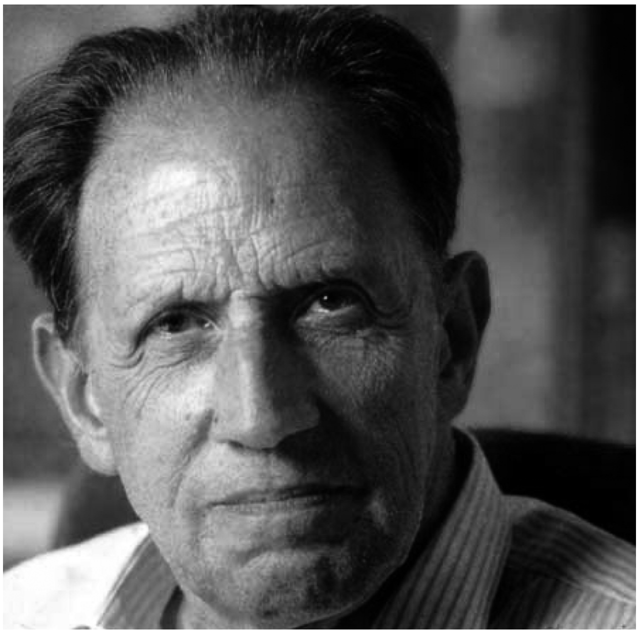
CONTRIBUTIONS to SCIENCE, **3** (2): 297–317 (2006)
Institut d'Estudis Catalans, Barcelona
DOI: 10.2436/20.7010.01.10 ISSN: 1575-6343 **www.cat-science.com**

biography and bibliography



Professor RAMON MARGALEF (1919–2004)*

Ramon Margalef, Professor Emeritus of Ecology of the University of Barcelona, Catalonia, and member for the Institute for Catalan Studies, passed away at age 85 on May 23, 2004. Margalef was the most important Catalan and Spanish limnologist, marine biologist, and ecologist of the twentieth century. He was a pioneer and outstanding researcher in these fields; and he contributed greatly to many branches of science, ranging from limnology and biological oceanography to theoretical ecology. Margalef has left us an enormous body of scientific literature, consisting of more than 400 published scientific papers and 20 scientific books. Even though not all of his papers were published in journals included in the Science Citation Index, for many years he was the most frequently cited Spanish scientist. In a list of 95 investigators from around the world, Margalef was considered to be one of the three most outstanding Spanish life scientists –the other two being Nobel Prize winners Santiago Ramón y Cajal (1852–1934) and Severo Ochoa (1905–1993). Margalef's book *Perspectives in Ecological Theory* (1968) and his articles "On certain unifying principles in ecology" (1963), "Life-forms of phytoplankton as survival alternatives in an unstable environment" (1978), and "From hydrodynamic processes to structure (information) and from information to process" (1985) are classics regarding their citations by other authors. In particular, "On certain unifying principles in ecology" is considered to be among the top ten articles of twentieth-century biology.

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A naturalist in the difficult post-war Spain

Ramon Margalef was born in Barcelona in 1919, and as a youth, as he later wrote, "lost time in Trade School and other foolishnesses". He studied French, German, and mathematics, but soon thereafter he became interested in natural history and biology, especially with respect to aquatic environments. The Spanish Civil War interrupted his education and in 1938, while he was still a teenager, he was recruited into the Republican army. At the end of the war, he was forced by the new government to serve an extended three-year-period in the military. Afterwards, he worked as a clerk at an insurance company while continuing his research on Iberian aquatic ecosystems as a student at the Botanical Institute of Barcelona. His training was mostly autodidactic. He read everything he could find on biology, physics, and other fields of science, which equipped him with an encyclopedic amount of knowledge. Margalef's earliest scientific publications, which date back to 1943, quickly established his talent and won him a scholarship, which allowed him to obtain a degree in Biology. In 1951, he defended his doctoral thesis on the "Temperature and morphology of living beings", which addressed many questions that nowadays continue to be asked and which interested Margalef all his life.

It is well-known that, in the 1940s, Margalef built his own microscope with an assortment of parts that he had bought at flea markets. What is not so well-known, however, is that, over the years, he also constructed several other instruments in order to automatically obtain plankton samples, mimic natural conditions in the laboratory, or automatically process data from his experiments. He applied to ecology what had once been said about physics: “The good ecologist should be able to screw down screws with a hammer and to sink nails with a screwdriver.” Proof of the high quality of his inventions (actual prototypes that were later modified and improved) was the fact that, for many years, the US government gave him –literally– a blank check to construct any kind of mechanical or electronic instrument he needed, devices that his colleagues referred to as “rain-making machines”.

During that early period, Margalef was an indefatigable researcher. Not only was he an outstanding naturalist, he was also capable of making connections between very diverse aspects of biology, geology, physics, and chemistry. It was obvious that he had a rare kind of intelligence, and that his knowledge exceeded by far that of his colleagues. Other scientists in higher positions were aware of the excellence of Margalef’s work and helped him to pursue his career. He often mentioned the German amateur naturalist Karl Faust (1874–1952), a businessman who settled in Catalonia in 1898 and who founded the Marimurtra Botanical Gardens in Blanes, Costa Brava; the eminent botanist Pius Font Quer (1888–1964); the zoologist Francisco García del Cid (1897–1965), the first director –from 1951 until his death– of the Institute for Fisheries Research; and Miquel Massutí Alzamora (1902–1950). All three offered him scholarships or helped him in his early research efforts.

After World War II, Margalef met with an American talent scout who had come to Spain in search of gifted scientists. This meeting proved to be crucial for Margalef. The American offered him the opportunity of unlimited travel throughout the United States and to other countries. Margalef took advantage of the offer to visit numerous research centers and to participate in many scientific meetings. Subsequently, several American universities encouraged him to move to the United States with his family, an invitation he would have accepted gladly in order to leave post-war Spain, which he considered to be a “shrunken society” with respect to science. Nevertheless, the opinion of his wife –Maria Mir, also a biologist, whom he had married in 1952 and who died just a week after her husband– prevailed. She was from Majorca and had strong personal ties to the island; for her, the United States was too far away from her homeland.

In 1950, Margalef began working at the Institute for Fisheries Research (Institut d’Investigacions Pesqueres, IIP, currently the Institute for Marine Sciences), a division of the Spanish Research Council (CSIC), of which he was appointed director in 1966. Margalef promoted oceanographic research and the Institute, which previously had focused its efforts mainly on fisheries, soon became a center of excellence in oceanography. He also converted the journal *Investigación Pesquera [Research in Fisheries]* into a prestigious journal of Spanish marine science. Similarly, his works on limnology, which appeared mainly in *Publicaciones del Instituto de Biología Aplicada [Publications of the Applied Biology Institute]*, bestowed on that journal an international reputation. When, in 1967, he was appointed to Spain’s first Chair in Ecology, at the University of Barcelona, he resigned his post at the IIP.

World renowned ecologist

At the University, Margalef established the Department of Ecology and trained several generations of ecologists, limnologists, and oceanographers. After two decades of a fruitful academic career, he retired and was appointed Emeritus Professor. Without the time-consuming commitments of teaching and active research, he generously shared his knowledge with colleagues and friends until shortly before his death.

Margalef trained hundreds of scientists in the classroom, in the laboratory, in the field, and at sea, lecturing them and carrying out joint research not only at the University of Barcelona and the Institute for Fisheries Research but also at other centers around the world. From 1971 to 2001, he directed around 40 doctoral theses, a number that does not do justice to his generosity, enthusiasm, and kindness when giving advice or suggesting methods to tackle difficult problems or the study of unexplored fields of science. Both young researchers and those not so young, who over half a century were fortunate enough to benefit from his guidance, will surely always remember Margalef’s unique approach to teaching and research.

The following wonderful definition of scientific research was written by Margalef (1981a; my translation):

> *Research should make knowledge advance over a wide field. It is exploration, play, and reflection at the same time, applied to every point of warp and weft. The research that I think about so often now could be applied either to improve the production of buttons or of a water purifier, to synthesize a new chemical compound, or to discover new relationships between natural phenomena or human activities, providing us in the process with newer, more succinct, and more generalized descriptions than we have had so far. This is a not totally unpredictable adventure, rarely for free yet positively addictive.*

A prolific author, with good command of half a dozen languages, throughout his life Margalef read thousands of scientific books, but he had a notable literary knowledge, too, especially of the classics. He also used his own books, which conveyed his ideas about the biosphere’s organization and functioning, to teach university students and society in general.

Two remarkable and thorough university textbooks written in Spanish by Margalef deserve special mention: *Ecología* (1974) and *Limnología* (1983). For many years, *Ecología* was considered to be the best book on this field of science ever written in any language. Margalef updated the ideas contained in that book in later works: *La Biosfera: Entre la termodinámica y el juego* [*The biosphere: Between thermodynamics and game*, 1980], *Teoría de los sistemas ecológicos* [*Theory of ecological systems*, 1991], *Oblik Biosfer* (in Russian; *A view of the biosphere*, 1992) and *Our biosphere* (1997). Margalef was also author and editor of many monographs, including *Introducción al estudio del plancton marino* [*Introduction to the study of marine plankton*, 1950], *Los crustáceos de las aguas continentales ibéricas* [*Crustaceans from Iberian freshwaters*, 1953], *Los organismos indicadores en la limnología* [*Indicator *organisms in limnology*, 1955], *Comunidades naturales* [*Natural communities*, 1962], *Ecología marina* [*Marine ecology*, 1967], and *The Western Mediterranean* (1985).

Margalef was also a great popularizer of ecology. Among his books aimed at general audiences, a few must be mentioned: *Ecología* [*Ecology*, 1981], which continues to be a bestseller; *L'Ecologia* [*Ecology*, 1985], published in Catalan on the occasion of a related exhibit in Barcelona; and *Planeta azul, planeta verde* [*Blue planet, green planet*, 1992]. He was also a frequent contributor to several encyclopedias of natural history, especially *Història natural dels Països Catalans* [in Catalan; *Natural history of the Catalan Countries*, 1984-1992] and *Biosfera* (first published in Catalan, later translated into Japanese and English; *Biosphere*, 1993–1998).

Margalef received numerous and significant awards for his research and teaching activities, including the following:

- Prince Albert I Medal, from the Oceanographic Institute of Paris (1972)
- A. G. Huntsman Award, from the Bedford Institute of Oceanography (Canada, 1980)
- Narcís Monturiol Medal Award of the Autonomous Government of Catalonia for Science and Technology (1983)
- Santiago Ramón y Cajal Prize, of the Spanish Ministry of Education and Science (1984)
- Naumann-Thienemann Medal, of the International Association of Theoretical and Applied Limnology (Societas Internationalis Limnologiae, SIL) (1989)
- Italgas Prize for Environmental Sciences (Italy, 1989)
- Catalan Foundation for Research Prize (1990)
- Alexander von Humboldt Award (Germany, 1990)
- Knight Commander of the Order of Alfonso X the Wise (Spain, 1990)
- International Prize San Francesco d'Assisi for the Environment (Italy, 1993)
- International Ecology Institute Prize, from the Ecological Institute (Germany, 1997)
- Cross of Sant Jordi Award of the Autonomous Government of Catalonia (1997)
- Honorary Forestry Engineer of the Polytechnical University of Madrid (1998)
- Rainier III of Monaco Prize (1998)
- ASLO Lifetime Achievement Award (2000)
- Spanish Council for Research (CSIC) Gold Medal Award (2002)
- Autonomous Government of Catalonia Gold Medal Award (2003)
- National Award for Environmental Sciences of the Autonomous Government of Catalonia (2004, posthumous).

Margalef was a member of several scientific academies in Spain and abroad, the National Academy of Sciences of the USA among them. In addition, he was an honorary member of several scientific societies around the world and was awarded Honoris Causa doctorates from several universities: Université d'Aix-Marseille, France (1973), Sarrià Chemical Institute of the University Ramon Llull, Barcelona (1983), Université Laval, Quebec, Canada (1987), University of Luján, Argentina (1994), and University of Alicante, Spain (1999).

In science, receiving so many international awards is somewhat unusual. It is even more unusual that professional recognition continues over half a century. Margalef's article "The theory of information in ecology" (1957, originally written in Spanish) was his introductory lecture as a new member of the Barcelona Royal Academy of Sciences and Arts (later published in its *Proceedings*) but it eventually reached a worldwide audience. In that article, Margalef suggested that the theory of information should also be applied to the study of species diversity in ecosystems. Due to the novelty of Margalef's approach, the article was translated into English and published in the journal *General Systems* (1958). At the time, ecology was still a young science, lacking both a theoretical reference frame and a corpus of stable paradigms comparable to those in other scientific fields. Margalef's 1958 paper, along with the article "On certain unifying principles in ecology" (1963) and the small book *Perspectives in Ecological Theory* (1968), which was translated into several languages, offered new and appealing ways of understanding ecology.

Margalef based his theoretical approach, which was holistic and integrative, on his extensive knowledge of aquatic ecosystems, which he had studied first as a naturalist, applying a botanical, zoological, and phytosociological perspective. Later, "tired of making lists [of species] to characterize different types of ecosystems", he took a more general approach and gathered information about the structure and workings of the biosphere, which he considered "a multishaped cover of life above some heterogeneous spaces that were also the matrix for evolution, and that were influenced by evolution itself in a feedback" (Margalef, 2004).

The International Society of Limnology awarded Margalef the Naumann-Thienemann Medal for "having shared his creative talents of discoveries, intuition, and synthesis of the ecological foundations of the limnological phenomena, and for his influence in the Hispanic world." Margalef, working on his own, set up the basis for studying the regional limnology of the Iberian Peninsula and the Balearic Islands, and later initiated the ecological research on one hundred Spanish reservoirs, which thus far remains the only thorough analyses of this type worldwide.

The study of marine plankton and primary production of the sea soon led Margalef to new quantitative approaches and to apply several new methods of evaluating the populations of microscopic organisms along the water column, such as consideration of species diversity, or other models derived from terrestrial ecology, e.g., the concept of ecological succession. Probably his most outstanding contributions to ecology were recognizing the spatial organization of phytoplankton and the crucial role of auxiliary energy in that structure. Prior to those observations, phytoplankton was considered to be simply a structure-less cell suspension.

Taking into account both space and the role of exosomatic energy in the structuring of biological communities was an approach that Margalef applied not only to the study of plankton, but also to other communities of the biosphere. This mode of thinking had proven to be advantageous in estimating species diversity and the connectance between different nodes of trophic webs. It also enabled him to study the patterns that could be elucidated from an analysis of ecological succession, which he first identified as an evolutionary framework in the development of the ecosystem. From these ideas, an ecological theory emerged that, like everything in science, has been subject to modification, refutation, and evolution. This theory was Margalef's major contribution to ecology as an established scientific discipline. From his first publications on ecological theory until his last book, Margalef's role in furthering our understanding of the functioning of the biosphere has been acknowledged internationally. In 1988, the National Science Foundation recognized Margalef's research on the dynamics of marine phytoplankton, which he carried out during the 1960s and 1970s, and declared that his work on these subjects had been several decades in advance and had provided the foundations for subsequent biological research in that field. Indeed, Margalef is one of the very few scientists who had contributed to both the theoretical and the practical development of a science.

A proper measure of this contribution can be found in the scientific publications of his colleagues, disciples, and friends, who in discussing their own research and expertise recognized their teacher's direct or indirect influence on their work in a series of publications; among others: Ros & Prat (1991), Margalef (1994), Gili *et al*. (2001), Ros *et al.* (2004), Zamora *et a*l. (2005), Armengol (2006).

Margalef excelled not only in the fields of limnology, marine ecology, and theoretical ecology, but also in biogeography, geology, human evolution, and human ecology. Including the human species in his general theory of the biosphere was among his most valuable but least-known contributions to ecology. He also played a major role in the popularization of ecology; as mentioned above, he wrote several popular-science books, was the author or editor of several encyclopedias, and participated in creating exhibitions aimed at the general public. In one of his articles advocating changes in the teaching of natural science, he stressed the importance of conveying the "simple facts about life and the environment not to forget in preparing schoolbooks for our grandchildren." (Margalef, 1984)

Natural-born teacher

Margalef was a natural-born teacher who captivated his students and conveyed a sense of enthusiasm concerning the field of ecology, at a time when it was still an elective subject in Spanish universities, just as limnology, marine biology, and other subjects often are now. Long before he was appointed to the Chair in Ecology, Margalef taught a wide range of university courses on disciplines belonging to his specialty. For example, in 1955, he lectured on Animal Ecology, Oceanography, and Marine Biology at the University of Barcelona and at other universities and research centers, especially in the United States. The level of these early courses was such that from them he obtained the material needed to prepare *Perspectives in Ecological Theory, Comunidades Naturales*, and *Ecología Marina*, all of which later became references in the ecological sciences. Later on, as the holder of a university chair, he wrote two manuals, *Ecology* and *Limnology*, as well as other undergraduate-oriented university texts (although recent generations prefer the more popularized, aforementioned ones).

Sometimes, Margalef's didactic contributions were more specialized, such as his discussion of the dynamics of exploited marine communities or his methods for carrying out oceanographic research, phytoplankton sampling, single-cell algae cultivation in the laboratory, the extraction of plant pigments, etc. (see his annexed Bibliography). Nonetheless, he was often reluctant to explicitly assume credit for his ideas.

For example, in the Foreword of a textbook on practical field and laboratory ecological work of which I was the editor (Ros, 1979), there is this explicit acknowledgment:

> *In his role as author of the course program, the head of the Ecology Department of the Barcelona University [Margalef] has […]designed these practical exercises and others; thus one can say that only formally, but not really, the textbook authors [half a dozen contributors, but not Margalef] are the practical exercises authors.*

I studied ecology as an elective subject as part of a degree in Biology during 1966–1967, immediately after Margalef had taught a course at the University of Chicago that provided the basis for *Perspectives in Ecological Theory*. The importance of this small book to modern ecology is inversely proportional to its mere one hundred pages, similar to the importance of Schrödinger's seminal but brief book, *What Is Life?* had for biology. Forty years ago, around the time Margalef was appointed director of the Institute for Fisheries Research (IIP), he taught a course in ecology that included trips to the IIP. These were extremely interesting tours that made us forget, at least for a couple of hours, the inflexibility of the classroom, and they allowed us to observe the laboratories where Margalef and other wise men carried out research in oceanographic science –an experience that would mark us for life.

I would like to share an anecdote that exemplifies both the state of Biology in Spain in the 1960s and what Margalef's classes were like. My classmates and I devised a system to make up for the lack of textbooks for most of the subjects we studied (a situation that has now inverted itself completely: there is a huge number of books available, in languages that are accessible to the students… who tend not to use them!). Some of us undertook the task of taking notes from courses in the different subjects, which we would then carefully prepare, reproduce, and exchange in different installments. Josep Maria Camarasa, who was in charge of taking notes for Ecology during the academic year of 1967–1968 (the last year before the completion of our degree), wrote in the prologue of his volume about the difficulties he faced in taking notes in Margalef's class, and even the few that he managed were difficult to understand.

Margalef was an atypical professor, or at least that is how he seemed to us. Even if he claimed to follow a detailed and explicit syllabus, he would often jump from one topic to another, making connections between topics that did not always seem to be related to the subject at hand. He rarely made use of the blackboard, and when he did it was in a way that did not allow us to take notes. In a typical episode, which I observed at least a hundred times, Margalef would explain something interesting and turn around to write it on the board, but he would do it at chest height and in such small handwriting that nobody could see a thing. We would wait for him to move over…to no avail! When he finally did move, his tiny hieroglyphics nonetheless remained covered or were erased while he continued with his explanation, but before we managed to copy anything down. While this was utterly exasperating for his students, at the same time it motivated us to search everywhere for ways to complement the subject. As a result, Margalef forced us into the habit of reading, not only about ecology but other subjects as well, from physics to scientific assay, from geology to statistics.

Margalef's autodidactic training as well as his scientific "wanderings" surely accounted for his ability to synthesize information regarding the workings of nature, and they resulted in a valuable legacy for his pupils: he was one of the driving forces –firstly– and an academic accountable –secondly– for the formation of the Seminar in Biology, the seed that would become the Library of the Faculty of Biology. He dedicated particular effort to establishing and funding the library for the Department of Ecology, which for decades remained one of the best ones in the Catalan universities and which also included many books on fields different to ecology. The reason for this broad-range approach is to be found in Margalef's own words (my translation):

> *I would wish that people read more, that better libraries were available and that students had a wider knowledge of languages […] Catalonia does not possess scientific bibliographical resources that are minimally adequate and modern IT techniques cannot replace the inspiring power of a book – I dare say of bone and flesh– on your lap…(Margalef, 1981a).*

This interest in promoting reading among students brings me to another anecdote, also involving an event that took place on several occasions. Sometimes, when the feared final exam arrived, Margalef would propose that, instead of writing it in one of the classrooms, it should be written in the library, where students could have free access to all the books they might need in order to answer the questions. This allowed Margalef to easily identify those who were used to looking up information and who knew where to find the answers. The "more typical" exams also did not escape from some amount of geniality, which was not always welcome by the frightened students. Once, for example, Margalef told his students to write down the question that *they* would like to answer (interestingly enough, the number of people who failed was not any lower than on other occasions). Another time, the entire exam consisted of one question: "What is Ecology?"

During his active life, practically until a month before his death, Margalef was frequently consulted and sought after for information, not only by his students but also by other professors and researchers, including those from seemingly distant professional disciplines, such as economics, geology, physics, and chemistry. His answer to most of their inquiries would always begin the same way: "I don't know much about that, but…", and then would come the treasure the person had been looking forward to: the last relevant bibliographic reference, the address of a researcher who was working on that subject, Margalef's thoughts on an area supposedly marginal to his scientific interests, and a series of research suggestions to help resolve the problem at hand as well as other, related ones that the inquirer probably had not stopped to think about. Part of this unique ability is reflected in his bibliography: most of his more than 400 scientific articles and books are about ecology, limnology, and marine biology, but his contributions to biogeography, micropaleontology, human ecology, and evolutionary biology are not scarce either.

Margalef was the living example that in order to be a good teacher it is necessary to be a good researcher, as he pointed out more than once (my translation):

> *A succession of teachers, teaching one another, who lack adequate contact with the outside world, produces a huge bubble without any content other than everyone's frustrations. Research is essential so that knowledge doesn't degrade and so that we remain eager to confer some novelty to our lessons. You don't replevy this research; you'd do it so far as the possibilities allow it to. (Margalef, 1981a).*

He contributed, as very few others, to building the scientific field that he taught, and he knew personally those scientists who during the second half of the 20th century shaped ecology, limnology, and oceanography. This direct relation to the protagonists of the history of these sciences (G. Evelyn Hutchinson, Robert H. McArthur, the brothers Eugene P. and Howard T. Odum, Josias Braun-Blanquet, to name a few) bestowed Margalef's classes with an extraordinary liveliness.

In the following texts, Margalef explained his view of the time he spent at the university (my translation):

> *[In] University […] I've spent half my life […] the truth is I have invested a lot of effort and enthusiasm, but it is also true that a considerable portion of my life at the university passed during relatively difficult or unsettled times, in which hardly favorable political conditions, a succession of different chancellors –some very good, others not so– and an administration that did not always make available the resources that had been granted to me were combined. There were also periods of turbulence and even rough conflict, but it is my duty to add that none of them was seriously detrimental to education…* (Margalef, 2004).
>
> *This text […] tries to collect the essential materials to construct the basis of ecology, with a certain amount of systematization and with the presentation of numerous examples […] It should be also added that the random character that university life has acquired during these last few years [he*

refered to years of political and social strife in Spain's campuses and to the endless strikes both by students and professors] makes one believe that a text can facilitate the continuity of studies (Margalef, 1974).

As much in my own investigations as in stimulating those of my students, I've tried to do what I could; I have good memories, but am not completely satisfied with the obtained results. I would lie if I said that they weren't worth the dedicated effort… (Margalef, 2004).

Margalef, *Gedankenexperimentator*

Much like other geniuses, Margalef excelled in proposing *Gedankenexperimenten*, in the style of "What would happen if….?" This allowed in-depth examination of many aspects of science that were not generally subject to actual experimentation. Despite the fact that some of these thought experiments seemed to border on science fiction, Margalef managed to exploit and convert them into classics of ecological theory, and some of them later became the basis of more formal studies.

One of the classic theoretical questions that Margalef posed had to do with the standard definition of the biosphere. Why is the biosphere a discontinuous, fragmented layer of many different organisms instead of a thin, giant amoeba that extends itself over land and water? The upper, autotrophic layer of this superorganism would be separated by just a few millimeters from the lower, heterotrophic one, the necessary width for the difference in redox potential that would allow production and respiration. That way, problems arising due to the huge distance that separates these processes in the ocean (see below) would not exist. But the physiological strain that a living layer with these features would endure –considering all the different environmental habitats over which it would extend– would be enormous and would, in turn, provoke its fragmentation into smaller units, each of which would be adapted to its immediate surrounding; in other words, this would give rise to the individuals of the different species that exist today. This monospecific, monoindividual, undiversified and thus seemingly impossible biosphere would be very efficient at photosynthesis, in the same way that biofilms and stromatolites are.

Of the many *Gedankenexperimenten* that Margalef suggested, I will only mention a few, with emphasis on two of them: the superprudent predator and the connectivity between elements of working systems.

The superprudent predator

There are many analogies about the functioning of a forest and of plankton –paradigms, respectively, of terrestrial and aquatic ecosystems. Both are organized in vertical columns that measure tens of meters in the forest and hundreds of meters in the water. Production (P) is quartered in the upper, illuminated part of each column, and respiration (R) occurs all along the column but is concentrated in the lower, darker part of it, with a clear inversion of the relationship between these processes regarding the extension of each system: P/R is in the order of 40/1 on land and 1/40 at sea, which corresponds to an average 80 m of trees' height for every 2 m of soil depth and around 100-m depth of the photic layer vs. the 3900 m of the aphotic one (which is also related to the slowness with which nutrients cycle in the ocean). There are also similarities regarding the proportion of the ocean surface that upwelling areas occupy in relation to the total ocean surface, and of the amount of total active xylem compared to the whole trunk surface area –less than 1‰ in both cases.

Nonetheless, the fundamental difference between the dynamics of primary production in the forest and those of planktonic ecosystems lies in the return of nutrients from the darker zone to the illuminated one: this process is carried out by the component organisms in the former and by physical forces in the latter. In both cases, gravity mediates the first stretch of the route, in the falling of leaves from the trees and the sinking of the corpses and dead cells of plankton, from the center of gravity of P to that of R. Yet, evolution has taken place in a way such that, on land, plants are responsible for the second part of the process, i.e., the ascent of nutrients from the level where R predominates to the one where P is possible. In fact, a tree can be considered as a machine that sucks water from the earth through evapotranspiration in the leaves and the conduction of sap through the xylem. This is the evolutionary response to the necessity of extracting nutrients from the soil and transporting them to the treetops. This is not possible in the ocean, where the huge distance between the surface and the seafloor –an average of 4 km– does not allow the development of any organism large enough to return the nutrients needed for primary production to the photic layer. Or does it? This was the big question that Margalef considered: did an organism that carried out the role of the tree ever exist in the ocean?

Concerning the aforementioned problem of distance, the tree's "altruistic" behavior has to be taken into account: the tree profits directly from the transport of nutrients it carries out, making it easy to see why evolution operated in this direction. Yet the theoretical marine organism imagined by Margalef would only benefit in a very indirect way from its activity: its fostering of primary production in the ocean would only prove beneficial to it after several trophic levels (at least two, if the organism was a carnivore).

In an analogy to Slobodkin's "prudent predator" –the carnivore that correctly manages its prey, preferentially eliminating old and sick animals from the prey population, thus obtaining a maximum sustainable return and, in turn, contributing to the adaptive evolution of its prey– a model that has many examples in nature, Margalef described his altruistic organism as a "superprudent predator".

Which candidate organisms in the sea fit this label? Margalef proposed a few possible ones; however, as with many of his incursions into theoretical ecology, his ideas were taken over and investigated by others, since interest in this line of research was not merely theoretical: the superprudent predator would also contribute to the biological carbon pump, with implications regarding the carbon equilibrium in water, the atmosphere, and its role in global climate change. What follows is a summary of the results obtained thus far.

The main candidates for the superprudent predator are: (a) big marine animals (whales, seals, fish, squids, etc.); (b) planktonic larvae of benthic or pelagic animals (with planktotrophic or lecitotrophic development); (c) planktonic organisms performing vertical migrations (especially copepods and krill); (d) planktonic organisms that package their excreta so that they sink or rise faster (especially copepods, appendicularians, and salps); and (e) marine organisms with horizontal migrations.

Big marine animals
Cetaceans, particularly sperm whales, and seals, who eat at depths of 200–1000 m and more and then come back to the surface to breath, would appear to be the ideal superprudent predator. In fact, they are unlikely prospects, since in order to rise from these great depths, they must get rid of a volume of feces that is almost equivalent to that of their ingestion of squid, fish, and other prey. Gray whales and walruses, by contrast, feed on amphipods and other benthic invertebrates through huge "bites" into the mud deposits of the ocean floor where these animals live, at depths from 100 to 200 m. In doing so, these animals raise immense sediment clouds that "fertilize" surface waters.

Planktonic larvae of benthic or pelagic animals
Around 80 % of pelagic and benthic marine animals have larvae whose development is either planktotrophic (they live a long time in the open ocean feeding on plankton) or lecitotrophic (they live a short while as plankters, but feed on their own yolk). It is tempting to propose that this movement from the habitat of the adult to the more superficial one of its larvae would provoke a net, upward transfer of organic matter, but it is quickly understood that the actual transport of organic matter is in fact downward. In the few cases in which the balance between the export of biomass (in the form of eggs or larvae) and its import (as juveniles who return to the adult habitat) has been evaluated, the results always favor importation: the animals send their larvae to nurse in surface waters, which are richer in nutrients and food, and the biomass of incoming juveniles exceeds that of outcoming larvae. Otherwise, it is improbable that evolution would have conserved such a generalized and complex mechanism.

Planktonic organisms with vertical migrations
As in the previous example, the supposed trophic benefit obtained from the vertical migration of planktonic organisms, such as copepods and krill, would not exist if the net flux of energy was upwards. Neither the migrating plankters nor the different species that together form what is known as the plankton ladder are therefore superprudent predators; rather, they are temporary exploiters of food resources, the more abundant as more superficial, and collaborators of the direct (top-down) functioning of the biological carbon pump.

Transport through fecal pellets
Many planktonic animals, especially copepods, appendicularians, and salps, that feed by filtering bacteria, phytoplankton cells, and other organic particles from their surrounding water package their excretory products with mucilage, increasing their density so that they sink faster. Other species package them with waxes, causing the fecal pellets to surface. Both methods achieve the desired effect of making the fecal matter disappear quickly from the animals' surroundings, thus avoiding the energy waste the filtration of already processed material would mean. Since the fecal pellets that rise to the surface return to it a small proportion of the nutrients that continuously sink due to gravity, the animals that produce them fulfill the requirement of superprudent predators. However, as will be shown below, animals that pack their feces in mucilage, thus sending them to greater depths, do so as well.

Animals with horizontal migrations
Many planktonic animals –passively– and pelagic and benthic ones –actively– have seasonal migrations between productive areas, where they feed, and other areas, where they live and reproduce. This causes a horizontal redistribution of oceanic production.

Besides these examples (walruses, gray whales, plankters that pack their feces in waxes), there are no organisms that directly return the organic matter that the ocean's surface loses continuously through sinking, impoverishing it in nutrients. Therefore, there are no altruistic superprudent predators in the sea. Nevertheless, there are species that introduce organic matter into the first part of the physical circuit (sinking due to gravity), packing it to accelerate the process, thereby enabling a faster return of nutrients to the photic layer (by means of the second part of this circuit, upwelling systems, fronts, tides, etc.), and redistributing the surface production by means of horizontal migrations.

Actually, this is what happens in terrestrial habitats: plants, which were described above as perfect nutrient-transporting machines, in fact profit from the physical mechanisms of heating, water evaporation, capillarity, etc. The same can be said for marine animals: they inject organic matter into that endless conveyor belt of water sinking-deep circulation-upwelling–surface circulation in the oceans, thus participating passively in the cycling of nutrients. If they did this actively, if they were authentic superprudent predators, they would require an external source of energy, and in doing so would violate the basic laws of physics.

Regularities in the composition of working systems, and other fields of interest

The study of the distribution of species' abundance and diversity within a community was one of the aspects of theoretical ecology in which Margalef left an important legacy. His contributions are not limited, as is usually thought, to the adoption of the Shannon–Wiener index, borrowed from the theory of information, or to the design of his own indexes –all of which he applied to analyze the thousands of samples of phytoplankton that he identified and quantified during his life (see Margalef, 1997)– but include the interpretation of diversity as a measure of structure, maturity, and biological wealth (currently known as biodiversity) of natural as well as artificial systems.

Margalef was also deeply interested in the diversity and connectance of functional, artificial systems. He directed two degree theses that analyzed this diversity and connectance in relation to the mechanical components of functional "Meccano" models, such as mills, looms, and automobiles (Marrasé, 1981), and of electronic circuits (e.g., amplifiers, audio compressors, receivers, transmitters) used in the construction of electronic devices (e.g., radio or television sets; Gutiérrez, 1981). The results not only demonstrated a substantial similarity between the natural and artificial systems, but also an inverse relationship between diversity and connectivity: the more elements (species, "Meccano" pieces, electrical and electronic components) a functional system has, the less related or interconnected they are. Connectivity in very diverse ecosystems, such as tropical rainforest or coral reefs, is extremely low (Margalef & Gutiérrez, 1983). The premise works the other way around as well: the fewer elements there are, the greater their interconnectivity. An electronic device cannot have all of its components connected (it would produce a short-circuit), nor can mechanical models (they would not move) or ecosystems, unless they are made up of such a small number of elements –the arctic tundra, cave faunas, or microcosms to name a few– that mutual dependence is an absolute necessity.

Problems from fields somewhat different than ecology were also the focus of Margalef's attention. He argued, for example, that the great transition between the Cretaceous period of the Mesozoic Era and the Tertiary period of the Cenozoic era (K-T), and the mass extinction that followed it, may not have been caused by the impact of a huge meteorite –the most accepted theory nowadays– but by the sudden release of an enormous amount of gases, mostly CO_2, from the oceans after millions of years of influx of organic matter from superficial and more productive waters and from deep anoxic waters that were maintained by a system of currents different from the present one. Recent episodes in African lakes, which have been accompanied by huge mortality rates among both people and animals, make this relatively rapid release of CO_2 into the atmosphere plausible –like a giant champagne bottle that is suddenly uncorked.

Two questions that interested Ramon Margalef during his last years and which he –had his health allowed him to– would have surely answered were what could be called "The flies of the 2, the 4, and the 8" and the "Topological inversion of landscape".

Shoes, nails, and envelopes, among other human-made objects, are not found in all the possible range of sizes: we have standardized them to specific ones instead. The same happens in nature, and we long ago established that different but related species, with a similar ecological role, are separated by certain differences in size. What was not so obvious was that some of these species of "standard" size appear to have a number of cells (in the wings of flies and butterflies, where they can be easily counted; in the body of some invertebrates; and in other meristic characters of plants and animals) that is the second, third, or fourth power of the number of cells of the smallest species: a species of fly for example has n cells, the species that follows it in size has n^2 cells, the next one n^3 cells, etc. To discover whether this was a generalized situation, which developmental mechanisms were behind it, and what significance it had in evolution were some of the challenges that excited Margalef's curiosity.

The "inversion of the dynamic topology of landscape" is the transformation having taken place on any western country: previously a natural territory, scarcely transited and dotted with just a few urban settlements, is now a *totum revolutum*, crammed with cities and speedways where all types of vehicles and information travel and where nature hardly survives among cropland, mining and industrial areas, wasteland and other landscape-altering attacks it suffers from our species. Margalef was particularly interested in how the flux of information is affected by this inversion: How do the frontiers between the natural, mature blocks and the more artificial, active ones behave? How are matter, energy, and information exchanged? In pondering these questions Margalef attempted to identify the scientific essence underlying that which may be obvious to a naturalist or a city planner –the holistic approximation of the phenomenon at hand.

These are examples of how the functioning of the world can be approached from a naturalistic attitude, through curiosity (generalized, panoptic, constant, and childlike), love for that which is being studied, and interest for the connections between different natural phenomena. Ramon Margalef contributed enormously to the task of solving many of life's mysteries, and he did it, as Valiela (1994) observed, because "his ideas made us think, something enviable for any scientist".

Epilogue

Ramon Margalef was an exemplary teacher and man of science, honored by the University of Barcelona, the various academies of which he was a member, the numerous research centers and universities that awarded him distinctions, and his country.

Margalef contributed remarkably to ecology, limnology, and oceanography, but liked to think of himself as a naturalist (Ros, 2004b). He was one of the great minds of the natural sciences and biology –in the tradition of those other great men, such as Darwin, Humboldt, Hutchinson and Mayr, to name only a few. Nonetheless, despite his vast and intense dedication to science, Margalef was not insensitive to worldly affairs:

> *For most topics that concern ecology, I like poets more than lawyers, and feel more inclined to phantasy, feeling and inspiration than to rigor, consistency, and even responsibility. In my views of environmental problems, I feel more attracted by the origin of the troubles and what they tell us about the workings of the biosphere than by their solutions… This is not plain callousness, but concern as to why action accepted as "ecologically correct" should most often contribute to accentuating the inequality of the opportunities available to mankind.* (Margalef, 1997).

The cover of one of Margalef's books (Margalef, 1992a) reproduces a fragment of a Catalan tapestry of the sixteenth century, in which a handcuffed elderly man seems to be studying some mollusk shells, unaware of the battle that is taking place around him. In the legend to the cover illustration, the author wrote that "to study biotic diversity in the face of adversity, much courage is needed." Margalef must have been referring to his own difficult first steps as a naturalist after the Spanish Civil War, in an environment that was all but favorable to research, whether in the laboratory or in the field. However, the scene can also be interpreted differently. Naturalists have been criticized for their seemingly exclusive pursuit of their own, highly specialized interests, as well as for being apparently impassive to the usually very distressing events of this world, which they tend to ignore by isolating themselves in the ivory towers of academia. Margalef was not that sort of scientist. He did not ignore his social environment; on the contrary, he applied his knowledge of nature to gain a better understanding of the world that surrounded him.

Stephen Jay Gould used to divide naturalists into two kinds: Galilean (from Galileo Galilei) and Franciscan (from Saint Francis of Assisi; Gould, 1991). Galileans delight in nature's intellectual puzzles, and the quest for explanation and understanding. They do not deny the visceral beauty of the world around them, but take greater pleasure in finding a scientific explanation for its wonders (Gould himself admitted to be an unrepentant Galilean). By contrast, Franciscan naturalists are the poets of nature; they exalt and indulge themselves in the beauty of nature with lyrical descriptions. Edward O. Wilson offered another perspective (Wilson, 1998): the world, in all its multifaceted complexity, can be explained from the same general principles, mainly physical, which can be applied both to science and to humanities. He named consilience the key to a unified understanding of all that surrounds us. A few years ago, I dedicated one of my books (Ros, 1999, 2004a) as follows: "To Ramon Margalef, a Galilean naturalist and a consilient scientist *avant la lettre*".

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