

Evolution at the ecosystem level: On the evolution of ecosystem patterns*

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Resum. A mesura que problemes ambientals com la superpoblació, la sobrepesca, la contaminació i la pluja àcida han rebut més atenció pública, l'interès s'ha centrat més en vincles biogeoquímics i en estudis integrals d'ecosistemes sencers. Ramon Margalef va reconèixer fermament la notable influència intel·lectual que es podria obtenir mitjançant la transferència, d'un camp a un altre, de les perspectives i avenços de cadascun d'ells. En aquest article voldria tractar la naixent unificació de la biologia de poblacions i la ciència dels ecosistemes. La gestió sostenible requereix que es relacionin les característiques macroscòpiques de les comunitats i els ecosistemes amb els detalls microscòpics dels individus i les poblacions. Sostindré que les diferències que han impedit aquesta síntesi són artificials i que les hem de superar per a poder construir una ciència que ens permeti afrontar la pèrdua dels beneficis que es deriven dels ecosistemes.

Paraules clau: Ramon Margalef · biologia de poblacions · ciència dels ecosistemes · sostenibilitat · dinàmica ecològica i evolutiva

Summary. As environmental problems like overpopulation, overfishing, pollution and acid rain commanded greater public attention, much focus shifted to biogeochemical linkages, and to holistic studies of whole ecosystems. Ramon Margalef recognized as forcefully as anyone the remarkable intellectual leverage one could gain by transferring the unique perspectives and advances from one field to another. In this article I discuss the nascent unification of population biology and ecosystems science. Sustainable management requires that we relate the macroscopic features of communities and ecosystems to the microscopic details of individuals and populations. I argue that the distinctions that have prevented this synthesis are artificial, and that we need to overcome them to build a science that allows us to deal with the loss of the benefits we derive from ecosystems.

Keywords: Ramon Margalef · population biology · ecosystems science · sustainability · ecological and evolutionary dynamics

Introduction

The history of ecology is firmly grounded in natural history. Darwin's voyage on the *Beagle* transformed our view of Nature, and set the stage for the emergence of the new discipline. Natural history was the cradle of ecology, and remains its foundation.

But understanding ecological patterns, and being able to manage precious resources, required understanding dynamics. So ecology embraced mathematical formalisms, in a partnership that facilitated general theory. The theoretical constructs developed nearly a century ago by pioneers like Alfred Lotka and Vito Volterra remain at the core of research in ecology

today, and are must-learning for all young ecologists, no matter how mathematical they are. Indeed, in turning to mathematical approaches, ecology was rediscovering and extending insights from demographic investigations from the 17th century and later Malthus and Verhulst, with roots reaching back even to Fibonacci five centuries before.

Meanwhile, evolutionary biology, the essential legacy of Darwin's writings, developed its own mathematical foundations. Ronald Fisher, Sewall Wright and J.B.S. Haldane pioneered the development of a synthetic mathematical theory that deepened our understanding of evolution, and provided a framework for the modern synthesis of genetics and evolution that is at the center of all biological understanding. Theodosius Dobzhansky crystallized this view in his famous essay titled *Nothing in Biology Makes Sense Except in the Light of Evolution* [6]. Thus, the parallel developments in the two fields of ecology and evolutionary biology suggested natural synergies between them, but those synergies have been only partially realized. I will return to this theme later in the lecture.

As ecology matured, it found partnerships elsewhere, in the physical sciences, where Ramon Margalef was one of the key

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figures in developing synthesis, as well as in engineering and molecular biology. Margalef recognized as forcefully as anyone the remarkable intellectual leverage one could gain by transferring the unique perspectives and advances from one field to another. He wrote, in an unpublished manuscript [28], “The reader may suspect that I distrust attempts to define the orthodox approach to the ‘true’ science.” It is the heterodox approach that he championed, the reaching outside the box, that breaks new ground in science. Ramon Margalef was always reaching outside the box, looking for insights from thermodynamics and wherever else he could find them, to shed new light on the problems of ecology.

As environmental problems like overpopulation, overfishing, pollution and acid rain commanded greater public attention, much focus shifted to biogeochemical linkages, and to holistic studies of whole ecosystems. A chasm developed between such research and the more traditional evolutionary research, which addressed phenomena at much lower scales of organization—those of individuals and populations—and generally at much longer time scales than seemed relevant to most of those concerned with problems of environmental degradation. (But there were exceptions, like Harold Mooney and Paul Ehrlich, previous Margalef Prize winners; Tyler Prize winners Herbert Bormann and Gene Likens [1,9,34], who tried to bridge the gap; and of course the great polymath G. Evelyn Hutchinson [12]).

The human footprint on our Earth looms large. It threatens our survival, and demands our attention... raising both ecological and evolutionary challenges. My comments when accepting this prestigious prize, like much of my current work, were on the interface between ecology and evolution on the one hand, and the disciplines of economics, sociology, psychology, anthropology and ethics on the other. These are the new partnerships that must be developed to deal with the threats to our environment [7,19]. However, in this article I want to discuss another and related dimension, the nascent unification of population biology and ecosystems science. I will argue that the distinctions that have prevented this synthesis are artificial, and that we need to overcome them to build a science that allows us to deal with the loss of the benefits we derive from ecosystems.

Towards a theory of sustainability

The central problem facing societies in the next decades, and probably in the next centuries, is assuring a sustainable future. Sustainability of course means many things. It means a future free of major destructive conflict. It means promise of stability in financial markets and energy and economic security. It means the maintenance of biological and cultural diversity. But, at the core, it means the protection of the goods and services we derive from ecosystems, and which support our lives and their quality. These services include all the things ecosystems mean to us:

1. The food, fiber, fuel, and pharmaceuticals we derive directly.

2. The indirect benefits of climate mediation, pollination, and sequestration of toxics as well as essential nutrients.
3. The aesthetic and ethical dimensions that humans assign to natural places, and to wild plants and animals.

Understanding what sustains these goods and services requires firstly understanding how they depend upon biological diversity and ecosystem functioning, and secondly what sustains those aspects of biological diversity and ecosystem functioning that are essential to providing goods and services. In any ecosystem, there are characteristic patterns and processes that sustain ecosystem services, and not all species are equally important in the maintenance of these patterns and processes. Some species would be barely missed if they were to disappear. Others, like the chestnuts that disappeared from the forests of the northeastern United States, may be missed for some of the services they provide; but their elimination will not result in cascading collapses that threaten the identity of the ecosystems. The loss of yet others, however, ranging from nitrogen-fixing bacteria to keystone predators like the sea otter of the west coast of the United States and Canada, would fundamentally change the nature of these systems. Thus we need to identify the patterns that are the signatures of these ecosystems, and to focus on the regularities while recognizing that control of those regularities rests at lower levels of organization, in particular species and functional groups, and in statistical ensembles of individuals and species. This implies a need to relate phenomena across scales, from cells to organisms to collectives to ecosystems to the biosphere, and to ask:

How robust are the properties of ecosystems?

How does the robustness of macroscopic properties relate to ecological and evolutionary dynamics on finer scales?

How do ecosystems self-organize over ecological and evolutionary time?

These have been the focus of my work over several decades [22,24], with many themes that resonate with the similar approaches and perspectives of Ramon Margalef [29–31]. Margalef pioneered the application of ideas from thermodynamics to ecological communities, recognizing fully the power of developing statistical approaches to the overwhelming complexity of ecosystems.

Population biology and ecosystems science

Historically, population biology and ecosystems science went their separate ways. However, as I have implied earlier in this essay, this is no longer acceptable, if it ever was. Sustainable management requires that we relate the macroscopic features of communities and ecosystems to the microscopic details of individuals and populations. What maintains the robustness of these macroscopic patterns, such as the cycling of key elements? Over ecological and evolutionary time, how do we explain the regularities we see at the level of ecosystems and the biosphere? What maintains homeostasis? James Lovelock, a highly original and independent scientist, proposed a solution,

which he called the *Gaia Hypothesis* [27]. There are many versions of Gaia, which has gone through a continual evolution of its own, both in Lovelock's writing and in that of others [14]; but the basic idea is that the biota controls the physico-chemical environment at just the right conditions for its survival. In the extreme form of this concept, the biosphere is viewed as a super-organism, selected for its macroscopic properties.

No ecologist would question the basic thesis that the biota affects the physico-chemical environment at various scales; this indeed is the essence of current concerns about the effects of humans on our environment, and in particular anthropogenic changes in land cover and pollution. The problem however is that Gaia describes macroscopic regularities and implies macroscopic regulation; but evolution operates at much lower scales of organization, through selfish competition among genotypes [3], and not for the 'benefit' of the whole system. Ecosystems and the biosphere are complex adaptive systems [23], in which heterogeneous collections of individual units interact locally, and change their genotypes or phenotypes based on the outcomes of those interactions. Patterns emerge, to large extent, from phenomena at much lower levels of organization—those of individual agents, small spatial scales, and short temporal scales—and then feedback to affect the processes on those scales. Hence, we need a theoretical foundation resting on our understanding of the principles of evolution, at the level of genotypes and populations, elucidating the features that underlie the robustness of the goods and services we derive from ecosystems. Lovelock is correct that we need to explain those regularities from an evolutionary perspective, but that explanation must be soundly based in evolutionary principles.

Evolution at the ecosystem level

Marine ecosystems provide an ideal context in which to address the challenges laid out in the preceding section, in part because of the rich theoretical history since Volterra, in part because of the increasing recognition that the management of declining marine resources requires an ecosystem perspective (NAS 1998), and in part because the wealth of data and analyses emerging for marine microbial metagenomics presents unique opportunities beyond what are available in any other ecological system. In marine ecosystems, characteristic regularities include the distributions of phytoplankton, zooplankton and fish at local to global scales; the availability and utilization of nutrients such as C, N and P; and the size-structure spectra across many orders of magnitude [2].

An impressive beginning to explaining the global distribution of phytoplankton has been carried out in the Darwin project [10], which unites ecological models of the oceans with a general circulation model and allows competition to operate to select among a suite of candidate phenotypes. The robustness of the macroscopic features of these systems is then shown to emerge from the microscopic interactions, over ecological and (to some extent) evolutionary time. My research group, led by Michael Raghib-Moreno and Juan Bonachela, has begun a

collaboration with the Follows group and others to embed this approach into an evolutionary framework, in which basic biophysical constraints define the set of feasible phenotypes. An adaptive dynamics approach [5,11] is then used to illuminate how evolution has shaped the assemblages we observe. To illustrate how this framework can help to address such issues, I turn to a simpler but equally important problem, the explanation of the Redfield ratios.

Marine ecosystems exhibit remarkable constancy in element ratios across broad regions, despite the fact that absolute levels may vary considerably. This is true of the water column, of the primary producers and of the consumers of those primary producers. Seventy-five years ago, Albert Redfield [38] noted the constancy of C:N:P ratios in marine organic matter, and the ratios still bear his name. The characteristic ratios are not the same for every species, but averages over species within marine ecosystems show for example the typical 16:1 ratio for N:P. Redfield asked to what extent these ratios simply reflected organismal evolution to element availability as determined by geological phenomena, and to what extent on the other hand the ratios in the water column were controlled by biotic processes, in particular nitrogen fixation. He favored the latter mechanism. Tyrell, Lenton, and others [17,18,42] verified Redfield's intuition that competition between nitrogen-fixing species and other phytoplankton can regulate oceanic N:P ratios to match the N:P requirements of the non-fixers.

The question of what determines these N:P requirements of phytoplankton remained. We [15,16] have used the adaptive dynamic framework to address this issue. Evolution in our approach is entirely at the traditional level of genomes and populations, and the environmental regularities emerge from this process of 'niche construction' [37]. This has echoes of Lovelock's view, but the patterns are shown to be emergent from evolution at the level of individuals and populations rather than representing any sort of selection at the ecosystem level.

The initial approach, which can be extended to an unlimited variety of problems associated with the evolution of ecosystem properties, is to separate time scales, assuming evolution acts slowly to set the parameters that govern different types in competition. On the fast, ecological time scale, a chemostat-like environment is considered, in which a monotypic species with given traits (stoichiometric requirements) reaches equilibrium with the available resources (Fig. 1). The system of equations representing this is shown in Fig. 2, where the equations describe P and N availability in the water column, P and N in storage in the organisms, and organism biomass (B). In this formulation, growth is according to Droop's equation (Droop1977), but limited according to Liebig's law by the nutrient in shortest supply relative to needs, and uptake (f) follows standard formulations.

On this fast, ecological time scale, it may be shown that the system goes to a globally stable equilibrium as nutrients become limiting [4]. Indeed, in general, one nutrient will become limiting first, as in the models of Tilman [43]; which nutrient that will be depends on the external inputs of nutrients, as well as on the trait characteristics (phenotypic parameters) of the biological species—in other words, on its stoichiometric needs.

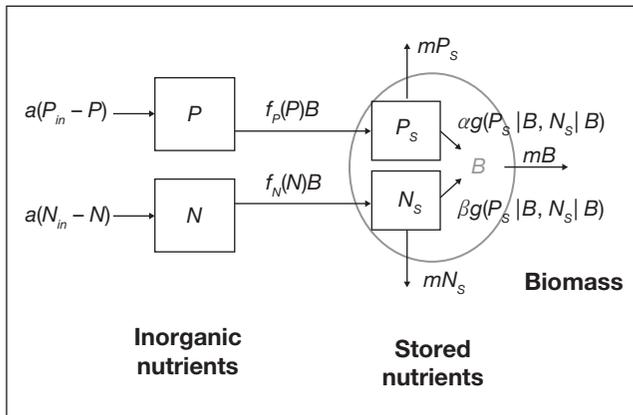


Fig. 1. Schematic for the model of N and P dynamics in marine ecosystems. After [16,17].

So far, I have not discussed the evolutionary time scale at all. Evolution is assumed to occur on longer time scales, as mutation or other diversifying mechanisms, including possible invasion by novel types, introduces a competition among types with different nutrient use ratios, constrained by biophysical tradeoffs. When this is permitted, the system invariably evolves to co-limitation, since any other situation is invasible by types less dependent on the limiting resource. This equilibrium approach provides an answer to what the optimal type will be, but it overestimates the observed N:P ratio. To resolve this dilemma, we recall G.E. Hutchinson's famous discourse on planktonic coexistence [13], in which he emphasized the importance of environmental fluctuations in mediating non-equilibrium coexistence. Hutchinson was focused initially on spatially uniform fluctuations, but coexistence is achieved even more easily in the presence of localized disturbances that create a non-equilibrium spatio-temporal mosaic, in which different regions are in different stages of ecological succession [25,26]. Thus we temporarily abandon the equilibrium constraint, and determine the stoichiometric allocation that will result in maximal growth; the type that grows fastest is one that has a lower N:P ratio, reflecting higher investment in ribosomes [40]. Combining the equilibrium and non-equilibrium approaches then provides a possible explanation both for the observed N:P ratios, as well as for the existence of species with different N:P ratios mentioned earlier; it also addresses a favorite topic of Ramon Margalef, the evolution of successional patterns. In particular, within a spatio-temporal dynamic localized distur-

bances transiently favor species with high investment in ribosomes and hence N:P ratios below Redfield, to be replaced in a successional dynamic by those with higher investment in proteins and hence N:P ratios above Redfield. The overall result is the coexistence of a range of species with N:P ratios neatly bracketing the observed range of N:P requirements, with the canonical Redfield ratio in the middle.

This example is interesting in its own right, since patterns of nutrient use are among the most essential signatures of ecosystem functioning. But more important for the points I want to make in this paper are that the methodology, combining ecological dynamics with evolutionary mechanisms, can be extended to a wide range of problems of interest. Hence, we have also used the approach to examine issues as diverse as seed dispersal [20,21], water uptake in arid environments [44], the evolution of nitrogen fixation [32,33] and the evolution of bacterial quorum sensing [35]. The procedure in all cases is to couple ecological dynamics on fast time scales with evolutionary dynamics on slow time scales in order to search for evolutionarily stable strategies, relaxing the time-scale separation when necessary to deal with transient phenomena. It's important to note that the dynamics may be more complicated than this. Some evolutionarily stable strategies may not actually be reachable in this dynamic. More interestingly, the system can converge to points that are not evolutionarily stable, but rather evolutionary branch points [11,20,21], giving rise to coexistence of strategies and more complicated outcomes. This is a rich area for investigation.

Conclusions and further thoughts

A central problem in achieving sustainability is to understand how to characterize the robustness of the macroscopic properties of ecosystems and the biosphere, in terms of microscopic ecological and evolutionary dynamics mediated at the level of organisms and populations. Ecosystems and the biosphere are complex adaptive systems, whose properties are emergent from interactions on ecological and evolutionary time scales, at organizational levels far below those of the whole systems. The problems encountered in addressing these issues involve public goods and common pool resources, and raise issues of the commons similar to those confronted in economic and social systems. This should not surprise us, because ecological systems are similar to economic systems in that individuals compete for limited resources, exploit others, and form consortia and partnerships.

Adam Smith wrote in 1776 that "By preferring the support of domestic to that of foreign industry, he intends only his own security; and by directing that industry in such a manner as its produce may be of the greatest value, he intends only his own gain, and he is in this, as in many other cases, led by an invisible hand to promote an end which was no part of his intention. Nor is it always the worse for the society that it was not part of it. By pursuing his own interest he frequently promotes that of the society more effectually than when he really intends to promote it." [39] But the notion of the invisible hand as justification

$$\begin{array}{l}
 \text{Ambient} \left\{ \begin{array}{l} \frac{dP}{dt} = a(P_{in} - P) - f_p(P)B \\ \frac{dN}{dt} = a(N_{in} - N) - f_n(N)B \end{array} \right. \\
 \text{Storage} \left\{ \begin{array}{l} \frac{dP_s}{dt} = Bf_p(P) - \mu \min(P_s/(P_s + \alpha B), N_s/(N_s + \beta B))\alpha B - mP_s \\ \frac{dN_s}{dt} = Bf_n(N) - \mu \cdot \min(P_s/(P_s + \alpha B), N_s/(N_s + \beta B))\beta B - mN_s \end{array} \right. \\
 \text{Biomass} \quad \frac{dB}{dt} = \mu \min(P_s/(P_s + \alpha B), N_s/(N_s + \beta B))B - mB
 \end{array}$$

Fig. 2. Mathematical representation of Fig. 1.

for a pure free market society has been stretched far beyond Adam Smith's original intent. Nobel Laureate Joseph Stiglitz has written that "the reason that the invisible hand often seems invisible is that it is often not there," [41] argues, with others, that Smith was fully cognizant of the limitations of free markets in achieving the common good.

The global economic crisis in recent years has taught us that a pure free-market economy carries dangers for the collective good; the invisible hand of Adam Smith does not protect society. These lessons are magnified for ecological and environmental systems: There is no goddess Gaia to ensure that biospheric evolution will lead to a sustainable future, at least not according to criteria that include the preservation of humanity.

The unification of population biology and ecosystems science means going beyond thinking about ecosystems and the biosphere as if they were evolutionary units, maximizing throughput or stability or some other systemic goal. Rather, they exhibit patterns emergent from processes at much lower levels of organization, and it is the maintenance of such patterns that preserves the goods and services we derive from ecosystems. With the aid of new mathematical approaches and vast new metagenomic data, we have the capacity to study the wide range of ecosystem patterns and processes that characterize the essential features of those systems, and to examine the robustness of those patterns and their role in supporting ecosystem goods and services. I have already mentioned a variety of applications of the approach, from seed dispersal to quorum sensing, from nitrogen fixation to nutrient use. These are all aspects of the biology of ecosystems that involve tradeoffs between individual benefits and the collective good. Other examples abound, including chelation and the production of siderophores, antibiotics and allelochemicals. Before us lie the broader emergent patterns that fascinated Ramon Margalef: the emergence of trophic webs, species diversity relations and successional dynamics.

Chapter 7 of Margalef's unpublished monograph was concerned with ecological succession, and the eighth and last chapter was termed "Evolution in the ecosystem." Near the end of that book, Margalef turns his attention to perhaps the greatest intellectual challenge facing us, understanding cultural evolution, acknowledging the similarities between the mechanisms that produce cultural and genetic evolution. Exploration of cultural evolution, especially the role of social norms in enforcing cooperation, is the next great challenge in achieving a sustainable future [8]; we need to turn these same methodologies to understanding how the social context influences individual behaviors, how that social context emerges from the collective behaviors of large numbers of individuals, and the conditions under which social norms and attitudes can suddenly change. In particular, we need to apply this thinking to address human patterns of consumption, and the achievement of cooperation in dealing with global environmental problems.

By marrying theory and empirical work, we can elucidate the patterns of key macroscopic measures within ecosystems, develop explanations of variation in those patterns, and devel-

op predictive models of responses to changing environments. Beyond that, we need to bridge the gaps across scales, from the ecological to the evolutionary, from the physical and biological to the cultural and ethical. Ultimately, only by providing such linkages between the microscopic and the macroscopic can we further the science needed to achieve a sustainable future.

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Professor Simon A. Levin, recipient of the Ramon Margalef Prize in Ecology 2010, pronounced the lecture entitled "Evolution at the ecosystem level: On the evolution of ecosystem patterns" at the Scientific Forum "How do evolutionary processes shape ecosystem patterns and why do ecosystems constrain them?", on 6 October 2010 in Barcelona.



The Autonomous Government of Catalonia created the Ramon Margalef Prize in Ecology to honor the memory of the Catalan scientist Ramon Margalef (1919–2004), one of the main thinkers and scholars of ecology as a holistic science, and whose contribution was decisive to the creation of modern ecology. This international award recognizes those people around the world who have also made outstanding contributions to the development of ecological science. More information: www.gencat.cat/premiramon-margalef.

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