiced a holistic approach to biology and sketched a grand picture of what life is. In the 150 years following the publication of his masterpiece, biology became fractionated into many branches, with the triumph of the reductionistic method. The apex of this tendency is well explained by the sentence "Life is chemistry" in the last editorial of John Maddox [47], a conviction that probably marked 25 years of direction of the most influential scientific journal of all time (*Nature*), condemning biology to be equal to chemistry. Along with this chemical tendency, which led to the triumph of chemical biology at one end of the span of life sciences, biology was also afflicted by physics envy [14], with the search for the "definite laws" that, following Darwin, rule the domains of the sciences of simple phenomena but that are very loose (and hence losing the status of laws) in the sciences of complexity. This led to incessant attempts to find formulas that might predict the behaviour of complex systems while performing what Darwin called "mere theoretical calculations".

These two extremes became (and still are) dominant in the life sciences and, most often, they do not communicate with each other, focusing on parts of the "grand Darwinian picture" (or even making accessory pictures, like the -omic ones), so losing the vision of the whole. The reductionistic practice has been (and still is) extremely fruitful, and the divergence from Darwinian thinking was crucial to achieve the actual progress; otherwise, we would still have a "vision from a distance" of what is life.

The time is ripe, however, to give new dignity to natural history, Darwin's discipline, not as a "return to the past" or an alternative to chemical or mathematical ways of studying life but as the reconciliation of all approaches under a common theoretical framework: the theory of natural history (i.e. the theory of ecology and evolution).

The logical primacy of natural history

The modern meaning of natural history is not far from Darwin's research protocol. He identified the pattern of evolution and considered ecology to be its ultimate cause, whereas he missed the proximate cause for it, later developed by genetics. Of course, Natural History, once it incorporates genetics, becomes the most holistic biological discipline, being the study of the patterns and the proximate and the ultimate processes that describe and explain the expression of life. This approach is very modern, also in the light of the ecosystem approach, which sees humans as members of ecosystems. Darwin referred to ecology as "the economy of nature" and this term should be considered in all its depth, in the light of current events. The triumph of the reductionistic approach led humans to develop their own "economy" and envisaged "definite laws" for it, aimed at predicting the behaviour of complex systems such as socioeconomic ones. The failure of this physics envy by economists is probably due to the current disregard for the "economy of nature". If the "laws" of the economy of humans are in contradiction with those of the economy of nature, it is overly naive to expect that the laws of human economy will prevail over those of nature's economy. Economics circumvented the problem by "externalizing" the economy of nature from the economy of humans. Ecological economics is calling for an economic appraisal of what nature is (giving a price to the goods and services that nature provides to humans), but it might be better to follow a natural history appraisal of what human economy is. It would become immediately apparent that the continuous growth advocated by all economic systems is an infantile expectation since our planet is a finite system, where infinite growth is impossible. The growth of human economy, furthermore, is often accompanied by the degrowth of the economy of nature (there is no free lunch, as economists teach us) and this will eventually lead to both economic and environmental disaster.

Natural history, in this framework, has logical primacy over economy and should incorporate it, so that all our actions are based on a sound evaluation of natural costs, especially those that involve the growth of the economic capital at the expense of the natural capital. This change in focus is the only possibility we have to escape from the disasters that our myopic view of the world is preparing for the future generations and also for the present ones.

Coda

Of course, life will find solutions to our disasters. We are not so powerful to disrupt the functioning of the ecosystems; we cannot even eradicate cockroaches (without poisoning ourselves)! We are the endangered species and our growth is the premise of our collapse, as Darwin said, and it is worth repeating it:

"*Even slow-breeding man has doubled in twenty-five years, and at this rate, in a few thousand years, there would literally not be standing room for his progeny*".

Probably Darwin made some mistake here, since we have strong indications that it is not a matter of a few thousand years for us to pay the bill of our meal on the planet. And the solution of searching for another restaurant (… planet) is both naive and unfeasible.

A Theory of Natural History is at hand, reconciling all aspects of biology (including humans in Nature), renewing the centrality of Darwin's figure, not only for the things he discovered but for his non-dogmatic method of how to make science.

Disclosures

The author declares that he has no disclosures.

Acknowledgments

The analysis of *The Origin of Species* was stimulated by the request to give a keynote lecture to celebrate the figure of Darwin during the 2009 congress of the Italian Society of Ecology (SItE).

This study was carried out in the frame of various projects on marine biodiversity which were funded by MIUR, Provincia di Brindisi, and CoNISMa. The views proposed here are based on work performed with the financial support of the European Union through the VECTORS, PERSEUS, COCONET, and MED-JELLYRISK projects. Alessandro Minelli (Padua) commented on an early version of the manuscript. David Reznick and an anonymous reviewer suggested some additions and corrected some mistakes.

References

1. Darwin CR: *On the Origin of Species by means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray; 1858.
2. Lamarck J-B: *Philosophie Zoologique, ou Exposition des Considérations Relatives à` l'Histoire Naturelle des Animaux*. Paris: Dentu et l'Auteur; 1809.
3. Darwin CF, Wallace A: **On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection.** *J Proc Linn So Zool,* 1858, **3:**45-62.
4. Reznick DN: *The "Origin" Then and Now: An Interpretive Guide to the "Origin of Species."* Princeton: Princeton University Press; 2010.
5. Buss L: *The Evolution of Individuality*. Princeton: Princeton University Press; 1987.
6. Mayr E: *The Growth of Biological Thought*. Cambridge: Belknap Press; 1982.
7. Elton C: *Animal Ecology*. London: Sidgwick and Jackson; 1927.
8. May RM: **How many species are there on Earth?** *Science* 1988, **241:**1441-9.
9. Boero F: **The study of species in the era of biodiversity: a tale of stupidity.** *Diversity* 2010, **2:**115-126.
10. Gehring W, Seimyia M: **Eye evolution and the origin of Darwin's eye prototype.** *Ital J Zool* 2010, **77:**124-36.
11. Ricklefs RE: **Natural history, and the nature of biological diversity.** *Am Nat* 2012, **179:**423-35.
12. Tewksbury JJ, Anderson JGT, Bakker JD, Billo TJ, Dunwiddie PW, Groom MJ, Hampton SE, Herman SG, Levey DJ, Machnicki NJ, Martinez del Rio C, Power ME, Rowell K, Salomon AK, Stacey L, Trombulak S, Wheeler TA: **Natural history's place in science and society.** *Biol Sci* 2014, **64:**300-10.
13. Kant I: *Metaphysical foundations of natural sciences*. Edited by Friedman M. Cambridge: Cambridge University Press; 1786, (printed in 2004).
14. Egler FE: **Physics envy in ecology.** *Bull Ecol Soc Am* 1986, **67:**233-5.
15. Cleland CE: **Methodological and epistemic differences between historical science and experimental science.** *Philos Sci* 2002, **69:**474-96.
16. Harte J: **Towards a synthesis of the Newtonian and Darwininan worldviews.** *Phys Today* 2002, **50:**29-34.
17. Gatto M: **On Volterra and D'Ancona footsteps: the temporal and spatial complexity of ecological interactions and networks.** *Ital J Zool* 2009, **76:**3-15.
18. May RM: **Simple mathematical models with very complicated dynamics.** *Nature* **261:**459-67.
19. Boero F: **Marine sciences: from natural history to ecology and back, on Darwin's shoulders.** *Adv Oceanogr Limnol* 2011, **1:**219-33.
20. Gause GF: *The struggle for existence*. New York: Williams and Wilkins; 1934.
21. Loreau M: **Linking biodiversity and ecosystems: towards a unifying ecological theory.** *Phil Trans R Soc B* 2010, **365:**49-60.
22. Boero F, Fresi E. **Zonation and evolution of a rocky bottom hydroid community.** *PSZN I: Marine Ecology* 1986, **7:**123-50.
23. Terlizzi A, Scuderi D, Fraschetti S, Guidetti P, Boero F: **Molluscs on subtidal cliffs: patterns of spatial distribution.** *J Mar Biol Assoc UK* 2003, **83:**165-172.
24. Möbius K: *Die Auster und Austernwirtschaft*. Berlin: Wiegandt, Hempel und Parey; 1877.
25. Mayr E: **Is biology an autonomous science?.** In: *Towards a new philosophy of biology*. Edited by Mayr E. Cambridge: Belknap Press; 1988:8-23.
26. Doak DF, Estes JA, Halpern BS, Jacob U, Lindberg DR, Lovvorn J, Monson DH, Tinker MT, Williams TM, Wootton JT, Carroll LI, Emmerson M, Micheli F, Novak M: **Understanding and predicting ecological dynamics: are major surprises inevitable?** *Ecology* 2008, **89:**952-61.
27. Pianka ER: **On r and K selection.** *Am Nat* 1970, **104:**581-88.
28. Dunson WA, Travis J: **The role of abiotic factors in community organization.** *Am Nat* 1991, **138:**1066-91.
29. Pérès JM., Picard J: **Nouveau manuel de bionomie benthique de la mer Méditerranée.** *Rev Trav Stat Mar* 1964, **3:**3-137.
30. Riedl R: **Water Movement (Animals).** In: *Marine Ecology*. Edited by Kinne O. London: Wiley Interscience; 1971:1123-56.
31. Hutchinson GE: **Concluding remarks.** *Cold Spring Harb Symp Quant Biol* 1957, **22:**415-27.
32. Andrewartha HG, Birch LC: *The Distribution and Abundance of Animals*. Chicago: University of Chicago Press; 1954.
33. Lafferty KD, Dobson AP, Kuris AM: **Parasites dominate food web links.** *Proc Natl Acad Sci U S A* 2006, **103:**11211-6.
34. Hairston NG, Smith FE, Slobodkin LG: **Community structure, population control, and competition.** *Am Nat* 1960, **94:**421-25.
35. Leck MA, Parker VT, Simpson RL: *Ecology of soil seed banks*. San Diego: Academic Press; 1989.
36. Boero F, Belmonte G, Fanelli G, Piraino S, Rubino F: **The continuity of living matter and the discontinuities of its constituents: do plankton and benthos really exist?** *Trends Ecol Evol 1996,* **11:**177-80.
37. Marcus NH, Boero F: **The importance of benthic-pelagic coupling and the forgotten role of life-cycles in coastal aquatic systems.** *Limnol Oceanogr* 1998, **43:**763-8.
38. Pulliam HR: **Sources, sinks, and population regulation.** *Am Nat* **132:**652-61.
39. Gaines S, Roughgarden J: **Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone.** *Proc Natl Acad Sci USA* 1985, **82:**307-3711.
40. MacArthur RH, Wilson EO: **An equilibrium theory of insular zoogeography.** *Evolution* 1963, **17:**373-87.
41. Hutchinson GE: **Homage to Santa Rosalia or Why are there so many kinds of animals?** *Am Nat* 1959, **93:**145-59.
42. Van Valen L: **A new evolutionary law.** *Evol Theory* 1973, **1:**1-30.
43. Boero F, Belmonte G, Bussotti S, Fanelli G, S. Fraschetti S, Giangrande A, Gravili C, Guidetti P, Pati A, Piraino S, Rubino F, Saracino O, Schmich J, Terlizzi A, Geraci S: **From biodiversity and ecosystem functioning to the roots of ecological complexity.** *Ecol Complex* 2004, **2:**101-9.
44. Boero F, Bonsdorff E: **A conceptual framework for marine biodiversity and ecosystem functioning.** *Mar Ecol-Evol Persp* 2007, **28**(Suppl. 1):134-45.
45. Pauly D: **Anecdotes and the shifting baseline syndrome of fisheries.** *Trends Ecol Evol* 1995, **10:**430.
46. Vellend M: **Conceptual synthesis in community ecology.** *Q Rev Biol* 2010, **85:**183-206.
47. Maddox J: **On the widespread distrust for science.** *Nature* 1995, **378:**435-8.