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THÈSE / UNIVERSITÉ DE BRETAGNE OCCIDENTALE
sous le sceau de l'Université Bretagne Loire
pour obtenir le titre de
DOCTEUR DE L'UNIVERSITÉ DE BRETAGNE OCCIDENTALE
Mention : Biologie marine
École Doctorale des Sciences de la Mer

présentée par
J. Coston-Guarini
Préparée à Laboratoire des Sciences de
l'Environnement Marin, IUEM, Plouzané

Epistemic values of historical information in marine ecology and conservation

THIS VERSION DOES NOT INCLUDE DATA APPENDICES

Thèse soutenue le 15 Décembre 2016
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A mon mari, Jean-Marc.

REMERCIEMENTS

This project re-examines the theoretical underpinnings of accepted frameworks in marine ecology.

I ask a simple question: do we need to know the history of ecology to progress?
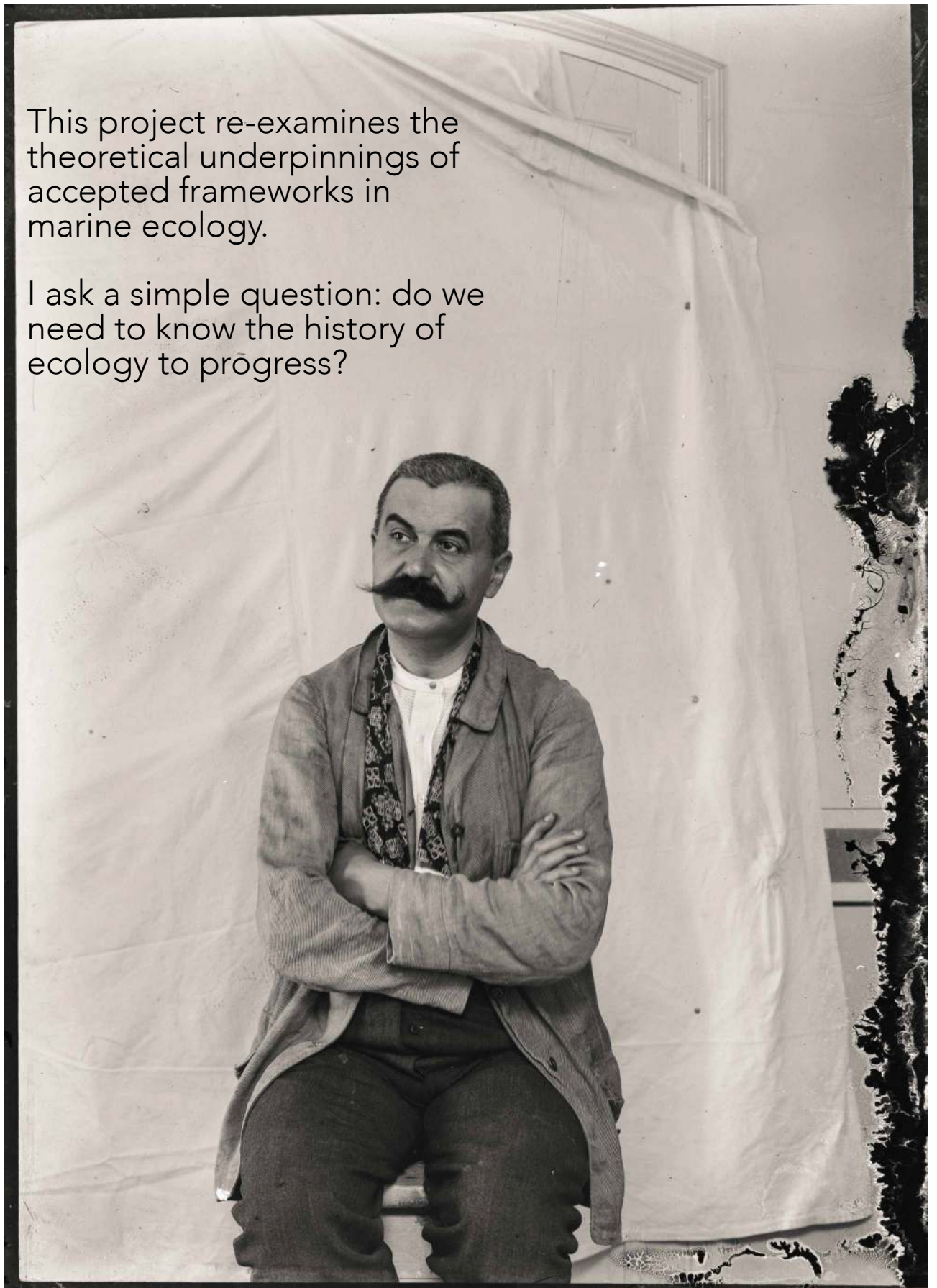
Ecology originated in works by natural historians with extremely wide-ranging interests, like those of the Roumanian marine zoologist, cave biologist, oceanographer and polar explorer, Emil G. Racovitza (1868-1947). Portrait, *ca.* 1910-1920, Banyuls-sur-Mer; glass plate negative; private collection.

EPISTEMIC VALUES OF HISTORICAL INFORMATION IN MARINE ECOLOGY AND CONSERVATION

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15 Dec 2016

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ABSTRACT

At a time when there is a critical need for globalized, shared information about the state of the biosphere, the ecological sciences are still not able to furnish adequate diagnostics or prognostics about ecosystem (dys-)functioning. How did this situation arise?

The project begins with a re-examination of the historical origins of ecology and the accompanying theoretical frameworks since the early 18th century. It revealed that ecology, like biology, has developed a scientific practice without fundamental and general scientific laws. Both modern disciplines arose from a mixture of observations and philosophies concerned with explaining not only the purpose of life but also why "lower" organisms exist to serve humanity. Meanwhile, preservationist, conservation and protection movements wrote a myriad of regulations and legal descriptions to govern the environment, yet pre-dating any tested ecological paradigms. In that sense, nature protection and resource exploitation could be characterized as vast experiments in ecology that began long before a science of ecology existed. Hence, today, a significant part of ecology advances under an operating principle that 'complexity cannot be the object of reductionism' and is mainly based on phenomenology. This practice renders results vulnerable to misinterpretation and manipulation (whether intentional or not) since conclusions are reached under strict *ceteris paribus sic stantibus* conditions. In other words, by restricting conclusions to "all conditions being otherwise equal", it is an accepted scientific practice in ecology that results may not be either transposable or comparable.

The research goal then is to understand how historical contexts influenced ecological practice today. To do this, I re-examined the central object of ecology - populations of individuals from the same species - using both reconstruction and recursive analyses. In a series of examples, I show that properties of ecological systems are often studied at the population level while underlying mechanisms happen at the individual one, and I attempt to demonstrate how this problem of scale has undermined progress in ecology.

In particular, the ecological theory that describes conditions of co-existence from the work of Gause (and also Lotka and Volterra) cannot provide a robust, unique explanation for the processes of competition because of analytical "short-cuts" made at the time of the original work. Individual-based approaches provide better representations of actual ecological processes and can accommodate a wider range of possible behaviors. They permit ecological interactions to be represented between individuals (whether they are from the same species or

not) and with the environment they perceive. I suggest that, properties can emerge from individual interactive dynamics at intermediate levels of groups of individuals that need to be redefined but which are not what is called population or communities.

Furthermore, a re-examination of the historical record of several different marine species produced additional insights concerning the effects of context for problems in conservation theory, including:

> • the identification of a species as invasive or extinct is highly sensitive to the working context of scientists and experts;

> • the reliability of species presence information is conditioned by the interest and expertise of the source of the reporting the information; and

> • if historical trends analysis suggests that an ecological niche is shrinking (either because of changes in the place or role of the organism in the environment), then there is no reason to expect that conservation measures of the species will be effective.

I conclude that the fundamental objects of ecology need to be reconsidered, as well as all the concepts of interaction-based processes that were derived from population-based reasoning (competition, invasion ...). Technological advances over the past two decades have made it possible to experiment with, and measure directly individual interactions. This should permit the development of a more functional body of theories - converging toward laws - concerning ecological interactions at the individual level. It should deeply affect applied ecology, such as how we evaluate and assess impact in environmental management. Finally, I also suggest that historical ecology is not about the simple act of collecting data from old logbooks. Historical ecology offers a means to reconsider past decisions, and to delve deeper into the foundational concepts of ecology and the conditions in which they arose. If physics has evolved by proposing fundamental (*i.e.* universal) laws and by constantly re-evaluating concepts and theories, then historical ecology could aim at performing this task for ecology, but from a retrospective point of view.

SIMPLIFIED SUMMARY

Understanding and predicting impacts of human activities on the biosphere requires knowing how past practices and uses may have altered the trajectory of ecological systems. Identifying trends is thus a fundamental topic in ecology and a practical necessity for evaluating protection measures. For many environmental variables like temperature, data series can be reassembled directly from calibrated, comparable sources. However, the living component in ecological systems has no equivalent standard measurement. And, as a result ecological sciences have developed a scientific practice without points of inter-comparison and reference points. There are only a handful of long-term (*i.e.* multi-decadal, pre-1970 start) observation series which target marine systems. This situation makes information about ecological conditions difficult to integrate with environmental change scenarios, because what is admitted as baselines are always changing, or are not evaluated at all.

Since at least the early 1980s, some ecologists have called on their colleagues to integrate the study of biological materials in museum collections (*i.e.* "museum ecology") to examine ecological trends. Since then, the diversity of observations which can be considered relevant for hindcasting has broadened considerably. Information can be compiled from disciplines like history, archeology, paleontology, phylogenetics, environmental sciences, climate sciences, and museum sciences, among others. What has only recently become evident is that each discipline has a different scientific practice that circumscribes how observations can be re-used. Thus, in addition to the significant amount of work involved in simply assembling data, we can add evaluating errors arising from aggregation and scaling problems, a need to establish portable reference measurements, and to develop new techniques to incorporate contextual frameworks from historical and social sciences. This work is fundamentally multi-disciplinary and interdisciplinary.

As ecology does not have its 'thermometer', it needs to develop conceptual probes to be able to draw conclusions which can be compared across space and time. I suggest that reconstruction of ecological trends depends explicitly on the historical context of ecological concepts that guided the original observations. The epistemic value of ecological observations should be treated explicitly. The overall goal is to arrive at a definition of an ecological system which can be calibrated and compared through space and time. It should then be possible to predict what will be missing, and better identify limits to the analyses of past ecological states.

A first step toward this goal is to re-examine the fundamental concepts applied today in their original context. I do this through a recursive analysis and constructive criticism of the epistemological progress of theories in ecology. Finally, I consider how the sociology of science may help develop a theory of collections and their processes of accumulation and loss. The objective is to be able to forecast where new data resources will be found for ecological studies by predicting the types of historical records expected in different institutional structures.

PROPOSITIONS

The original purpose of this project was to investigate the epistemic value of heritage collections for addressing modern scientific questions about environmental change in marine ecosystems. The main challenge is to address processes of knowledge assimilation within a specific scientific discipline, marine ecology. If the sociological representations can suggest a means to answer the question of how science works, then it does little to help us identify how to value the information which is unpublished and ignored in these analyses. Thus a part of this work concerns the actual methodological approach to the evaluation and description of scientific production. A knowledge model is proposed, which is neither sociological, nor historical, but is inspired by both of them. Database and object collections permit exploration of questions about how historical context that may have biased observations used for current analysis of ecological and environmental trends.

The lessons of the contextual analysis are pulled together to address questions of ecological interest. The role of these sources of information and their value to current questions are tested in a series of investigations regarding ecological applications. These questions concern past exploitation and future preservation and conservation of this region. The goal is finally to lay the foundation of a discipline of historical ecology that can address both practical questions about how the ecosystem has evolved and to be able to better predict how it may change in the future. The main approach uses recursive techniques to re-examine concepts and reconstruct ecological trends.

The results can be summarized in the form of three propositions that constitutes the core of this project.

FIRST PROPOSITION: the absence of a body of fundamental scientific law specific to ecology, impairs the scientific progress in this field. Therefore, I propose that one of the major challenges and objectives of ecology should be to discover laws, *i.e.* revealing fundamental mechanisms. In addition, the main challenge of historical ecology should be to examine concepts and theories to understand why they did not lead to establishing a corpus of laws.

SECOND PROPOSITION: the absence of possibility to inter-calibrate data when reconstructing trends makes it necessary to construct conceptual probes that 'measure' the quality of the available information regarding the knowledge at the time it appears (*i.e.*

examining the consistency of the concepts at the time they were established), as well as the level of bias induced by the context in which investigations were performed. Series should be systematically associated with a model to hindcast recursively data (*i.e.* at each time *t*, are reconstructed previous data from the knowledge at this point in time).

THIRD PROPOSITION: To progress, ecology should abandon historically ill-defined concepts that were elaborated at the species or species' assemblage(s) level (like niche, competition and biocenosis …) to focus on the actual interactions that develop between individuals and their environment. Ecology should therefore not study objects other than individuals and with having the single goal of finding emergent properties at different levels of interacting groups. All our results revealed that the initial focus on populations (loosely defined as a group of individuals of the same species living in a geographic area) has not led ecologists to propose useful properties that constitute fundamental knowledge in the discipline and that are not subject to systematic re-evaluation.

PROLOGUE, Crete Island, 2013.

How do we do Science? What do we value in scientific work? We rarely sit down to think about where the theories and ideas we take for granted came from, or what other ideas may have been promoted or discarded along the way. This is the domain of historical and epistemological studies, not of scientific research proper, or is it?

This project is an undisciplined journey around the edges of humanities and ecological sciences, so let me start by telling a story …

Three years ago, I participated in a summer school for field ecology held on the island of Crete. Earlier in the year, I'd been working on a couple of teaching and exhibition projects about the "pourpres" of the French zoologist, Henri de Lacaze-Duthiers (1821-1901). These are experiments he did in the 1850s and 1860s using the photosensitive molecules extracted from crushed Muricidae snails to make photographic transfer images onto fabric. When he published his results, he made something of a sensation because he claimed to have re-discovered how the Romans made Royal or Tyrian purple dyes.

This production of natural pigments constitutes an early example of a large-scale exploitation of marine organisms not related directly to consumption, and also the industrialization of a chemical process. Crete was an important center for this industry from about the 3rd millennium BC and numerous archeological sites exist all over the island. I thought this would be an ideal short field project for the students to do mixing history and field ecology. So I proposed that the students estimate the local density of one of the species exploited by the purple dye industry: Hexaplex trunculus. I contacted the local expert to get some idea about where we could find them, but to my surprise I was told the project was a bad idea because there weren't any left and it was even suggested that the species might be extinct locally.

All the articles I'd read considered this a ubiquitous species in the Mediterranean. Was there a link between this "extinction " and the purple pigment industry on the island? More practically, did I have to come up with another project for the students? I was somewhat doubtful about such strong declarations, so we went looking for them anyway. After just a few diving explorations, there they were, right where they should have been. We went ahead with the project and instead of relying on local expertise and local biodiversity surveys from the scientific literature, we added interviews with local residents who recounted to us their fishing techniques, how they gathered the snails for meals and even recalled using the mucus-like secretion from crushed shells to mark their clothes many decades earlier.

What happened that summer intrigued me - I had inadvertently stumbled onto the Achilles heel of ecological research: the absence of a law-based scientific practice in ecology can lead experts to conclude on the extinction of

the species based on lack of observations. It was an important lesson for me. Ecology depends on someone noticing a particular organism exists in the environment and recording that observation somewhere. Ecology, perhaps more than any other natural science, depends on who is doing the observing. The basic data of ecology - species presence and distributions - are highly dependent on context. This was the genesis of my inquiry into historical contingency and ecology.

<center>***</center>

Ecological studies have long been plagued by both a strong reliance on argumentation based on the ecologist's personal experience - either expertise or intuition - and unstable, fluctuating definitions of concepts which are not rooted in direct comparable measurements. Theories and principles are built on concepts like species and ecological niche, which have their own very unstable epistemological developments. In recent years, ecologists are being increasingly solicited to provide responses for societal challenges about environmental impact and protection of species, but prediction and reconstruction of trends have never been ecology's strong suit because it has developed without a law-based scientific practice. This situation renders rebuilt series vulnerable to incorporating misconceptions about different ecological objects, like the example of the Murex in the anecdote. Wouldn't it be more 'scientific' to be able to reconstruct population trends from first principles about ecological interactions? Then numerous difficult questions arise: How does missed information affect the interpretation we have of an ecological problem? What kinds of bias exist about the presence of species in an area under study? What does the measurement of interactions concern and what functions describe their relationship with the objects of ecology?

To explore these problems and how they limit progress in ecological theory, I will draw on the experiences of philosophers, historians and archeologists who have long recognized the importance of evaluating the cultural contexts which are attached to objects and concepts when reconstructing the past.

PART I. Ecological ways of thinking

SUMMARY

This first section discusses the epistemological background of ecological sciences. In the following pages, the objects of study of ecology are not considered in terms of aquatic, marine or terrestrial, but as common objects shared by all the specialties and sub-disciplines. The implications of the absence of laws in ecology for establishing baselines is discussed. The section closes with the development of a profile of ecological research practices.

From this discussion of the background and development of ecological studies, I highlight the difficulties with the objects of study in ecology that have arisen over the past century. I suggest that the strong focus on statistical concepts of populations and communities cannot lead to the development of a body of ecological laws because the parameters observed are outcomes of interactions between individual organisms. This is thus a return to early ideas about the importance of both seasonal conditions and the conditions of the individual's surroundings as suggested by John Lawes (1814-1900; who began the experiments at Rothamsted, England), and even Ernst Haeckel (1834-1919) himself.

CHAPTER 1

A CONTROVERSIAL DISCIPLINE

"One of the consistent difficulties of
ecology is that, like beauty, it is in
the eye of the beholder"

-- McIntosh (1985): 31

Ecology is a relatively young science, and like Biology, is a 19th century invention. It is built on the empiricism and phenomenological approaches of 19th century practitioners, who themselves were trained in European natural history traditions.[1] But biological studies were already shedding the attitudes of prior centuries[2] in the 1830s, when Biology split from natural history, like Physics and Chemistry had before it. By the time Darwin published his theory in 1859, Biology concerned mostly either the "chemical" physiology[3] of Justus von Leibig (1803-1873) and its application to agricultural production, or making detailed observations of organism morphology and physiological functioning in the context of medical research. These activities, often associated with new industrial developments, had the effect of making Natural History appear outdated, and even, as McIntosh wrote, "The term *naturalist* took on a pejorative tone."[4]

Natural history studies continued under new terms after the 1859. When Ernst Haeckel (1834-1919) invented the word ecology, his definition of a science about interactions captured an essential part of Charles Darwin's (1809-1882) ideas, and in a sense, saved natural history. Since underlying natural selection are all the interactions between living organisms and their surroundings, Haeckel in his enthusiasm for Darwin's work, neatly supplied a single word for complex semantic concepts implicit in Darwin's idea about the processes of evolution. Haeckel drew on not only Darwin, but also his own re-analysis of a central idea in natural philosophy: the definition of individuality and the object of study in biology.[5] He integrated the ideas of a natural historian and geographer he admired greatly, Alexander von Humboldt (1769-1859)[6], who by mapping the distribution of species in different latitudes proposed explanation for the different associations observed. He was also "undoubtedly influenced by Buffon's definition of bionomics and John Stuart Mill's and St. Hilaire's definitions of ethology"[7].

Thus, the scope of ecology was vast from the very beginning. To create 'ecology' Haeckel used a prefix that derives from the Greek 'oikos', (the dwelling, household, or family, οἶκος),

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[1] Much of this brief overview of ecology's origins is found in the very comprehensive work of McIntosh (1985).
[2] By this I refer to the standard, politically acceptable point of view that Nature is apprehended correctly through a melange of aesthetic, moral judgements and theoretical, objective reasoning that characterized the 16th, 17th and 18th centuries.
[3] Today, this would be organic chemistry.
[4] McIntosh (1985): 45
[5] Richards (2008): -
[6] Footnote 3, p. 21 Richards (2008)
[7] Park (1946): 313

extending the sense of house or household to organisms as well as Man. The concept "oikos" refers to a sociological unit of Greek society that encompasses the persons of a household as well as where they lived together. The prefix was well chosen by Haeckel to describe the type of knowledge he had in mind about organisms and their environment:

> ["Unter Oecologie verstehen wir die gesamte Wissenschaft von den Beziehungen des Organismus zur umgebenden Außenwelt, wohin wir im weiteren Sinne alle 'Existenz-Bedingungen' rechnen können"].

> Par écologie nous comprenons toute la science des relations de l'organisme avec le monde extérieur environnant, où nous pouvons nous attendre tous les « conditions d'existence » au sens large.

> By Ecology we can understand "the entire science of the relationships of the organism to its surrounding external world, wherein we understand all 'existence-relationships' in the wider sense" [8]

So, to study organisms in their environment is to study the relationships that organisms develop between themselves and with their environment - this is the general framework that he proposed to complement Darwin's idea. A single example, like that of the pygmy seahorse (*Hippocampus bargibanti* Whitley, 1970*)*, is enough to illustrate some of the complexity implicit in this framework: removed from their environment, these organisms would be described according to their morphology as fish with "body-segments [that] imitate the yellow and orange clumps of spicules of the gorgonian"[9]. The same organism considered in their environment, are described by their capacity to hide by mimicry in the gorgonians where they live[10]. Clearly, the dividing line between ecology and biology would involve a precise definition of what is the whole organism, and what are the parts of the organism.[11] This touches a sensitive point in biology about how to identify the living and non-living parts of Nature and it implicates a debate that raged for centuries under terms like materialism and vitalism.[12] It is also a fundamental distinction that informed arguments about the classification of the natural world, the Great Chain of Being, and philosophies about how to investigate natural phenomena.

It seems reasonable to consider how individual investigators would have been constrained by their capacity to make observations on such complex topics in the mid-19th century. First, and foremost, this suggests problems of inventing new concepts and experimental approaches to collecting and making observations. Scientists work within paradigms shared among groups of

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[8] English translation from Richards (2008). Original citation appears in Haeckel (1866) Vol. 2, 286-287.
[9] Anon (1969)
[10] Anon (1969); Gomon (1997)
[11] Petersen (1928); Sears (1960)
[12] Similar issues are still present in criticisms and concerns about Synthetic Biology today (Kwok, 2010; Cameron *et al.* 2014).

investigators. These conceptual frameworks of commonly held assumptions are recognized within institutions as scientific disciplines. But a discipline does not exist without both a name *and* a transmitted scientific practice. For instance, throughout the 19th century, ecologists shared with oceanographers many of the same battles for recognition and positions within both Universities and other research institutions.[13] When Haeckel invented the neologism 'ecology' he certainly did not foresee the difficulties that future ecologists would have to define this new field of study. For him, it was a logical extension of studies about evolution.

Thus, even if the word "ecology" originates in the work of Haeckel[14] on morphology, evolution and adaptation, the practice of ecology as an academic discipline began almost a generation later, between 1895 and 1905. At this time, two important textbooks appeared. First was a very influential textbook on plant biogeography[15] by the Danish botanist, J. Eugenius B. Warming (1841-1924) who also taught the first university course in ecology. Warming has even been named as the person responsible for the "revival" of the word ecology.[16] Shortly thereafter, the American botanist Frederic E. Clements (1874-1945) published a foundational text on research methods[17] as a follow-up to an earlier work where he introduced the quadrat, the idea of the species as a unit of study, and basic statistical tools to treat data.[18] Many other workers contributed fundamental concepts as well during the period leading up to the publication of the textbooks (Table 1-1), but these two works directly impacted the training of future ecologists and therefore the subsequent development of the discipline. Since both men were working on terrestrial systems, later workers, like G.F. Gause[19], often attributed a leadership role to terrestrial-based ecologists for the development of new concepts; but if we examine what domains the ecologists who proposed many new and original concepts were actually working in, the characterization becomes more nuanced (Table 1-1).

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[13] Deacon (1971); McIntosh (1985)
[14] Haeckel (1866)
[15] Warming (1895)
[16] Sears (1960): 195
[17] Clements (1905)
[18] Pound and Clements (1898)
[19] Gause (1934): 4

Table 1-1. Concepts in ecology that attempt to encompass aspects of the unity of living and non-living systems.
Non-exhaustive list of terms invented to express the unity of living and non-living components and the complex interactions between them. Primary sources: McIntosh (1985), Real and Brown (1991), and Chase and Leibold (2003). TEcol = Terrestrial ecology, MEcol = Marine ecology.

Concept	Year appeared	Author associated with	Nationality	Original domain of concept
Nature	--	--	--	--
Population growth	1798	T. Malthus (1766-1834)	British	Demography
Environment	1827	--	German	translation to English of German "Umgebung"
Ethology	1854	I.G. Saint-Hilaire (1805-1861)	French	Natural History
Evolution and natural selection	1859	C. Darwin (1809-1882)	British	Natural History
Biotope	1866	E. Haeckel (1834-1919)	German	Marine zoology
Ecology	1866-1873[1]	E. Haeckel (1834-1919)	German	Marine zoology
Biosphere (1)	1875	E. Seuss (1831-1914)	Austrian	Geology, Geography
Biocoenosis	1870-1877	K.A. Möbius (1825-1908)	German	Marine zoology
Food web	1880	L. Camerano (1856-1917)	Italian	Natural History
Microcosm	1887	S.A. Forbes (1844-1930)	American	Limnology
Environmental	1880-1890, 1967	--	--	--
Bionomics	1885-1900	--	French	English translation of French 'bionomie'[2]
Conservation	1890-1915	G. Pinchot (1856-1946)	American	Forestry
"Plantesamfund"	1895	J.E.B. Warming (1841-1924)	Danish	Biogeography
Ecological succession	1899	H.C. Cowles (1869-1939)	American	TEcol, Limnology
Physiography	1901	H.C. Cowles (1869-1939)	American	TEcol
Population interactions	1910-1926	A.J. Lotka (1880-1949) & V. Volterra (1860-1940)	American, Italian	Mathematics, Chemistry
Food chains	1913, 1927	V.E. Shelford (1877-1968) & C.S. Elton (1900-1991)	American, British	TEcol, MEcol
Biome	1916	F.E. Clements (1874-1945)	American	TEcol
Environmentalism	1916-1923, 1970	--	--	Psychological theory (Nature vs. Nurture)
Biosystem	1918, 1939	A. Thienemann (1882-1960)	German	Limnology
Niche (1, habitat)	1914-1919	J. Grinnell (1877-1939)	American	TEcol
Bioenergetics	1925	A.J. Lotka (1880-1949)	American	Mathematics, Physics
Niche (2, functions)	1927	C.S. Elton (1900-1991)	British	Ecology
Bioecology	1927	W.P. Taylor (1888- ?)	American	Ecology
Biosphere (2)	1926-1929	V. Vernadsky (1863-1945)	Russian	Geology, Chemistry
Ecosystem	1935	A. Tansley (1871-1955)	British	TEcol
Trophic dynamics	1942	R. Lindeman (1915-1942)	American	Limnology
Biogeoceonosis	1945	V. Sukachev (1880-1967)	Russian	Biogeography
Niche (3, hypervolumes)	1944-1957	G.E. Hutchinson (1903-1991)	British-American	Limnology
Dynamic equilibrium	1962	F.W. Preston (1896-1989)	British-American	TEcol
Systems ecology	1964	H.T. Odum (1924-2002)	American	TEcol
Island biography theory	1967	R.H. MacArthur (1930-1972)	American	TEcol
Metapopulation	1969	R. Levins (1930-2016)	American	Mathematics, Agriculture
Ecosphere	1970	B. Commoner (1917-2012)	American	TEcol
Chaos	1974	R.M. May (1936-	British	TEcol
Neutral theory	2001	S.P. Hubble (1942-	American	TEcol

[1]Ecology appeared in English-language texts *ca.* 1873.
[2]Bionomics was a short-lived synonym for ecology among English-language ecologists. French marine benthic ecologists continued to use the term well into the 1960s.

By the end of the 19th century, as biology, physiology, and zoology settled into comfortable university departments with designated chairs, laboratories and teaching programs, attempts to put ecology (and ecologists) in one box or another largely failed in the early decades of the 20th century.[20] It became a persistent challenge within the research community to fix where ecology belongs. Even now, on the website for the Nature Publishing Group, "Evolution & Ecology" is cited twice: once under Earth & Environment, and a second time under Life Sciences (Figure 1-1). The situation was even more unclear in 1895: W.A. Herdman (1858-1924) tried to illustrate all the different areas touched by the "Field Naturalist" working in Zoology (Figure 1-2). In this sketch, which is meant to illustrate an opening address for a Zoological section of The British Association, he uses "bionomics" as a loose synonym of ecology. His illustration succeeds to convey a general impression of how confusing the connections between biological research specialties had become, while also showing the tremendous possibilities to contribute in multiple domains of knowledge. It also indicates the importance Darwin's theory held for all the areas of study listed.[21] In addition, ecologists themselves proclaimed from time to time their frustration with the lack of clarity in their domain. Victor Shelford (1877-1968) in 1913, famously admitted feeling "hopeless" about the absence of a clear framework for ecology when he wrote his landmark text on field ecology.[22] Half a century later, another American ecologist, E.P. Odum (1913-2002), lamented that Ecology appeared lost on institutional organizational charts under 'Life sciences' or just 'Biology'.[23] These may seem like arcane details of the historiography of scientific disciplines, but access to funds, techniques, methods and new tools, depends on institutional support, continuity and visibility. *Where* to look for ecology matters.

Partly, some of the difficulties come from when ecological concepts arose. Many themes are quite common in literature prior to Haeckel's invention of the word in 1866 (see Table 1-1 for some examples). As a case in point, ecology was nearly invented a couple of decades before Haeckel, when Justus von Liebig's book on the applications of organic chemistry for agriculture[24] was published on the heels of the invention of aquariums.[25] In the two decades that followed, a fad for aquariums and aquarium-keeping swept across England and western

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[20] Sears (1960): 197

[21] This priority given to evolution is presented in a similar way by the later analysis of Paul B. Sears in his presentation of the early history of the American Society of Naturalists, Sears (1960): 193-195.

[22] Shelford (1913): Preface, p. v.: "The organization of the data here presented is the result of many attempts and failures which at times made the task seem hopeless."

[23] Odum (1975): 4.

[24] von Liebig (1840) released to great fanfare in three languages simultaneously: English, French and German.

[25] The French biologist Charles des Moulins (1798-1875?6) was experimenting with ways to keep small populations of invertebrates alive in his laboratory. Moulins described in a short publication how adding different sorts of plants and algae refreshed the water in his "petit étang factice" (his little imitation pond; Des Moulins, (1830): 261). He reported that the animals in his container remained alive and healthy for many months when kept in this way.

Figure 1-1. Where does Ecology belong? This is a snapshot of the journal topic selection menu listed on the Nature Publishing Group website in Fall 2016. Notice that ecology appears (with evolution) twice: once under Earth Sciences and then under Life Sciences. The difficulty of choosing where ecology belongs among the spectrum of scientific disciplines persists today. This phenomenon has been discussed periodically in the scientific literature throughout the 20th century by working ecologists, as well as by the historian Robert Kohler and the ecologist-historian Robert McIntosh.

See page at this address: http://www.nature.com/npg_/index_npg.html.

EVOLUTION

OCEANOGRAPHY — — — — — — — — — — — — — — (PHYSICS
&
CHEMISTRY

FISHERIES

GEOGRAPHY
GEOLOGY

CHALLENGER
EXPEDITION

WORK OF
BIOLOGICAL STATIONS

BIONOMICS

EXPERIMENTAL
EMBRYOLOGY

CYTOLOGY

PALEONTOLOGY

LOCAL
FAUNAS

EMBRYOLOGY

HISTOLOGY

DISTRIBUTION

SPECIOGRAPHY

HABITATS

COMPARATIVE
ANATOMY

LIFE
HISTORIES

ANATOMY

STRUCTURE

MEDICAL

FIELD NATURALIST

Figure 1-2. W.A. Herdman's (1858-1924) arrangement of fields of study concerned by zoology in the latter half of the 19th century. In his Opening Address commenting on the changes in natural history and marine zoology since 1851 he stated: "That excessive specialization, from which most of us suffer in the present day, had not yet arisen; and in the comprehensive, but perhaps not very detailed, survey of his subject taken by one of the field naturalists of that time, we find the beginnings of different lines of work, which have since developed into some half-dozen distinct departments of zoology, are now often studied independently, and are in some real danger of losing touch with one another." He uses "bionomics" as a loose synonym of ecology, calling it : "One of the most characteristic studies of the older field naturalists, the observation of habits, has now become, under the influence of Darwinism, the "Bionomics" of the present day, the study of the relations between habit and structure and environment - a most fascinating and promising field of investigation, which may be confidently expected to tell us much in the future in regard to the competition between species, and the useful or indifferent nature of specific characters."

Redrawn from diagram in Herdman, William A. "The British Association. Section D. Zoology. Opening Address." Nature 52, no. 1351 (1895): 494–501. Citations p. 495.

Europe[26] accompanied by numerous publications describing how to create and maintain salt-water and fresh-water aquaria[27] at home. It was a British chemist (R. Warington, 1807-1868) who worked out the chemistry of the aquarium principle by 1850.[28] After experimentation, he realized that the oxygen produced by the plants supported the animals, and that the conditions would remain stable as long as the number of animals was not too high. His publications appeared in 1850 and 1851.[29] Rehbock has argued that new discoveries about the chemical nature of physiological processes like respiration and growth discovered at the end of the 18th century, did not appear to interest British naturalists until *after* publication of Justus von Liebig's work in "physiological" chemistry.[30] Rehbock proposed that when von Liebig discussed these processes in terms of how they could benefit farming and animal husbandry, this made the chemistry seem more relevant to naturalists who wished to keep animals alive for study. Meanwhile, von Leibig had actively promoted the idea of chemical equilibrium being part of the balance of nature. Thus, aquariums were held up as *de facto* evidence for the existence of this balance.[31]

If many ecological concepts were established early in the history of the discipline, then it is with some consternation that after more than a century of effort, we cannot yet answer satisfactorily many apparently fundamental questions such as:

> *What does it mean, ecologically, that the biological diversity measured in region X is higher than in region Y? How does the presence of a specific resource affect community structure and distribution? What does a change in species or community distribution indicate? When do interactions between individuals affect densities of populations? When do perturbations effect permanent changes in population cycles? What are the common units (portable variables) of ecological interactions? How does the distribution and density of species observed at one instant of time differ from what is expected in a given area or volume of an environment?*

The eminent theoretical ecologist Robert May also discussed some of these same questions and issues with respect to conservation of biological diversity (Table 1-2). These are questions that arise from the way in which we conceive of Science and the role of prediction in producing knowledge.[32] Unfortunately for early ecologists, determining relationships of cause

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[26] Rehbock (1980); Hamlin (1986); Kisling (2000); Lorenzi (2009).

[27] P.H. Gosse's lavishly illustrated volume (Gosse, 1854) is considered the center-piece of the aquarium-keeping movement which began in Victorian England. A color digital scan version of the 1856 edition is visible on the Biodiversity Heritage Library at: http://www.biodiversitylibrary.org/bibliography/4841#/summary. Other important early popularizers were H.D. Butler, S. Hibbard, H.N Humphreys, E. Lankester, and G.B. Sowerby.

[28] Hamlin (1986): 132-135

[29] Warington (1850); Warington (1851)

[30] Rehbock (1980): 525

[31] Even if it was obviously false since the aquarium owner intervened constantly to maintain the balance, Hamlin (1986).

[32] The terrestrial ecologists Jeff Houlahan recently published an essay on the topic of prediction in ecological research that was inspired by the reporting on the reproducibility crisis in psychology (Houlahan *et al.* 2016).

Table 1-2. "Unanswered questions in ecology", after Robert May (1999).
The Australian theoretical ecologist Robert May compiled a list of topics and issues about the leading edge of ecological research at the close of the 20th century. All of these issues remain current research topics in ecology. The one issue that has progressed significantly is the construction of global biodiversity databases (final topic in this list).

Questions	Issues raised
What determines population density?	Concerns the absence of "predictive understanding of why the population density" of a species has a particular value, nor what this value depends on.
What determines the spatial structure of populations?	How does the spatial expression of population dynamics depend on other spatially structured variables, such as habitats, interactions with other populations and environmental conditions?
Can ecological processes be studied at short time periods and small spatial scales?	Are the practical limitations of an ecological experiment (field or laboratory) dictated by institutional structures limiting the ability to apprehend ecological problems?
What are the relationships between stability and complexity in ecological communities?	Since "real ecosystems are not randomly constructed" there must be relationships between complexity, stability, structure and function which explain why the disappearance of one species provokes important changes, while under other conditions it does not. More importantly the measurement of stability and complexity remain approximate.
What do food web patterns mean for ecosystem structure and function?	What is the usual length of a food chain? What is the link if any with the length of a food chain and population dynamics of the species included? "How many species does a given species interact with?" Does this have a relationship with the total number of species in a given food web?
What does the relative abundance of species mean for conservation?	Can we predict commonness and rarity of species in ecosystems under "normal" or perturbed conditions? What is the meaning of the relative species richness values for describing community assembly processes?
Are there functional relationships between species numbers, sizes, ranges?	What could be the consequences of biological diversity decreases? Is the species-area relationship an expression of a fundamental property of ecosystems? From what interactions does this derive? Can these be used to predict extinction?
What are the interactions between biogeochemical cycles and balances and ecological trends?	Can these be studied at global-scales? What are the driving ecological interactions? Does the frontier between biological reactions and ecological ones need to disappear?
How can sociological and ecological approaches be combined to better apprehend conservation problems and priorities?	Will require a global biodiversity information infrastructure. What is the common ground that exists between economic, sociological and ecological frameworks? How can traditional ecological expertise become more relevant to conservation debates?

and effect between observations made in the field (*e.g.* distribution patterns of organisms) and processes that could be studied experimentally (*e.g.* predation, production, dispersion) were poorly adapted to analytical methods available in the 19th century. It was not seen as possible or even desirable to simplify natural environments for ecological study. While the biologist was dissecting organisms into constituent parts and systems, the ecologist focused on the whole set of conditions of existence of organisms in their environment. Furthermore, the traditional separation between academic institutions and applied schools contributed an odd

twist to the development of ecology during the same period. In essence, techniques like plot manipulations and long-term observations both arose in applied contexts.[33] Agricultural, fisheries and aquaculture laboratories developed experimental methods to applied problems that would not be integrated into ecology until decades later.[34] Early ecologists tried to follow, observe and understand the complexity of ecological systems in their 'natural' cycles through description of single study sites with little emphasis on comparison. With hindsight, these studies of variations provided enormously detailed life histories of small plots of land, without advancing the theoretical understanding of population dynamics much beyond the level of intuition.

Ecologists would not move to encompass the complexities of ecological functioning with analyses beyond enumeration until mathematicians became interested in ecological problems. Hence, process simulation began with Lotka and Volterra's two species models in the mid 1920's and 1930s (Table 1-1). A generation later, in the 1950s and 1960s, the first computable models and new techniques like isotopic tracers from "radioecology" demonstrated the simulation of trophic cycling was possible.[35] At the same time, scales of evolution were considered to be much longer than ecological scales, and hence would not have to be taken into account. Dobzhansky's famous essay "Nothing in biology makes sense except at the light of evolution" was only published in 1973[36], then becoming identified with the moment in time when biologists started to modify how ecologists perceived evolutionary processes.

So should we consider that ecology really begins in 1950 or 1970? Definitely not. But given the technological changes that appeared after WWII, it is perhaps not surprising that historical perspectives have been absent in ecological studies.[37] The amount of new instrumentation available alone radically changed all scientific disciplines in less than a decade. Quasi-simultaneously, societal demands for precise, actionable information about the state of natural resources, their protection and management expanded. Many American ecologists, like Paul B. Sears (1891-1990) advocated for better integration of ecological "principles" and public policy in the United States.[38] He and other influential ecologists, such as the Odum brothers[39], joined the burgeoning environmental movement in the US that culminated in the passage of the National Environmental Protection Act at the end of 1969. Nonetheless, early alliances between the policy-making community and research ecologists were not nurtured in

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[33] Probably the most well-known examples being the work at Park Grass Experiments at Rothamsted begun by J.B. Lawes (Silvertown et al., 2006), the Continuous Plankton Recorder samplings, and the fisheries stock assessments organized by the International Council for the Exploration of the Sea (ICES) for the North Atlantic.
[34] See recent volume on this topic edited by Phillips and Kingsland (2015).
[35] Neel and Olson (1962)
[36] The American Biology Teacher 35(3): 125-129.
[37] Sears (1960); McIntosh (1985)
[38] See Sears (1960) and the numerous other short editorials contributed while he was editor of Science Magazine.
[39] HT and EP Odum were authors of the most widely used textbooks in ecology in the US between about 1950 and 1980.

subsequent decades, contributing to a rising perception of incomprehension between these communities around policy failures.[40]

To appreciate the effect of the absence of a historical perspective in ecology, an example that has been widely discussed is the rarity of long-term ecological series for either terrestrial or marine environments.[41] As pressure has mounted to be able to reconstruct past conditions to improve management of natural resources, the role of recent, historical past conditions in determining present ones has been the object of increasing attention. As Daniel Pauly wrote in his eloquent commentary on the moving baseline problem in fisheries[42]: "[…]each generation of fisheries scientists accepts as a baseline the stock size and species composition that occurred at the beginning of their careers, and uses this to evaluate changes". He concludes his short essay by evoking what is perhaps one of the strongest criticisms of ecological paradigms yet, that: "frameworks for incorporating of earlier knowledge in the present models" should be developed to be able to "evaluate the true social and ecological costs" of natural resource exploitation.

Returning to the final days of natural history, just before both 'Biology' and 'Scientists' were invented, let us also reconsider the 1825 article of French geographer and natural historian A. Dureau de la Malle (1777-1857) who described 30 years of observations of forest plots he owned.[43] This is the same work that Lawes cites as having inspired his experiments at Rothamsted.[44] In his presentation, Dureau de la Malle reports on various interventions and measures the responses of the populations and communities he observes. He provides rough estimates of the times required for "recovery". Finally, he wonders if he has not discovered the existence of a general law of nature concerning reproduction and population recovery. His article has all the hallmarks of an ecological study being conducted 80 years later. This is evidence of a remarkable conceptual stability in the way natural processes were being studied, which at the same time also calls into question our notions of conceptual progress for ecology. And, ironically, it is also this same type of observation, so disparaged in the mid-20th century[45] and now locked away on museum shelves and in archives, that furnishes much of the data required today by ecologists reconstructing past trends to better understand how to predict future changes.

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[40] Christie (2011)
[41] Edwards *et al.* (2010)
[42] Pauly (1995): 430
[43] Dureau de la Malle (1825)
[44] Lawes *et al.* (1882)
[45] Sears (1960): 195-198

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CHAPTER 2

OBJECTS OF STUDY IN ECOLOGY

"If the human species, as is
reasonable to suppose, shall in the
progress of time, people equally the
whole surface of the earth, the
history of the beaver, in a few ages,
will be regarded as a ridiculous
fable."

-- Buffon (1756) Tome VI: 62

What are the objects of study for an ecologist today? By the end of the 19th century, ecological studies crystallized around three primary categories of observations:

1. there are patterns in biological diversity associated with climate;

2. both populations of organisms and environmental conditions fluctuate;

3. organisms adapt to the conditions of their existence.

The apparent simplicity of this list is deceptive. For example, what is the place of evolution with respect to ecology and the explanations it provides for diversification? As we saw in the early diagram from Herdman (Figure 1-2), "evolution" was considered as an overarching theme relevant to all work with living organisms. And, throughout the 20th century ecologists and biologists engaged in roughly parallel investigations. Evolutionary biology focused on understanding the parts of the developing organism, an approach which expanded rapidly into studies at cellular and molecular scales after the re-discovery of Mendel's work and the description of the molecular structure of DNA. In contrast, ecologists were mainly concerned until the early 1990s with evolution from a paleontological viewpoint: that is, addressing morphological changes of the remains of adult and juvenile organisms over very long time scales.[1] Since then, the situation has changed radically.[2]

Not only did ecologists and biologists simply not work at the same time scales, but their objects of study were not the same. As Robert Kohler has shown, these differences impacted strongly the scientific practices[3] of both disciplines, and the effects continue to be felt today. The biologist delved into the physiological functioning of selected 'model' organisms and developed laboratory-based experimental approaches. While the ecologist worked from the organism outward to the environment it inhabits, investing great effort in building snapshots of observed complexity in 'natural' environments.[4] The frontier then, whether one considers it real or a convenient approximation, lies in how the individual organism is studied.[5]

Usually, the objects of study in ecology are organized according to the context they are being

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[1] See for example the descriptions in the volume edited by Ricklefs and Schluter (1993).

[2] The comparison between the point of view expressed in Ricklefs' work of the 1990s and this later article on micro and macroevolution provides an example of how ecological and evolutionary studies have converged around the topic of diversification and extinction Reznick and Ricklefs (2009).

[3] Kohler (2002)

[4] Like Odum's series of diagrams of the different conditions surveyed in his Silver Springs study Odum (1957), or Shelford's earlier work on animal communities Shelford (1913).

[5] In one of the last articles by the great fisheries biologists, C.G. Johannes Petersen (1860-1928) he wrote eloquently on this topic just before his accidental death (Petersen 1928).

studied in (Figure 2-1). All ecological objects concern scales of time and space and thus are conceived as nested, hierarchical structures (*e.g.* the biosphere is larger than a biome - defined by climate type, itself larger than a landscape, because the biosphere contains the set of all biomes, which contains sets of landscapes). One example concept, "habitat", is highlighted in each of the different schemes to illustrate how the point-of-view changes the perception of the object:

- as a concept of scale (Figure 2-1a), habitat is the smallest relative unit inserted into successive spatial scales above (which can be used to describe a specific - usually rather homogeneous -type of environment);

- but if we construct a diagram based on placing ecological objects in an ecosystem (Figure 2-1b), then habitat becomes part of the biotope definition (that is the abiotic conditions) and is related to the biological objects concerning species through the niche (that describes the conditions necessary for the existence of a population);

- and because of that, in the third part (Figure 2-1c) where the ecosystem is placed within a system of evolutionary diversification processes, "habitat" becomes the means through which biological processes, such as growth and mortality, interact with the biological entities of populations and individuals (hence can be used to define the boundaries of a community).

Many authors have commented that studies in ecology are plagued by both wobbly definitions and capricious theoretical developments[6], touching a sensitive topic: the place of ecology relative to other sciences and its infallibility.[7] Indeed, several of the central objects of study in ecology (population, communities ...) cannot be perceived as entities that can be manipulated directly; a theoretical and usually inferential framework is necessary to investigate them. If the objects of ecology in Figure 2-1 were placed on their respective epistemological continuums their context-dependent definitions become susceptible to historical contingencies, such as different interpretations promoted by various schools of ecology (see Highlight). Seen from this perspective, it is obvious that ecology is built from conceptual objects that regularly exceeded the technical capabilities to observe, analyze and ultimately define what they are at different historical periods. In a very real sense, ecological objects have been 'discovered' before their nature could be examined analytically (Table 1-1).

In addition, ecosystems and niches are considered as objects of ecology but they are more like a category of concepts, than 'real' objects we can store on a shelf: they require being formulated within a systemic framework and their manipulation and study depends explicitly on being able to translate the concept into a computational framework. Hence, the placement of the niche in Figure 2-1b is a relatively recent clarification resulting from an important review volume

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[6] One particular example is the compilation of M.W. Palmer about the different hypotheses (he lists 120) which lay claim to explaining species richness variations (Palmer, 1994). More recently, Brian McGill reviewed all the different ways species abundance distributions are treated (McGill *et al.*, 2007), and Scheiner (2013) has gone so far as to call ecology "idea-free"!

[7] A small selection of the many articles written on different aspects of this topic since the 1970s: Peters (1976); Southwood (1980); Houlahan *et al.* 2016.

SCALES OF SIZE

(a)

NESTING OF ECOLOGICAL OBJECTS

(b)

NESTING OF ECO-EVO PROCESSES PRODUCING BIODIVERSITY

(c)
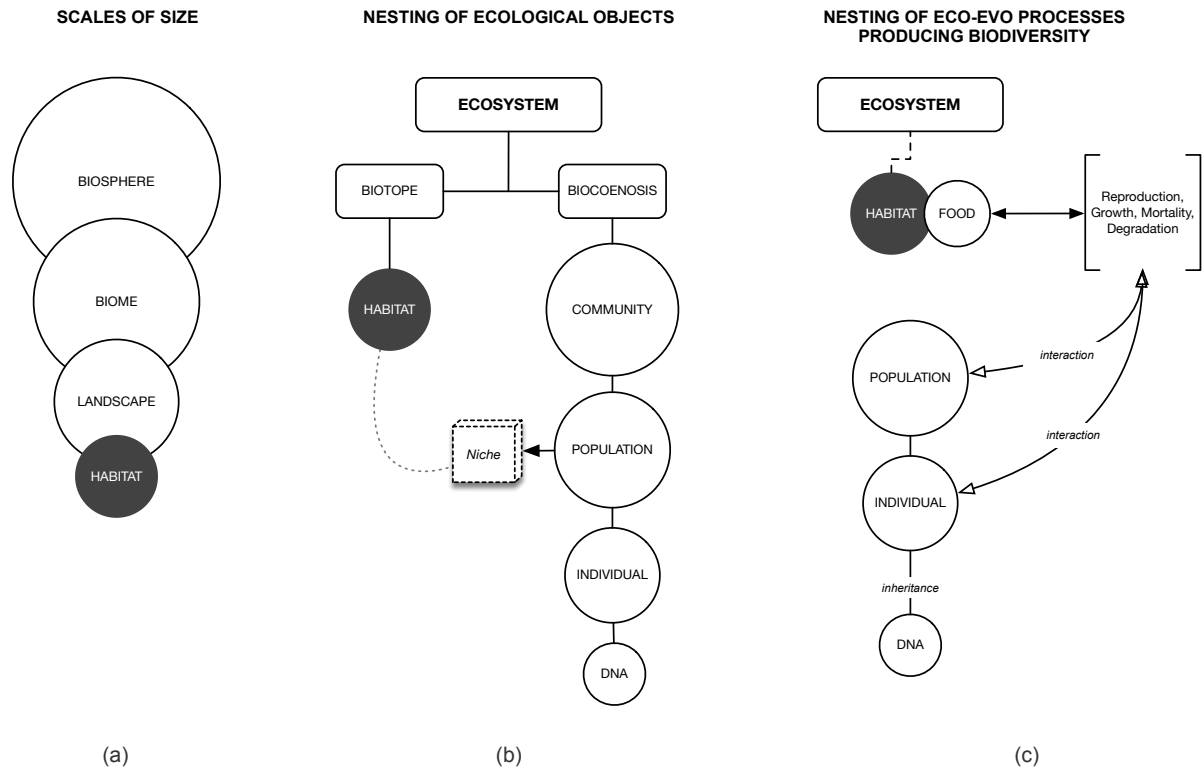
FIGURE 2-1. Theories in ecology use ecological objects having nested scales and concepts.

(a) The relative sizes of the four main environmental systems recognized in ecological theories: biosphere being the largest and habitat the smallest. (b) Ecological objects are concepts that also have explicit nested relationships. This is an example of how objects in community ecology may be organized for studying conditions of co-existence and species distributions across different regions. In this diagram, the biotic factors (under biocoenosis) permit the totality of populations in the biocoenosis to co-exist. The biotope contains the abiotic factors of the habitats of each species, and the association between biotope and biocoenosis are what constitutes the ecosystem. (c) Finally ecological objects have their own dynamics and are used in evolutionary theory to explain diversification through interactions (e.g. competition) and inheritance processes.

Habitat appears in three different contexts and is often confused with another important concept, the niche. In 2003, Chase and Leibold's seminal volume on ecological niches succeeded to replace the concept in a more comprehensible framework than earlier authors, like Hutchinson. Simply stated, the niche contains all the conditions required for the existence of a species. It therefore connects the habitat and population. This resulted in a renewed interest for using niche theory to predict species distributions and for conservation planning.

produced in 2003 by Chase and Leibold.[8] These authors proposed a definition of the niche that revised Hutchinson's n-dimensional hypervolumes of the 1950s, which was, in practice, unusable. Chase and Leibold suggested that the niche could be defined as containing all the conditions required for the existence of a species and the feedbacks the population has on those conditions. This means in an ecosystem framework (Figure 2-1b), the niche provides a functional link between the population and their habitat. The work they did immediately struck a chord in the conservation and resource management communities, where there has been a strong renewal of interest in using niche theory to *predict* species distributions.[9] Difficulties encountered in these attempts to apply theory have since led to reviving another earlier concept of the ecological niche (the resource-utilization niche)[10] which links quantification of the species' population dynamics and its structural interactions with the resources (*sensu largo)* actually exploited in their immediate environment.

To counter some of these epistemological challenges in ecology, authors like E.G. Hutchinson and Robert May, have tried proposing direct questions (*e.g.* How many species are there on Earth?) as a stimulus for fundamental research.[11] But, does enumeration really stimulate scientific progress? Or is it hand-waving that distracts from underlying issues? Robert May and others have argued these types of numbers are important for some "big" questions, like estimating a rate of global extinction or trying to put an economic value on a volume of seawater. However, as far as the processes underlying diversification and extinction (leading to changes of biological diversity) are understood, the answer to his question could only be a discussion about the kinds of species concerned and when. It does not in any case seem a cause for May's 'embarassment' as he himself suggested.[12] Nonetheless, where do we go after the counting is done?

I would argue that these grand statements are meaningless. If ecology is about 'the conditions of existence of the organism in its environment', or said, in other terms, the science of the *interactions* between the organism and its environment (resembling something like the diagram in Figure 2-1c), then ecologists should manipulate, as a primary object, organisms. Organisms could be described by one individual when it functions autonomously, but could be assimilated to a colony when individuals are not dissociable from each other, or when their functioning depends directly on each other (*e.g.* corals, sponges). Consequently, properties at the level of groups of organisms are only outcomes of the individual's 'reaction' to different, varying environmental conditions (including interactions between organisms). These interactions between the organism and their proximal environment translate into survival and reproduction, which are, when integrated over a population, the two pillars of ecological selective value (or ecological fitness) of the species as a

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[8] Chase and Leibold (2003) provide a detailed description of the evolution of the concept.

[9] Unfortunately, because in reality the conditions required for the existence of a species may be mostly unknown, other concepts have substituted, like the environmental envelope, or the "ecological niche factor" to predict habitat suitability. These analytical tools use widely available and global databases of basic environmental measurements, like temperature, salinity, chl *a*, water depth, cloud cover, etc. as means to predict species ranges over large distances.

[10] MacArthur and Levins (1967)

[11] May (1988). Hutchinson (1959) proposed a slightly different type of interrogation, asking *why* there should be so many kinds of animals. As a side comment on how banal the enumeration approach to diversity has become, a search on Google Scholar (5 October 2016) returned more than 4 million hits on the title of May's 1988 article and its variants. I have to wonder if this is really a fruitful area of research or just a good title.

[12] May (2010)

parallel of the biological selective value for genotypes or phenotypes. This emphasizes an important issue. Nothing suggests that it is possible to work backwards from the number of different species to the interactions, because ecology, like biology, has at the center of its preoccupations a complex, dynamic and adaptive object: the living organism.

Groups of organisms as objects of study. The focus in current ecological studies is on the object of 'population' (individuals of the same species in a defined space) and the place and the function of that species in its environment (including other species; what is summarized by the term 'niche'). These studies seek to explain the viability - in the broadest sense - of the population and, ultimately, changes in the distribution of biological diversity (part of the first category of observations referred to at the start of this chapter).

In this context, biological populations have a number of attributes (Table 2-1) that control or affect their size in time and hence the probability of the persistence or extinction of a species, as well as their dispersion and the evenness of their occurrence in a unit area.

Table 2-1. Attributes of biological populations and processes operating on them
List of common population attributes used in population dynamics models, their generic definitions, and the processes actually being represented at the individual level (inspired by table in Odum 1975, pp 122 – 123). Note this list does not account for processes of resource utilization by the organism (*i.e.* consumption, degradation, energy allocation …).

Population attribute	Description	Process at individual level
Birth rate	probability that a new individual is produced in the population per unit time	reproduction
Death rate	probability that an individual dies in a population per unit time	mortality
Mortality rate	number of individuals that die per number of individuals likely to die per unit time	mortality
Dispersal rate	numbers of individuals that immigrate or emigrate per unit time per number of individuals likely to move; can also be represented as a diffusion rate (*e.g.* m^{-2}, s^{-1})	transport (passive, active)
Growth rate (population)	number of individuals reproduced per number of reproducers in a population per unit time	production
Growth rate (individual)	change in size of individual per unit time	growth
Density	numbers of individuals per unit area or volume	---
Distribution	how groups and individual organisms are arranged (distributed) per unit area (random, uniform, patches)	---
Age distribution	the relative proportion of individuals of different ages (demographic structure)	---
Genetic character	probability of producing descendants	mutation, inheritance

Populations of living organisms can be described by dynamic variables like abundance and biomass, yet simulating variables at the population level while all ecological processes and interactions occur at the individual level (Table 2-1), creates the paradoxical situation that process-oriented models of population dynamics are mainly phenological and cannot have any properties which allow generalization. Besides, when dealing with population dynamics models ecologists must keep in mind that while describing the change in population abundance and distribution over time, causes should be found at the individual levels and from all the different interactions that can exist between them and their environment. For example, because resources are limited in a finite given area (or volume), net population growth could be expressed as an

exponential curve[13], which becomes limited when the carrying capacity is reached and producing the familiar S-shaped 'logistic' curve.[14] This characterization relies on the following equation, describing the dynamic of the state variable N(t), the state of population at time *t*:

$$\frac{dN(t)}{dt} = rN\left(1 - \frac{N(t)}{K}\right)$$

This formulation assumes that r, the net growth rate of the population (balance between reproduction and mortality, in time^{-1}) is constant, that individuals are not synchronized (neither for reproduction, nor for mortality) that all individuals are susceptible to reproduce and die at any time (including doing both at the same time!), that the carrying capacity, which is the maximum quantity of individuals that the biotope can support (in units of N) is constant, and that an intra-specific competition coefficient (competition for the resource among individuals of the population) is both homogeneous among individuals in the population and is equal to 1. Respecting all these assumptions is not realistic, but it is treated as a measure of the process of production at the population level. Yet, implicit in population model is knowing everything about the physiology of individuals which makes up the population and how the individuals are distributed relative to an energy resource during the period of production, among many other conditions. As a result, any global measures of biological production averaged over large regions and long-time scales provide inadequate descriptions of the underlying variability.

In addition, Robert May in 1976[15], explored the dynamics of the logistic model, when the continuous model is converted into a discrete model (implying that the generations of the breeding population do not overlap, which, he suggested, is the case of insects in temperate areas). He found that the dynamic behavior of the discrete model varies with parameters' values and can even become completely chaotic when r increases. In this case, the variations of the state of the population are not different (from an observers' point of view) from completely random variations, even if the dynamics remained completely deterministic. Therefore, even our example of a very "simple" model, but which rests on unrealistic hypotheses and develops complicated dynamics that may not be identifiable, appears to have little utility in ecology.

So then why use populations at all? Populations became the central object of ecological studies because it is at this level that the emergent property of 'species (co-)existence' emerges. The population is considered as the basic ecological object involved in adaptive dynamics and evolution.[16] A population is primarily a statistical concept[17] but it became also a biological one. Any single individual can belong to a population as long as it fulfils the criteria which is

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[13] Malthus (1798). Thomas Malthus (1766 − 1834) a political writer described what he projected as the miserable results of overpopulation in his "Essay on the Principle of Population" (1798). Overpopulation in this case is defined as producing more offspring than can survive with the given resources. For Malthus populations were regulated (higher mortality) by divine intervention.

[14] The logistic curve, first described by the mathematician Pierre F. Verhulst (1804-1849) in the early 19th century (Verhulst 1838; Bacaër 2008).

[15] May, R. 1976. Simple mathematical models with very complicated dynamics. Nature 261: 459-467.

[16] See for example the presentation of Dobelli M. and Dieckmann U. 2005. Adaptive dynamics as a mathematical tool for studying the ecology of speciation processes. J. of Evolutionary Biology, 18: 1194-1200.

[17] The idea of a population as a rational unit of study emerged from British political movements in the 17th century concerned with documenting the activities and costs associated with society Bacaër (2008).

characteristic of what is defined as a population. Textbooks have defined population "as a collective group of a particular kind in the community"[18] or all the individuals of a particular species in a delimited area (the "target" population). Organisms can be grouped according to

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HIGHLIGHT: Ecological divergence

Important differences arose between European and American schools of Ecology in the late 19th and early 20th centuries. Although both schools recognized dynamics as an important part of ecology, their paths of investigation diverged early on. For example, American ecology was and still is strongly influenced by the writings of Frederic Clements, especially his ideas about ecological succession and climax communities, while European ecologists are much less so. McIntosh (1985, Chapter 2) suggests that the ideas of succession, which arose in American centers of plant ecology on the plains of the Mid-West, were concerned more with following dominant species and identifying "formations" of plants that indicated the stage of succession relative to a hypothesized equilibrium condition. Whereas European plant ecology was focused on discovering plant "associations" (resembling a continuity of natural history studies) and thus had a stronger emphasis on collecting taxonomic information, rather than functions. Hence, Clements' ideas held less interest for European ecologists engaged in documenting complexity.

There are also disparities in vocabulary. A striking difference in terminology concerns the Germanic terms, biotope (German: Biotop) and biocoenosis (German: Biocönose). Many of the difficulties are discussed in Gisin (1949). Neither word ever gained much traction in American texts, whereas in Europe both terms are prominent. 'Biocoenosis' first appeared in reports by Karl Möbius in the 1870s written for the Minister of Agriculture about exploitation of oyster and mussel banks on the northern coasts of Germany (Möbius, 1870; Möbius, 1877). Widely used American textbooks on Ecology replaced this term with community (see Odum, 1953; Odum, 1975). Similarly, the term "habitat" in US texts is used as a synonym of Haeckel's term 'biotope' (Haeckel, 1866). Even today, North American texts on theoretical ecology still contain no mention of either term (e.g. May, 1976; Case, 2000).

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observed similarities (whether they are morphological, anatomical, physiological or genetic). The population, related to one particular species (based on the single criteria of cross-reproduction and on their individual capacity to produce more individuals of the same kind) is assumed to be able to maintain itself indefinitely when reproduction compensates (on average) mortality. Given the over-arching concern with evolutionary questions which runs through all of modern ecology, placing populations at the center appears to offer a coherent framework of investigation.

The other grouping for which evolutionary aspects are assumed to be predominant is communities. The concept of communities was first introduced into ecological research by Karl Möbius with another term, biocenosis (see Highlight). It was further popularized by Frederic Clements in his vision of communities and the existence of a dynamic equilibrium in ecology. He advocated a view that the community of species together may function, or be organized like a single organism. He suggested that the groups of organisms which appear to be made up of stable associations *(i.e.* these associations could be identified, like geologic strata, in many different places) would represent the visible outcome of adaptive, evolutionary processes. And therefore, the community could also be expected to have patterns of distribution like species. Clements' argument is that the associations between the species of a particular community are so interdependent that the species may adapt and co-evolve within this higher level of organization. One of the pioneer works on communities is the experiment performed by Simberloff and Wilson[19] on arthropods in the mangrove islands of Key West (Florida, USA). This experiment consisted of eliminating the arthropod community of four islands of mangroves by fumigation,

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[18] Odum (1975): 122
[19] Simberloff and Wilson (1969)

and observing recolonization afterwards. Recolonization took two years, and in 3 cases over 4, arthropod communities reached equilibrium (measured in terms of species richness) close to the values established prior to the experiment. However, this theory denies the existence of ecological processes like competition. So even if there was an important theoretical development from this work (island biogeography theory), when Evelyn C. Pielou (1924-2016), suggests that identifying a community relies on the ecologist to first identify a "convenient entity" which the ecologist then "considers as homogeneous in some intuitive sense"[20], this seriously challenges the vision that a community can be a fundamental object of study and is a controversy that continues to this day.[21]

At present, a community is defined as a set of populations, hence an assemblage of individuals from different species inhabiting the same environment (*sensu largo*) in the same space, geographically speaking. In principle, the community represents all living individuals (and species) in the same environment, but it can be restricted to a group of individuals sharing a set of functional interactions in their environment or sharing the same resources. Hence, despite the reservations expressed by Pielou, the community is maintained as an object of study, precisely because it circles back conveniently to our definition of ecology, as encompassing the *interactions* between the organism and its environment. In spite of the history of doubts about the ability to identify and study communities, advances in evolutionary biology may return community ecology to its evolutionary roots.[22] Some of these problems are also starting to gain wider recognition, as ecological knowledge about communities expands in conservation. However, because the term 'ecological community' implies a definition of an ideal but non-precise distribution area, it has tended to be replaced by 'species assemblage' (referring only to a referenced area, usually related to habitat) as global databases like GBIF (Global Biodiversity Information Facility) and OBIS (Ocean Biogeographic Information System) become part of the ecologist's toolbox.[23]

Nonetheless, both groupings, the community and the population, embody similar problems of how to observe, analyze and compare them. For most of the history of ecology, and despite the sophisticated statistical methods developed, these groupings continue to depend on the intent and skill of the observer.[24] In spite of occasional calls for change, there have been little or no

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[20] The full quote is: "Before delving into the mathematics, it is necessary to contemplate the word "community" and what is meant by it. In the present context it means all the organisms in a chosen area that belong to the taxonomic group the ecologist is studying. The chosen area is usually one that the ecologist regards as a convenient entity and is willing to consider as homogeneous in some intuitive sense." Pielou (1977): 269. Her quote echos an earlier sentiment expressed by Gisin in 1949: "*De fait, la biocénotique, dont la méthode comparative conduit à la circonscription des groupements biologiques, représente une première étape dans les recherches écologiques. Elle ne fait en somme que rassembler les données d'une vaste expérience instituée par la nature quant à, la localisation des êtres.*" Gisin (1949): 93.

[21] In a review of the state of community ecology (Lawton, 1999) characterized it as having "the worst of all worlds" (p. 181), creating a "mess" because all the "contingency is itself too complicated to be useful", was countered by (Vellend, 2010) who wrote that "even theoretical community ecology can be considered a mess for much the same reason" (p. 185).

[22] Johnson and Stinchcombe (2007)

[23] A typical study in conservation, like the recent Parravicini et al. (2014) uses global databases of reef fish species occurrences where no indication of community is given. Findings are thus discussed in terms of assemblages, not communities.

[24] Doak et al. (2008) stated about ecological dynamics and prediction that: "[…] the extent and frequency of major "surprises" in ecological systems argue for substantial humility about our predictive abilities, and that current effort to enumerate uncertainties must be better tempered with the recognition that ecological models fail to capture many instances of population and community dynamics." And that "[…] an ecological surprise occurs when an

means invested in repeating earlier observations.[25] The rarity of long term experiments in community ecology suggests that the scientific practice did not value replication. Hence, it could be considered that the body of ecological works are probably long overdue for re-evaluation.[26]

Interactions. Despite a strong tendency to focus on different objects of ecology in designating specialties (community ecology, landscape ecology, population ecology, …), ecological studies are primarily concerned with observing and understanding interactions. The majority of these interactions concern the property of (species) co-existence. For instance, when the members of a community find all the conditions for their coexistence in the environment, the community is then qualified as a biocenosis. The property of co-existence implies persistence in time and space of the populations and that interactions taking place in the biocenosis are not leading to exclusion.

Usually, ecological interactions are listed in textbooks as: competition, predation, parasitism, commensalism, mutualism, symbiosis, *etc*. In other words, these terms describe how the interaction is qualified, but not how it is measured, nor the processes involved. For example, mutualism, identifies two species that interact each other increasing their mutual benefit in terms of growth, or survival, or reproduction ... that are not explicitly defined. Besides, interactions are often considered to be exclusive of other antagonist ones. So, mutualism implies that there is no competition among individuals of the populations. This is consistent with the large body of literature on interactions[27], which has focused on classifying interactions in terms of species on one another (and thus reasoning at the level of a population and within communities). Thus ecologists tend to treat the populations in communities as homogenous units developing homogeneous interactions. But how is the genetic diversity within the population[28] taken into account in this conception of interactions? Especially when direct effects are clearly defined as the effect of one individual on another - a definition that should include characterization of their genetic heritage as well as behavioral markers and biological state.

Mostly ecologists use the term 'interaction' as a catch-all for what must ultimately be a series of actions and reactions between ecological objects. The vocabulary of ecological interactions arose in the latter half of the 19th century. At this time, zoologists began developing terminology to describe observations about how plant and animal "societies" interacted and mixing vocabulary between sociological and biological contexts was quite common.[29] Even the means to classify

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experienced biologist with clear, well-informed expectations faces outcomes or patterns that strongly contradict these expectations." This article provides a long list of examples of the fallibility of ecologists' "experience" being confused with objectively tested truths.

[25] This was a major theme in the Russian biologist Georgy F. Gause's (1910-1986) ecological works between 1930 and 1950. See also footnote 26.

[26] This has been presented under a different aspect by Scheiner (2013), who suggests that the absence of engagement in "the heart of the scientific enterprise: theory testing" is undermining ecological progress.

[27] For example, Menge (1995) and references therein.

[28] See Table 1 of Johnson and Stinchcombe (2007) where these authors summarize the implications of questions like these in their proposition for a new synthesis of community ecology and evolutionary biology. For example, how would the recent work of Jacquet *et al.* (2016) on diversity-stability relationships change if genetic diversity was included in their analysis?

[29] Mutualism was even co-opted by anarchists as a sociopolitical slogan in the late 19th and early 20th centuries. Sapp (2004) goes on to explain how this politicization affected negatively the teaching of this concept and another term in biology (symbiosis) at this time.

interactions were initially fixed by a sociologist (E.F. Haskell, 1906-1986) with his co-action compass[30] of human interactions. His approach was taken up by the Odum brothers in their extremely popular textbook on ecology by the early 1950s.[31] Interactions are thus presented between two entities as positive or negative with respect to each entity and have a 'direction', but they are rarely quantified. While the visualization of interactions as a compass permitted gradients of interactions strengths to be represented, it nonetheless did not clarify the definitions beyond this.

One category of interactions which has fared better in terms of measurable quantities, concerns exchanges within food webs and between trophic levels. Usually described at the species-level (*e.g.* "plant-herbivore", "host-parasite" or "predator-prey") they indicate the transfer of matter and energy between living organisms and its transformation or assimilation. Trophic levels summarize the interaction between the organism and the resources it uses to survive. Unlike the general categories of interactions, trophic studies came into their own as both stable- and radio-isotopic tracer analyses became widely accessible. Trophic functions combine behavioral information with the trophic level. Thus the species which scavenges (a behavior) and sustains its growth by consuming non-living organic matter is assigned a trophic function as a recycler or participating in degradation. However, conceiving of trophic levels as a hierarchy undermines the structural metaphor of the food web and over-emphasizes the verticality of an ecosystem in many instances, ignoring the fact that trophic relationships in communities are made of many weak interactions and few strong ones, which leads to metaphorical short-cuts applied to very specific contexts (*e.g.* top-down or bottom-up controls in food chains) that obscure the cyclic nature of ecological systems.

Behavioral studies on interactions were codified between the 1920s and 1950s, culminating with the publication of Tinbergen's 1963 text entitled "On aims and methods of Ethology".[32] He proposed a means to explain behaviors through structured consideration of possible proximate or ultimate causes, and diachronic or synchronic perspectives.[33] This approach aims to distinguish between individual and evolutionary contexts; in this manner, he laid out how different interpretational contexts affect both the questions asked and the explanations given. Tinbergen sidestepped the debate between biologists and ecologists about the frontier between their disciplines, and permitted all scales of study to be admitted as explanation. This was an important advance, but behavioral studies continued to operate within a somewhat murky theoretical framework. Behavior was defined by Tinbergen as "the total movements made by the intact animal".[34] However coming up with an operational definition that has no taxonomic bias has been far less successful. In 2009, making a parallel to the ongoing debate about the definition of

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[30] Haskell (1949). His initial grid representation (called the 9 co-actions) was proposed in an earlier 1947 publication. Haskell was a sociologist and anthropologist who left mainstream academia by the end of the 1940s to pursue a personal ambition of building a unified science in which scientific specializations would disappear.
[31] Odum EP. 1953. The Fundamentals of Ecology. WB Saunders, Philadelphia. 384 pp. Later editions were co-edited with his younger brother, Howard T. Odum.
[32] Tinbergen (1963)
[33] Today this approach is called Tinbergen's Four Questions.
[34] Tinbergen, 1955; cited in Levitis *et al.* (2009).

"species", and the need for common definitions, Levitis and co-authors identified 25 different definitions for behavior in use![35]

For an ecologist, individuals are considered to have an organized and functional structure, and are defined to be alive when they exhibit a metabolic activity; they develop capacities of autonomous replication, and these capacities condition interactions they have with other organisms and their environments. Interactions decomposed into actions and reactions can be biochemical, biological, behavioral responses to environmental cues. Today, thanks to the wide array of means available to monitor the activities of living organisms,[36] through this enhanced capacity and broadened spectrum of data acquisition, two essential questions arise: what precisely are the relationships between ecological processes, interactions and species populations, and how do these depend on the perceptual capacities and sensibilities of an *individual* organism? Some definitions of ecology as "…the study of living organisms at the level of the population and the community…"[37] are in complete disagreement with these ideas. Indeed, focusing on populations and communities may have distracted ecologists from studying interactions where they occur: at the individual level. In addition, today, there remains very little clarity on units of measurement of interactions in the literature.[38] In their majority, changes in biomass or numbers or densities of individuals of different species being studied are used. But these measures can only be rough 'stand-ins' for underlying processes.

Ecological systems. Even if interactions remain somewhat ill-defined, ecological systems, in particular *ecosystems*, depend directly on them. For ecology, the year 1935 marks the replacement of the vague concept of 'environment' with the concept of an ecosystem. Tansley's original discussion,[39] which is deeply informed by long-standing arguments about how living organisms should be studied, is a scathing criticism of the inclusion of vitalist ideas in the "whole" as described by Clements. Tansley, sets aside any concerns about ill-defined roles for spiritual causes, and argues for a materialist approach: the object of the living organism in a system of other entities, whether these are other living organisms or parts of the habitat. According to the principle that each living organism is in a continuous relationship with its environment (among which are other organisms), they form a set of interacting components, which has a particular structure and functioning and within spatial boundaries which can be precisely defined. He qualifies the ecosystem using system approaches, even if a general theory of system was the object of later work of von Bertalanffy. Mainly, he has set one of the fundamental features of ecosystems "which are, from the point of view of the ecologist, the basic units of nature on the face of the earth".[40]

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[35] Levitis et al. (2009). These authors proposed to use the following definition based on a survey of researchers working in behavioral sciences: "[…] behaviour is the internally coordinated responses (actions or inactions) of whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses more easily understood as developmental changes." (Levitis et al., 2009: abstract). It remains to be seen if this is adopted.

[36] Le Galliard, Guarini and Gaill (2012)

[37] Southwood (1980)

[38] An example of the variety of information collected about mutualistic interactions, see Table 1. in Bronstein (2009). A recent comparison of the methods of analysis of animal movements by Gurarie et al. (2016) discusses the importance and problems inherent for interpreting individual animal movements.

[39] Tansley (1935)

[40] Tansley (1935): 299

The real target of Tansley's presentation is the framework of ecological succession and the early 20th century debates around dynamic equilibrium. His goal was to replace the vague, romanticized supraorganism metaphor of community favored by Clements, with a concept that would enable ecologists to link the persistence of the system to the existence of a stable equilibrium state. Along the way, using 'ecosystem' transformed ecological studies into something more analytical, efficient, and modern. 'System' was perfectly in step with newly industrialized research laboratories of the mid-20th century. It dispelled (briefly) persistent criticisms of ecology as a throwback to 18th century natural history. Ecosystems could be described at any scale. Within this conceptual framework, organisms are considered as both whole and elementary pieces of ecological systems. Tansley attempted to convey a message long-sought by ecologists' intent on mimicking the scientific success of physics[41] of having discovered a form of universality. Ecosystems could be anywhere and contained all scales of observation.

Meant as more than a buzzword though, the choice of 'system' explicitly requires links exist between entities or objects of study. From this idea, a new science of ecosystems arose focused on understanding the functioning of the ecosystem and the transfers, or fluxes, of energy and matter[42]. When links were assumed to be able to represent ecological interactions, ecosystem process-based models were born (Figure 2-2). These models replace interactions with mathematical definitions of how the state variables of a system (describing objects or compartments) are related. The ecosystem is then a conceptual definition of a natural phenomenon and not a 'thing' or a supra-organism to be discovered through description (like a community). It appeared quickly that is could not be a basic unit either, because it is not irreducible and mutually exclusive to any other ecosystem, but it fits perfectly with the ideas of Lotka, Volterra, Gause and other scientists working on a "physical biology"[43] in the 1930s. Later, American radioecologists employed to predict how radioactive elements would circulate in the environment, used the ideas of Odum to develop the earliest known simulation model of a multi-compartment dynamic ecosystem.[44] Their approach set the basic elements of ecosystem functions. Ecosystem functions became structured by the conversion of solar energy to chemical energy by autotroph organisms from photosynthesis, the flux of this energy to fuel production of organic matter from inorganic nutrients, and the transformation of inert materials into living matter. This prompted closer connections between ecology, biochemistry and chemistry (*e.g.* photosynthesis leads to the production of sugars and oxygen, from a source of carbon) which had been hinted at since the 19th century by the early aquariologists like Robert Warington tinkering with their miniature worlds.

Working in between the complexity of 'real-world' systems and simplified ecosystems.
Ecosystem provided a single word for all earlier concepts that attempted to represent the

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[41] See discussions on this in McIntosh (1985).

[42] Besides R. Lindeman's (1915-1942) important work on lake ecosystem dynamics, published between 1939-1942, the influential energy flow diagrams of H.T. Odum (see for example, Odum, 1957, Figure 7) helped to spread these ideas, among US ecologists.

[43] Gause (1934).

[44] "It seems natural to generalize the concepts of compartment models to include whole populations of organisms and masses of environmental materials such as air, water, soils, or organic litter lying over the soil which together constitute the ecosystem covering a specified area of the earth's surface." Neel and Olson (1962): 2. See also Figure 1 of the same publication.

essential unity of biological, organic entities and their non-living, abiotic, environment. However, no matter how complex the models were, they appeared to be quite distant from any ecological properties[45], and seemed to deviate from the initial goal of ecologists to explain how associations of different organisms, their attributes and possible interactions, produced the observed distributions of populations (hence, species) on the planet. The number of species and the complexity of a large variety of environments in the 'real-world' were cited repeatedly to be unsuitable for theory and models. Therefore, while classical and evolutionary biogeography focuses on observed species distribution, neglecting interactions as structuring factors[46], ecologists, and mainly quantitative ecologists, focused on small systems of interactions, involving few species in simplified environments, that they can study both *in vitro* and *in silico*. But, what good were two species predator-prey models when communities contained dozens? For example, changes in any of the rates of the population attributes listed in Table 2-1 will produce oscillations in the population abundance over time, even extinction.[47] In addition, when loss of species becomes a societal concern, can models of ecological interactions help understand or explain the consequences of different human behaviors on the ecological quality of the environment? Or, if the distribution of species is understood in relation to how well their conditions of existence are fulfilled in a particular environment, how would disturbances in these conditions affect density-dependent selection pressures and the relative fitness of different sub-populations? What are the roles of behavioral traits in these outcomes?

Simplified ecosystem models do not seem to be able to represent such complexity, and complex ecosystem models have properties that are very difficult to characterize exhaustively, and always come across as far from what can be observed in Nature. Nonetheless, simplified models can provide an important theoretical support for experimental investigations. In the 1930s, G.F. Gause designed his experiments with protists and bacteria in microcosms to match the mathematical model constructed to represent it.[48] The goal of all these careful observations and controlled experiments was the discovery of scientific laws and principles that would enable ecological forecasts. Many, many experiments were executed using this and similar approaches by other ecologists, but few developed associated models as Gause did. In addition to simplification of the experimental system, there have also been pseudo-controlled experiments attempted at field sites, when for example a small area of land would be cleared and the stages of its recolonization could be monitored (like Charles Darwin's small plots in his back lawn) or the amount of nutrients available on plots could be manipulated, like in the Park Grass experiments.[49] Even very large scale experiments, involving entire islands cleared of one group of organisms can be treated this way.[50] However, no unified framework of ecosystem modeling has emerged to date from these approaches, which suggests that new tactics are needed.

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[45] May (1973)
[46] Hubbell (2001)
[47] May (1976), May, R. Chapter 2. Models for single populations. 4 - 26.
[48] Gause (1934)
[49] Lawes et al. (1882)
[50] Wilson and Simberloff (1969)
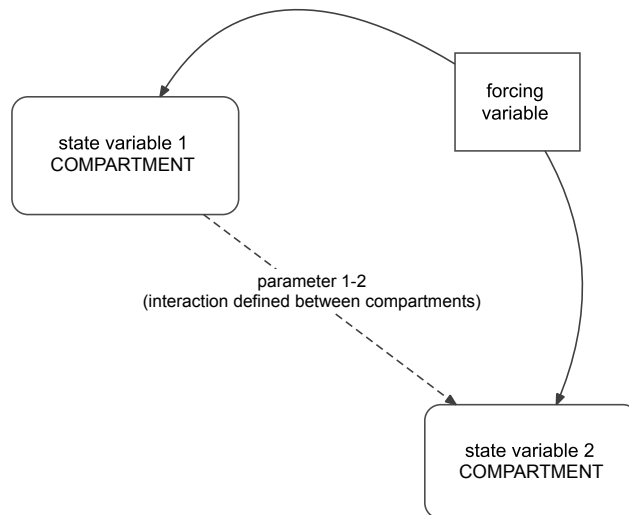
FIGURE 2-2. Anatomy of an ecological model

The simplest representation of an ecological interaction between two state variables, has at least one parameter and a forcing variable. The forcing variable describes the external forcing by dynamic environmental conditions such as light, temperature, or tides. State variables, represented as compartments, are written as a function of the parameters, forcing variables, or other state variables, for a given time interval. Because these vary dynamically, they are written as differential equations. Forcing variables are fixed externally, and are not affected by the model calculation of the interaction being represented between the state variables. A forcing variable may come from actual measurements or be generated by other models (a classic example would be the North Atlantic Oscillation). Parameter values may be taken from literature or data. The model is calibrated by comparison of model output and any data available from observations or experiments.

Modified from Figure 2, in Coston-Guarini et al., 2016a.

Despite these difficulties, it is important to cite that there are two ecological themes for which ecosystem models are absolutely necessary to support experimental work:

1. The origin of life and synthetic ecology. In the origin of life, ecosystems were assumed to be initiated by simple life forms, unicellular without nucleus and few rudimentary organelles. Many questions, from the conditions for the formation of first cells, to the development of first populations, are subjected to experiments and models.[51]

2. Life support systems for space travel. Many developments have been done on life support systems using the form of simplified ecosystem in which humans are just one component.[52] Despite of decades of combined efforts, the development of an operational device remains unachieved, an ample illustration of the difficulty of controlling ecosystems.[53]

Together these two topics have generated many studies on minimal ecosystems that are in their majority, theoretical. They have, nonetheless, many important applications for understanding fundamental processes related to functions, fluxes of matter and energy, and the coexistence of species, as I shall demonstrate in Chapter 6.

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[51] Krakauer and Sasaki, 2002. Proc. R. Soc. Lond. B 269: 2423–2428.
[52] Tong, L., Hu, D.W., Liu, H., Li, M., Fu, Y.M. Jia, B.Y., Du, F.Z., Hu, E.Z. 2001. Ecological Engineering. 37(12): 2025-2034.
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CHAPTER 3

TROUBLES CAUSED BY THE ABSENCE
OF ECOLOGICAL "LAWS"

"To kill is nature's first law"

-- Shelford (1913): 8

Is Ecology in an existential crisis? In 2013, the British ecologist, Georgina Mace wrote in an essay that was published in the journal Nature, that "a new kind of ecology is needed" from which "general conclusions" can be made.[1] Two years later, David Inouye, an American ecologist, weighed in on "The next century of ecology"[2] in an editorial published by Science. Both were at the head of the largest organizations of professional ecologists in their respective countries and give their visions of future ecological research: a more open and interdisciplinary ecology, a growing importance for ecological information in societal decisions, and emergence of prediction and forecasting as a new research *leitmotif*. However, the oft decried both the profusion and confusion of ecological models, theories, and paradigms[3], which leads to dead-ends, suggesting that the discipline is probably not on the verge of becoming a predictive science. This was recently driven home by an event recorded from the 2013 national meeting of the Ecological Society of America (ESA).[4] Anthony Ives, the ESA's MacArthur award winner for 2012, asked the audience if ecological researchers should focus on describing scientific laws: two-thirds said no. Clearly, there is a fundamental division among ecologists about the scientific framework in which they operate.

Traditionally, ecology has not been a science focused on prediction.[5] Yet, finding why theories do not make good predictions is to "separate what works from things that don't work".[6] So if this is not happening, then some of the concern expressed about the relevance of ecology may not be unwarranted. Possibly this concern is also about a current research funding climate driven by key words like "innovation", "new technologies" and "risk management". Given the origins of ecology, the unstable institutional and disciplinary context, as well as the difficulties in defining the objects of study reviewed in the previous chapters, some of this questioning about the relevance of ecology is justifiable today. But even if this type of frustration appears regularly today in blogs,[7] debate about the nature of ecological research has been simmering in

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[1] Mace (2013): 192

[2] Inouye (2015)

[3] A small selection of articles on the topic: Palmer (1994); Goldberg (1995); Graham and Dayton (2002); Hansson (2003); Scheiner (2013).

[4] O'Dwyer, J. 2015. The Hidden Power of Laws of Ecosystems. Nautilus Issue 29. http://nautil.us/issue/29/scaling/the-hidden-power-laws-of-ecosystems.

[5] This has been recognized as a short-coming for several decades, Houlahan *et al.* (2016) provides a summary of salient aspects of this debate.

[6] Keddy (1992): 235

[7] One of the most widely read blog in Ecology, Dynamic Ecology (https://dynamicecology.wordpress.com/), run by Jeremy Fox, Meghan Duffy and Brian McGill, often deals with this topic.

the literature for several decades; many authors expressed their wish to synthesize ecological knowledge into universal principles and scientific laws.

Eighty years ago, E.F. Haskell suggested that part of the problem lies with the semantic construction of ecology.[8] In a phrase, he suggests that ecologists are looking in the wrong place, and that the forest of poorly defined, qualitative terms have no direct relation to underlying processes the ecologist wishes to study. Furthermore, Haskell (p. 4) points out that "Mathematization of a scientific theory is not an addition to it, like a graft on a wild tree, but a change in the nature, […] a somatic transformation." In other words, using mathematics to represent a theory, which was previously only a descriptive statement (even a metaphorical one, like the supraorganism of Clements), transforms its very nature from something that is understood only by those who have read the same textbooks, to one based on common (dare I suggest, universal?) definitions.

In a review of the state of ecological theories dating from 1976, Peters wrote that there are no theories of ecology, but only tautological arguments.[9] All of the major theories of ecology are dismantled by him in this paper: competitive exclusion, predator-prey models, monoclimax and succession, diversity, Hutchinson's niche, spatial heterogeneity and stability. In each case, he describes how the original arguments are only *ad hoc,* and cannot be used to make predictions from empirical studies. Returning to the conclusions of Peters (p.11):

> "Tautologies may be useful logical aids, but they cannot replace true theories. Unless ecologists are careful to distinguish the two, their confusion may produce a body of thought resting on metaphysical rationale rather than empirical, predictive science."

Peters' work was met with dismay at the time it was released.[10] Nonetheless, not only his work but also the body of astute (and somewhat repetitive) critiques of ecological work, have been largely unheeded. Why? One reason could be that it can be difficult to admit that part of the bargain of doing scientific research is accepting that we might be wrong.[11] Another answer may lie with the responses to these publications: the critics offer *only* criticism, and few solutions.

Over the past decades, the failure to discover or develop Ecology as a predictive, laws-based science has been ascribed to:

- failure to replicate

- failure to develop comparative studies

- failure to quantify or use hypothesis testing

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[8] Haskell (1940); McIntosh (1985). It is unclear if this is the same EF Haskell who proposed the co-action theory of interactions later (1949).

[9] Peters (1976). This paper and several others eventually led to the publication of a book "A critique for ecology" (1993). The first chapter reviews the literature of earlier crises in ecology.

[10] A small selection of reviews and counter-reviews of the work: Lawton (1991), Beal *et al.* (1993), Scheiner, (1993), Shapiro (1993).

[11] This is what the sociologist R.K. Merton ascribes to the quality of humility necessary to be a 'good' scientist in his 1973 model of science communities Gingras (2013).

- failure to study process

- inadequate data coverage, data collection

- absence of common paradigms (*e.g.* contextual dependence of terms, Figure 2-1)

- absence of historical perspective (revision, recursion)

- absence of mathematical language

- inherent complexity of Nature

- over specialization of ecologists (and thus lack of collaboration)

- no applicable use demonstrated

Some of these challenges may be resolved with new technological solutions (*e.g.* the expansion of global databases of environmental and ecological observations). So perhaps we are looking at a Kuhnian problem of the mismatch between technical and theoretical development? Certainly, organizing internationally-sourced global databases has encouraged the normalization of descriptions and measurements. Ecologists have begun producing new comparative studies from these data that could not have been possible only a few years ago.[12] Meta-analyses highlight discrepancies in the assumed responses of different organism groups to climate change, as well as problems of data granularity.[13] Other reasons on the list (the absence of mathematical language, hypothesis testing and replication) are less of an issue today than even a decade ago because of changes in computing tools.

If a predictive ecological science is a desirable objective, then why hasn't a body of laws specific to ecology come about (yet)? The very persistence of the issues identified by Haskell, Peters and a host of other authors implies another underlying problem exists: ecologists are not trained to work within a unified conceptual framework of common principles. Indeed, the paradigms of scientific progress in ecology do not rest on testing and building a body of universal scientific law.[14] Ecologists use the laws of physics and chemistry, but they have none of their own. When Houlahan *et al.* (2016) stated in their abstract, "Models are where ecological understanding is stored and they are the source of all predictions – no prediction is possible without a model of the world", these authors seem to miss the point that models are not the problem (models are only as good as the current paradigm), but the *way ecology is done is the problem*, *i.e.* its scientific practice has not been concerned with building a predictive science from the beginning.

Styles of reasoning, ways of knowing and epistemological paths. Several authors (and a majority of the ecological community if the poll held at ESA in 2013 is representative) have questioned if laws are really necessary to do good science. This poses a very fundamental question: what does <u>good</u> scientific work look like? Classical ideas about 'good' scientific

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[12] Some examples from the marine realm include: Halpern *et al.* (2008); Lester et al. (2009); Lotze and Worm (2009); Micheli *et al.* (2013).
[13] See for example, Poloczanska *et al.* (2013), Figure 4.
[14] Lange (2005)

research are based on the approaches of Descartes, Galileo and Newton, and the breakdown of a problem into smaller and smaller parts (the fundamental units, or "atoms" of a discipline) that can be studied independently. The original 'entity' (or whole) is reconstituted using the mathematical relationships derived from studying these units: the whole is the 'sum' of its parts. These mathematical relationships make up the body of scientific laws used in disciplines like physics and chemistry. That this has not yet happened in ecology along with the absence of fundamental laws continues to fuel debates on the status of ecology relative to physics, for example. Thus, on prediction, Keddy wrote in 1992:

> "Physicists can build bombs and solar panels. Chemists can make napalm and plastic. In each case their knowledge leads to obvious outcomes-and if they are wrong, the bridges fall down, bombs fail to explode, and so on. But what of ecologists? What, if anything, are outcomes of our work, and how would anyone know if we were wrong?"[15]

In essence, we have reached the crux of the epistemological conflict at the heart of ecology hinted at earlier. Accordingly, the science of systems (as described by Ludwig von Bertalanffy[16]) becomes important when the limits of observation and analysis are reached. Tansley's ecosystem concept is therefore a critical step forward in ecological theory.

We cannot expect that scientific progress can be a linear, orderly progression. Knowledge creation and epistemological progress are dynamic, iterative processes. One possible conception of these relationships is proposed in Figure 3-1. The diagram shows how scientific knowledge could be created through interactions between groups of practitioners. Envisioned as continuum, scientific knowledge does not exist separately from all other forms of knowing. Unlike other models of knowledge creation which are philosophical constructs, this schematic arose during the initial discussions of a theory about collections (or material knowledge).[17] The goal was to transform the representation of a collection from a physical description of the amount of space required to store it, into a set of probabilities that this collection contains physical evidence for each link and/or compartment shown in Figure 3-1. There are four different points of departure for a scientific inquiry: three stances on knowledge manipulation and creation (practitioner+user,[18] applied theory or 'engineer', and 'scientist' where theoretical

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[15] Keddy (1992): 235

[16] The conditions of classical scientific methods "are not fulfilled in the entities called systems, i.e. consisting of parts "in interaction. […] The methodological problem of systems theory, therefore, is to provide for problems which, compared with the analytical-summative ones of classical science, are of a more general nature." von Bertanlanffy (1968): 19.

[17] The goal of this project (presented at several European conferences on university heritage between 2011 and 2013) was to create a method for estimating the relative scientific value of objects likely to be held in university heritage collections for re-use in new research topics. This was designed to augment standard museological or archivists' descriptions of collections with a description of their potential as a research instrument instead (*e.g.* Wissenschaftsrat, (2011)).

[18] This is similar to "tacit knowledge" proposed by Polanyi in 1958 (Personal Knowledge: Towards a Post-Critical Philosophy. University of Chicago Press.) This type of knowledge is considered the most difficult to transmit in written or verbal forms (as in skills that are transmitted or learned through demonstration and shared experience). It shares some similarities with "local ecological knowledge" that has been widely promoted in ecosystem-based management.
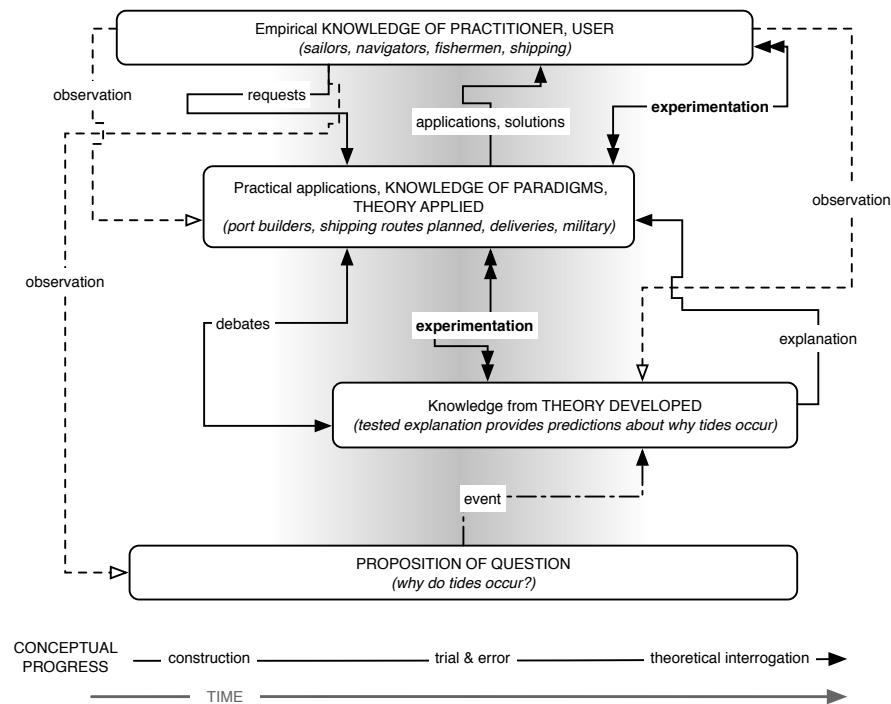
Figure 3-1. Proposition for the construction of scientific knowledge from four different points of departure, or 'ways of knowing'. The points of departure for a scientific inquiry are: knowledge manipulation and creation (practitioner+user, applied theory or 'engineer', and 'scientist' where theoretical development of explanation and prediction happen) and a fourth category (the challenger, or questioner, who is either already a member of one of the three groups or an outsider) that provokes investigation from any of the three other nodes. Each node could also represent a different community (user, manipulator-builder, researcher, general public). Pathways of exchange are indicated with labelled arrows. In this diagram no single group functions in isolation and no hierarchy implied.

Knowledge creation is thus represented as a dynamic, iterative process, dependent on the individual experiences and intentions of people involved and historical contingencies. The conception we have of knowledge creation affects profoundly what the scientific practice of different disciplines values as evidence, including the role of theory, prediction and laws. It also guides how both collectors and managers decide what artifacts and objects are worth saving in heritage collections of different sources and types. These processes determine what types of evidence are considered valuable of past scientific activities and what the historical record of a particular discipline consists of (see also Figure 8-3).

development of explanation and prediction happen[19]) and a fourth category (the challenger, or questioner, who is either already a member of one of the three groups or an outsider) that provokes investigation from any of the three points of view. Interactions may lead to "technology transfer", learning and additional new knowledge. Finally, no single group functions in isolation.

Depicting knowledge creation in this manner, is somewhat at odds with the wishes expressed by ecologists advocating a law-based practice and systematization of ecological frameworks cited earlier. Few of these authors see application and use as central to the advance of knowledge. They prefer to argue for new experimental facilities, or tighter integration of experimental and theoretical studies. Nonetheless, use is where theories and their explanatory power (truthfulness) are tested. Secondly, in Figure 3-1, I assume a diverse set of ideas exists at any time among different members of a scientific community regarding a particular question of theory. It is therefore expected that there will be many barriers to a common adoption of new paradigms because the community of ecologists is itself divided into different specializations or movements, as well as being separated geographically and culturally. Hence, the absence of a law-based scientific practice, which implies the absence of a common acceptation of paradigm (*e.g.* Figure 2-1), could amplify differences among ecologists and augment the probability of different epistemological paths within the discipline (*e.g.* different usages of biocenosis and community, Highlight, Chapter 2).

These differences can be even more profound. Prior to the late 19th century, the styles of reasoning in scientific investigation were very different from the relatively standardized methods in use today. The historian James Elwick has discussed how different reasoning styles and the norms of scientific practices co-existed in natural history, and later biology in England, France and Germany. One group of workers, the "analysts"[20] decomposed systems into smaller and smaller parts; organisms becoming collections of smaller and smaller parts. The whole organism was simply considered as an aggregation of these parts. This style of reasoning was prevalent among persons working in museums with collections, for example, and according to Elwick, "analysis:synthesis" norms were imported from France to England in the early 19th century. He contrasts this with the "palaetiological" research style popular in Germany[21] used by those investigators who worked with aquaria and vivaria to make observations over long periods of time of the developmental stages of single organisms or in microcosms. Then, the analyst-type reasoning pre-dates the palaetiological style among British naturalists simply because the tools necessary for maintaining organisms alive, were almost unknown in England prior to about 1840. As Elwick recounts (Elwick, 2007: 57):

> "In 1848 and 1849 Carpenter failed to get much support. But over the next seven years palaetiology came to challenge analysis:synthesis as a useful style for life researchers. During this time vivaria began to spread throughout Britain – made

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[19] These types of knowledge are very close to declarative and procedural knowledge, and are explicit knowledge. Declarative knowledge is about knowing facts and procedural knowledge is knowing how to accomplish something.

[20] Elwick (2007)

[21] "von Baerian embryology in 1837" Elwick (2007): 38.

cheaper by the removal of the glass tax in 1845, publicized at the Great Exhibition, and exemplified in the opening of the 1853 "Fish House" marine aquarium at the Zoological Gardens."

Thus each approach proceeded from a different theoretical framework, with different tools, and values different types of evidence when examining the same object of study (the organism).

Finally, these possibilities of multiple origins and parallel paradigms raise many questions about disregarding the significance of the epistemological context of earlier works in ecology when they are re-used in meta-analyses and for hindcasting (Table 3-1). Besides differences in the techniques and standards of analysis and evidence, the central problem is to evaluate correctly the original *intention* of the creator of earlier works. This is therefore a sociological and historical question.

Table 3-1. Common data re-use issues in environmental and ecological sciences
Historical ecology studies must consider a suite of issues when preparing data for a reconstruction study. These problems engender a number of important research challenges for ensuring the quality of the data and its usability in other research contexts.

Issue	Remarks
Provenance and traceability	Critical for determination of ownership, assigning legal responsibility, giving credit and preserving context of the original object. Ensures the traceability of uses and results during re-analysis and can be used to track changes with entity versioning.
Data dispersion and gaps	Gaps in records, gaps in time, lack of spatial overlap, fragmentation. Gaps also appear from an incomplete or impeded discovery process. Proposed remedies include: international data warehousing and discovery infrastructures (like GBIF specimen records, the Dryad data repository, GenBank, Fishbase) and portals (*e.g.* OBIS). This infrastructure is fragile and not sufficiently guaranteed over the long term (*e.g.* the now defunct US National Biological Information Infrastructure). When is interpolation valid?
Data heterogeneity and interoperability	Need for equivalences and cross-calibrations. For example, data collected by researchers for different purposes is considered heterogeneous when there are no equivalences available. Can also refer to different data types (i.e. isotopic, genomic, temperatures, qualitative sources ...) or data collected using conventions prevalent in different disciplines or different cultures and time periods.
Scale of data, scaling properties	What is the scale of the original data? Local or regional? Usually in terms of spatial resolution for a particular calculation.
Systematic errors, uncertainties	Bias estimates may be addressed through reconstruction, but how can it be consistently estimated? How to address error propagation in re-analyses? Strong demand for reporting standards in data workflows.
Absence of known reference conditions	Need for overlapping calibrations between different measurement methods, instruments and tools. Important for evaluating applicability, bias and interoperability. Missing units of measurement.
Absence of common standards for quality control, quality assurance, and in cataloguing (metadata)	All of the other issues depend explicitly on the development and communication of QA/QC standards. Errors are to be expected in most data holdings*. Need for normalized, traceable workflows (data provenance, analytical and data transformation methods) that can be used as a reference for the results derived.

e.g. analysis GIS errors in FishBase summarized in Robertson, 2008.

Scientific laws and the construction of knowledge. The notion of laws in science can be assimilated to the search for answers to a generic question: How does Nature work? Until René Descartes (1596-1650), most of the European intellectual world held Aristotelian views, which were associated with the vitalists.[22] Vitalism is concerned with identifying questions like:

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[22] This period is sometimes termed the time when "Nature was not yet like a machine".

what is aliveness? What is the mind and where is it in the body? Vitalists were fundamentally opposed to the Materialists (materialism, as in matter), who evoked only mechanistic explanations for observations. Each of these natural philosophies sought to answer two inseparable questions: what is something made of (the matter) and what is it made for (the purpose)? 'Matter' for the vitalist is not separable from its final purpose, it therefore has a final or ultimate cause to be discovered by the natural philosopher.[23] A compromise between views of materialists and vitalists was forged in the metaphor of Nature is like a machine.[24] This divergence in philosophical movements may reveal something of the difficulties encountered in defining living organisms (regarding inert matter) and the complexity of detecting a purpose (determinism) for aliveness. This new vision permitted both mathematics and science to be freed from the necessity to determine an 'ultimate' purpose, thus in investigating how Nature works, material concerns could be treated separately from vitalist questions about the spirit. This paradigmatic shift ushered in the Modern Age, post Descartes.

Concurrently, with this new practical view of natural philosophy, the ideal of a *scientific* law originated through the work of 16th and 17th century physicists and chemists (or rather alchemists). Scientific laws as originally conceived by Francis Bacon (1561-1626) are similar to laws in jurisprudence; Bacon was indeed both a lawyer and politician and he wrote the work outlining his new method for scientific inquiry[25] while in political exile. Bacon describes his vision for practical, scientific progress made through the systematic study and classification of facts. Eventually, according to his approach, both experimentation and classification would lead to the discovery of universal laws governing the relationships between the facts produced.

Using the word 'law' instead of rule, axiom or principle, invokes the inviolability of jurisprudence. This is certainly not accidental given the virulence of the confrontations between the different camps. However, this position launched another debate about what exactly a scientific law is for the "special (or inexact) sciences".[26] A simplistic version[27] of these arguments is that they are structured by opposing views on how laws govern: the externalist or internalist view (Figure 3-2). In the externalist point of view, laws are statements that govern

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[23] This conception led to the formulation of theories like the "Great Chain of Being" and the multiplication of classification systems, including all natural objects and phenomena (*e.g.* fire, water, minerals, organisms) as well as cultural objects (*e.g.* religious artefacts, decorative objects) used to organize the *cabinets de curiosités, Wunderkammern,* and Wonder-rooms that proliferated across Europe at the same time.

[24] The dualism of René Descartes. While this idea provided natural philosophers with a new defense for their studies, the pressure to conform to Church doctrines continued to be felt until well into the 19th century, especially for biological questions.

[25] Bacon's *Novum Organum Scientiarum* (1620) advocated a method based on ordered empirical investigations and use of instrumentation. He argued Science would not progress unless it used inductive reasoning based on objective evidence provided from experimentation. This he said would prevent human bias interfering in scientific progress. Both Bacon and René Descartes (1596-1650) criticized strongly Aristotelian methods (based on syllogism) that had dominated Western thought up to this time.

[26] The philosophical category of sciences that are postulated to be reducible to physics (that is social sciences, economics, psychology, biology, ecology, …). This is often referred to as the "Unity of Science" hypothesis for which Ludwig von Bertanlaffy with his systems theory was a staunch supporter.

[27] This is an extreme simplification of the nuanced debates among philosophers of science. For a more complete overview see Mumford (2005) and Dumsday (2012) as well as the entry in the Stanford encyclopedia of Philosophy on Ceteris Paribus laws (Reutlinger, Alexander, Schurz, Gerhard and Hüttemann, Andreas, "Ceteris Paribus Laws", The Stanford Encyclopedia of Philosophy (Fall 2015 Edition), Edward N. Zalta (ed.), http://plato.stanford.edu/archives/fall2015/entries/ceteris-paribus/).

(a) Externalist view

Universal governance is necessary

(b) Internalist view

Universal governance is unnecessary; laws are needed to fully describe cause and effect and the 'true effect' of phenomena in testable frameworks

TIME

(c) Laws provide an explanatory framework for reconstruction and prediction

Figure 3-2. Diagram of principal philosophical issues concerning laws in Nature and scientific laws, espoused by historians and philosophers of science. The central issue is where governance is placed, either internally or externally relative to the thing being governed. In the case of juridical laws we encounter in our cultural lives, the externalist viewpoint dominates (a). Scientific laws on the other hand are often considered as internalist (b). This is because while there are many concepts described semantically as scientific laws (rules, principles, axioms ...) identification of where governance occurs is much less clear. Is the law part of the object? external to the object? or does it mediate the relationship between the object and not-the-object? And to confuse matters further, these differences are often not clearly enunciated.

These philosophical debates have important repercussions for scientific practices. Scientific laws provide a framework for the explanation of phenomena (why they occur, cause and effect). The actual phenomena or event(s) remain the same (that is they are independent of the knowledge of the existence of the law by the scientist), even if the law (and its explanation) are invalidated. For ecology, the absence of a law-based framework weakens reconstructions of ecological trends, since there is no stable explanatory framework within which trends are tested. Thus, in (c) if the explanation changes, then the measurement, observation and even object of study may also change. Similar ideas have been discussed by Kuhn (1962) in his work on paradigm shifts and by Daston and Galison (2010) in their history of objectivity.

the behavior of other objects through direct power over the objects and a means of enforcement. This power embodies countermeasures designed to punish and regulate behaviors. Among 18th and 19th century natural philosophers and historians, this was also a reasonable conception of natural laws. Montesquieu, for example, considered there could be no distinction made between a natural law and civil law.[28]

Currently, scientific laws are considered as internalist (Figure 3-2), because where and how governance occurs is not clearly identifiable in the philosophical framework. In a view expressed by Mumford[29], scientific laws are intended to govern the properties possessed by various entities: the connections laws supposedly indicate are thus already built into the properties themselves. But, is the law part of the object, external to the object, or does it mediates the relationships the object has? These differences are often not enunciated or even known. It has been suggested that a mechanism of governance may not in fact be necessary for scientific laws at all. None of these issues have come to clear resolutions, something which seems normal since philosophers are not usually directly involved in the scientific work underlying the discovery of laws, but are analyzing the situation, *a priori*.

For ecology, Colvyan and Ginzberg (2003) have even argued that the concern expressed about an absence of laws in ecology is because there are important misconceptions about laws held by ecologists.[30] Some of their comments may or may not be warranted, but this raises a fundamental concern about what the meaning and function of scientific laws are for working scientists? In other words, could a statement about a "law" function as a rhetorical tool (a simple analogy with juridical governance) rather than a declaration of a description of a fundamental behavior? The philosopher Marc Lange has written extensively about this using ecology as an example.[31] He suggests laws in the special sciences, and for ecology in particular, could exist only under *ceteris paribus*[32] conditions, a phrase used to describe the situation of law-like statements in the special sciences for which exceptions to behaviors are permitted. In other words, and in contrast with Physics, this means that "a law need not be associated straightfowardly with a regularity".[33] The logical implication of this, is that these statements cannot be fully reduced or expressed by the laws of fundamental physics. Instead, Lange suggests collections of law-like statements represent a type of conceptual stability within a discipline.

Based on the work of Lange, it appears worthwhile to examine how the word "law" appears, or has been used within different scientific disciplines, including ecology. Finding there was no scholarly compilation of statements of laws, I used the open, crowd-sourced lists created by Wikipedia users to collect some basic information. The results are plotted in (Figure 3-3a).

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[28] Citation from Montesquieu's [Charles Louis de Secondat (1689-1755)] *Esprit des lois (*1748) in Hoquet, 2010, #33801): 53 - "Laws, in their most general signification, are the necessary relations [rapports nécessaires] arising from the nature of things." This work is better known for the ideas about the necessity of separating the three branches of government. It influenced the writers of the French constitution after the Revolution.
[29] Mumford as described in review of Lange (2006).
[30] Colyvan and Ginzburg (2003)
[31] Lange (2002); Lange (2005); Lange (2006)
[32] "other things equal", or "all other things being equal" in a scientific context
[33] Lange (2002): abstract

The first observation that could be made is that there are many terms that fulfill the same function in scientific work (*e.g.* principles, axioms, rules).[34] Each word invokes a relative level of inviolability along a continuum from laws to hypotheses. Secondly, statements of laws listed fall into four very broad categories: cultural, mathematical, natural history and physical laws (which also includes chemistry). The category of "cultural laws" are statements framed as laws which are not derived from scientific works. Categorizing statements into different disciplines becomes quite difficult when looking at publication records covering several hundred years because of epistemological processes (in this case increasing specialization and paradigm shifts) and socio-economic ones (institutionalization of research). Thus, on Figure 3-3a only six law statements from this list could be classed into the category 'Natural History'.[35] Finally, and perhaps most surprisingly, the use of laws is clearly a phenomenon which has enjoyed a certain popularity during the 19th and early 20th century.

How were scientific laws presented in early works on Natural History? Considering the historical distribution of laws (Figure 3-3a) and the position expressed by Lange, whatever we think about the necessity of scientific laws and how their governance works, scientific practice would be affected by how scientists themselves perceive these ideas in a particular discipline. Thus, if we 'believe' that a law explains something we observe, we also 'believe' that laws are discoverable, even if we are ignorant of their existence. This is sometimes called Galileo's Defense. When he was put on trial for his defense of a heliocentric solar system, he is said to have stated that even if the Pope didn't believe him it didn't make his statement any less true.

In this line of reasoning, the colossal 18th century work on natural history, entitled *Histoire Naturelle générale et particulière : avec la description du Cabinet du Roy,* or just Buffon's *Histoire Naturelle,* provides an unique example for analysis (see Highlight and Table 3-2). An emblematic work, it represents an attempt to present a unified system describing how Nature works, viewed through the lens of 18th century politics and scientific practices. Buffon's work was well-known throughout Europe and many early editions were lavishly illustrated in a distinctive style[36] that helped secure its popularity; during the 18th and 19th centuries there were so many different versions published that today there is still no definitive edition.[37]

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[34] The Wikipedia user constructed table of eponymous scientific laws (https://en.wikipedia.org/wiki/List_of_scientific_laws_named_after_people, viewed on 20 June 2015) lists the following terms in addition to "law": theorem (60), equation (20), principle (13), function (5), rule, (5), axiom (4), effect (4), paradox (4), distribution (3), formula (2), invariant (2), lemma (2), operator (2), all other terms only occur once. Only statements labelled as laws are plotted on Figure 3-3a (total number in list was 240).

[35] Grimm's Law (Linguistics), Buys Ballot's Law (Meteorology), Fitts' Law (Biology), Mendel's Laws (Biology), Zipf's Law (Linguistics), Archie's Law (Geology).

[36] The work continues to be cited for the quality of the illustrations. For example, the 'Quadrupeds' volumes contain unusual posed illustrations showing the internal structure and external appearance of different animals (de Baere 2007; Chansigaud 2009: 66-69).

[37] The series was re-edited until the end of the 19th century, as well as being translated into German, Russian and English. The various editions can have different illustrations (color or black and white engravings; anatomical illustrations were dropped from less expensive re-editions), vary in size, and completeness (Chansigaud, 2009). A scholar's edition is in progress (see *Éditions Honoré Champion*, Paris).
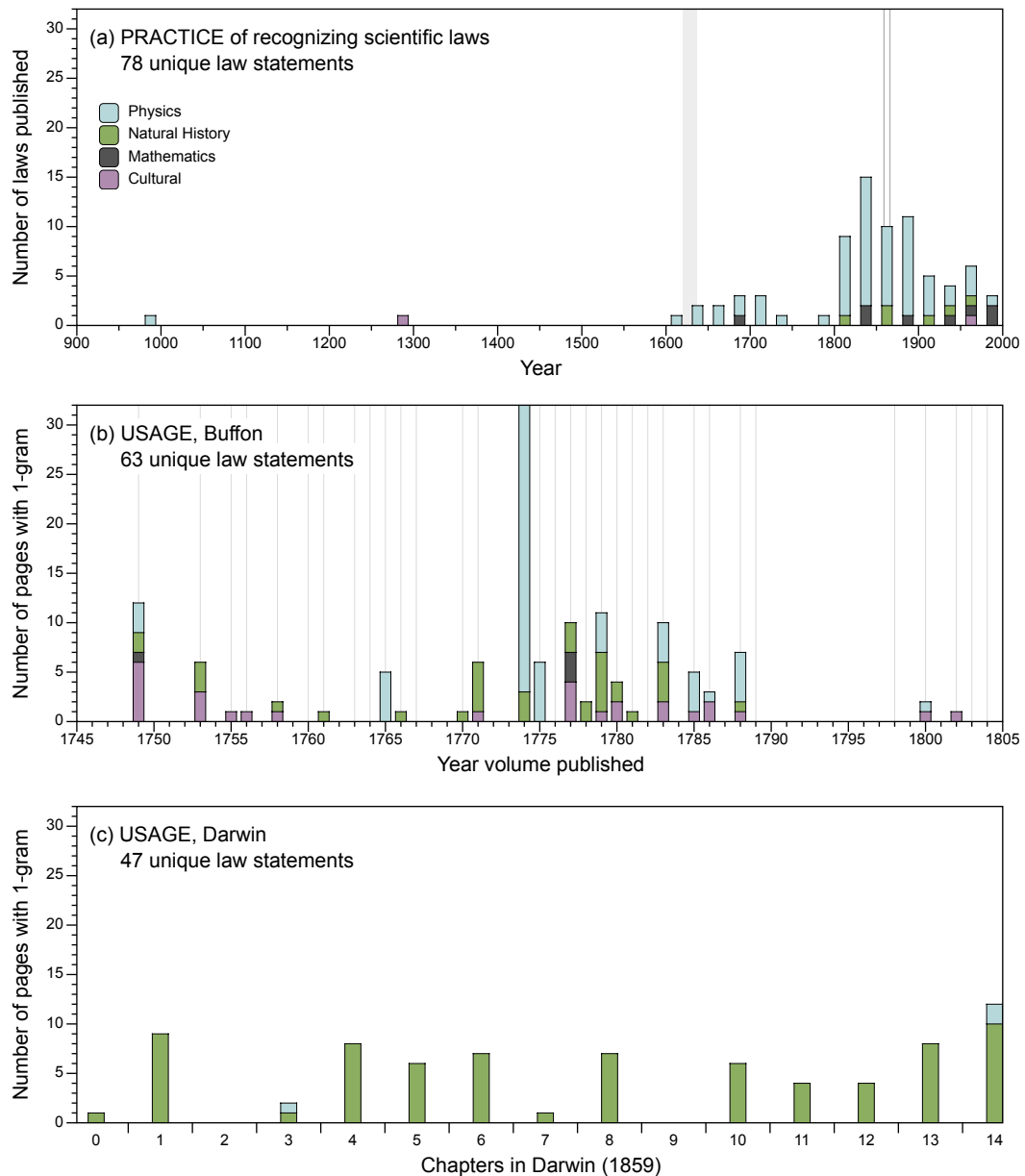
Figure 3-3. Usage of "law" in different scientific contexts. Each plot groups the instances of law into one of four broad categories of usage: Physics (and chemistry), Natural History, Mathematics, and Cultural. Laws assigned to the Cultural category are either references to jurisprudence or religious laws in the texts examined. While there are some scientific laws recognized prior to the year 1000, these statements appear to be a 19th and 20th century phenomenon.

(a) The most comprehensive list of scientific laws I located was the list of eponymous scientific laws created by Wikipedia users (viewed in June 2015). All statements and sources were checked against original published sources and with Pickover (2008). Numbers of laws are binned by intervals of 25 years since precise publication dates were not always available. The light gray interval represents the time between Bacon and Descartes' publications on the scientific method. Publication of Darwin's and Haeckel's seminal works are also indicated (1859, 1866). Most laws fall in the domain of Physics as expected.

(b) Distribution of phrases with the word "loi" from Buffon's Histoire Naturelle, grouped using the same categories shown in (a). Only 41 of the 44 total volumes were available in the online corpus (www.buffon.cnrs.fr). The gap between 1790 and 1800 is because Buffon's death and the Revolution Française and its aftermath temporarily halted publication. Laws in Physics have the highest number of occurrences. (c) Plot of the distribution of the 1-gram "law" by chapter in Darwin's 1859 edition of the Origin of Species. Darwin also uses the word law liberally throughout his work, but almost exclusively in a Natural History context. The majority of phrases refer to his ideas about morphological changes during growth, variation, and heritable traits. Of the 47 statements in Darwin, there are 44 which he describes as Natural History laws (the remaining three belong to Physics).

Table 3-2. List of the volumes in Buffon's *Histoire Naturelle* (HN) and dates of first printing.

There are substantial changes in all subsequent editions of this work over the 19th century. A definitive scholar's edition does not exist to standardize citations. Information is sourced www.buffon.cnrs.fr and digitized versions available on Gallica.fr (*Bibliothèque Nationale de France*).

Volume title	Publication year	Tome N°	Volume N° of Total	Total pages of text (from Gallica, not including indices)
Tome I : Premier Discours - De la manière d'étudier et de traiter l'histoire naturelle -	1749	1	1	612
Tome II : Histoire générale des Animaux, Histoire Naturelle de l'Homme -	1749	2	2	603
Tome III : Description du cabinet du Roi, Histoire Naturelle de l'Homme -	1749	3	3	530
Tome IV (Quadrupèdes I) : Discours sur la nature des Animaux -	1753	4	4	560
Tome V (Quadrupèdes II) : La Brébis -	1755	5	5	311
Tome VI (Quadrupèdes III) : Avant-Propos; Le Chat -	1756	6	6	379
Tome VII (Quadrupèdes IV) : Les Animaux carnassiers -	1758	7	7	378
Tome VIII (Quadrupèdes V) : Le Cochon d'Inde -	1760	8	8	402
Tome IX (Quadrupèdes VI) : Le Lion -	1761	9	9	375
Tome X (Quadrupèdes VII) : L'Ondatra et le Desman -	1763	10	10	368
Tome XI (Quadrupèdes VIII) : LEléphant -	1764	11	11	450
Tome XII (Quadrupèdes IX) : De la Nature Première Vue -	1764	12	12	451
Tome XIII (Quadrupèdes X) : De la Nature Seconde Vue -	1765	13	13	441
Tome XIV (Quadrupèdes XI) : Nomenclature des Singes -	1766	14	14	411
Tome XV (Quadrupèdes XII) : Les Sapajous et les Sagoins -	1767	15	15	207
Tome XVI (Oiseaux I) : Discours sur la nature des Oiseaux -	1770	HNO-1	16	496
Tome XVII (Oiseaux II) : L'outarde -	1771	HNO-2	17	560
Tome XVIII (Oiseaux III) : Le Crave ou Le Coracias -	1774	HNO-3	18	502
Tome XIX (Oiseaux IV) : Le Serin des Canaries -	1778	HNO-4	19	590
Tome XX (Oiseaux V) : L'Alouette -	1778	HNO-5	20	546
Tome XXI (Oiseaux VI) : L'Oiseau-mouche -	1779	HNO-6	21	702
Tome XXII (Oiseaux VII) : Les Pics -	1780	HNO-7	22	554
Tome XXIII (Oiseaux VIII) : L'Ibis -	1781	HNO-8	23	498
Tome XXIV (Oiseaux IX) : Le Cygne	1783	HNO-9	24	438
Tome XXV (Minéraux I) : De la figuration des Minéraux -	1783	HNM-1	25	557
Tome XXVI (Minéraux II) : Du Bitume -	1783	HNM-2	26	602
Tome XXVII (Minéraux III) : De l'Argent -	1785	HNM-3	27	636
Tome XXVIII (Minéraux IV) : Jaspes -	1786	HNM-4	28	448
Tome XXIX (Minéraux V) : Des forces de la Nature en général, et en particulier de l'Électricité et du Magnétisme -	1788	HNM-5	29	368
Tome XXX (Suppléments I) : De la Lumière, de la Chaleur et du Feu -	1774	S-1	30	542
Tome XXXI (Suppléments II) : Servant de suite à la Théorie de la Terre, et de préliminaire à l'Histoire des Végétaux	1775	S-2	31	564
Tome XXXII (Suppléments III) : Servant de suite à l'Histoire des Animaux quadrupèdes	1776	S-3	32	330
Tome XXXIII (Suppléments IV) : Servant de suite à l'Histoire Naturelle de l'Homme	1777	S-4	33	582
Tome XXXIV (Suppléments V) : Des Époques de la nature -	1779	S-5	34	615

Volume title	Publication year	Tome N°	Volume N° of Total	Total pages of text (from Gallica, not including indices)
Tome XXXV (Suppléments VI) : Servant de suite à l'Histoire des Animaux quadrupèdes,	1782	S-6	35	405
Tome XXXVI (Suppléments VII) : Servant de suite à l'Histoire des Animaux quadrupèdes,	1789	S-7	36	364
Tome XXXVII (Reptiles I) : Histoire générale et particulière des Quadrupèdes ovipares.	1788	HGPQO-1	37	651
Tome XXXVIII (Reptiles II) : Histoire des Serpents	1789	HGPQO-2	38	527
Tome XXXIX (Poissons I) : Discours sur la nature des poissons -	1798	HNP-1	39	679
Tome XXXX (Poissons II) : Discours sur la durée des espèces -	1800	HNP-2	40	696
Tome XXXXI (Poissons III) : Des effets de l'art de l'homme sur la nature des poissons -	1802	HNP-3	41	622
Tome XXXXII (Poissons IV) : Troisième vue de la Nature -	1802	HNP-4	42	772
Tome XXXXIII (Poissons V) : Discours sur la pêche, sur la connoissance des poissons fossiles, et sur quelques attributs généraux des poissons -	1803	HNP-5	43	871
Tome XXXXIV (Cétacés) : Vue générale des cétacés -	1804	HNC-1	44	373

The author, Georges-Louis Leclerc, Comte de Buffon (1707-1788), was a wealthy and politically savvy personage. He was nominated to head the *Jardin du Roi*[38] in 1739, only six years after having become a member of the *Académie des Sciences* based on his mathematical studies of probability.[39] From his position as chief of the royal natural history collections (which included not only objects, but also botanical gardens and a zoo) he was well-placed to write such a comprehensive work. Buffon was charged with producing a catalog of these collections. Instead, he produced a narrative to explain the Nature by developing a series of general principles from specific examples in the royal collections. When the first volumes finally came out, he was roundly criticized by his colleagues and rivals for the style and content of the work.[40] They criticized his "*système*"[41] (his version of a unified description of natural phenomena) and his prose was called opaque and overwrought.[42] Later analyses have suggested that the writing style and importance given to illustrations were a means to ensure the series' popularity with diverse publics.[43]

Still, camouflaged in Buffon's prose[44] are many new ideas (see Highlight). He develops comparisons between different types of not only organisms but also processes, by making liberal re-use of principles in physics and chemistry, as well as statistics and mathematics. The volumes of the *Histoire Naturelle* contain dozens of references to proto-theories about

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[38] This institution became the *Muséum National d'Histoire Naturelle* after the French Revolution.

[39] Egerton (1967): 189

[40] Egerton (1967): 189-263; Hoquet (2010): 34. See also the collection of citations by Lamoignon-Malesherbes, d'Alembert, and Diderot on the CNRS site dedicated to Buffon, available at http://www.buffon.cnrs.fr.

[41] "[…] le goût des systèmes, plus propres à flatter l'imagination qu'à éclairer la raison est aujourd'hui presqu'absolument banni des bons Ouvrages." D'Alembert (1751).

[42] For example, single sentences often continue over several pages and terminology changes continuously. Thankfully for the modern reader, the volumes are fully indexed.

[43] Borsari, (2011) in her literary review of the *Histoire Naturelle* has said that Buffon's writing style while aiming to create a connection with non-scientific readers, also provides all the detailed notes necessary for the expert to appreciate the presentation. It thus attempts to connect with both audiences in the same work.

[44] In spite of the remarks of Borsari, it remains unclear if this was intentional, an artifact of Buffon's writing style, or both.

adaptation and climate. Many times his reasoning is quite convoluted; nonetheless, it is difficult to judge *a posteriori* his ideas about organic evolution nearly two centuries before molecular biology was invented. Hence, despite the lukewarm reception by his peers at the *Académie des Sciences* in Paris, recent re-evaluations of this corpus emphasize its importance for the development of life sciences.[45] The ideas he expressed crystallized existing concepts within a single framework and strongly influenced some of his contemporaries[46] and successors[47] in how they discussed the distribution of species.

Buffon's *Histoire Naturelle* thus offers a singular opportunity to examine how scientific laws are used in this moment in time in a very broad natural history context (Figure 3-3, Tables 3-3 and 7). Buffon's text pre-dates several important changes in the 19th century: the re-organization of university teaching and degree programs structured by disciplines, the spread of industrialization and urbanization, and finally the social movements for the preservation of

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HIGHLIGHT. New ideas introduced by Buffon to Natural History

The American historian of science, Frank N. Egerton has summarized the new ideas in Buffon's texts which later play a role in the development of ecology and evolution. Buffon:

argued that the only true object of study in nature could be the individual organism and not groups of organisms;

was against the Linnaean hegemony of a taxonomy based on morphological characters;

developed an idea of the species which was based on a historical succession, the ability to mate and produce offspring and rejected the idea of a species as a fixed object;

proposed that there were places where particular animals or plant originated (centers of creation) and that changing climates may have permitted migrations;

suggests the size of an organism can limit the capacity to multiply when he remarks that large organisms are less numerous than small ones; and

developed an idea of population growth and demography related to the mass produced (Histoire Naturelle, Vol. 2, Ch. 2 - The Elm).

Buffon was well aware of the dynamics of natural systems but believed there were fixed limits in which they fluctuated. As such, he argued for a physiological conception of the description of organisms. This led him to begin to tabulate information about the life histories of different animals, including the basics traits of population dynamics (sex ratios, breeding periods, gestation, sexual maturity, numbers of offspring, lifespan, mortality) and introducing various causes for population increases and declines (predation, disease, famine, climatic events). But he presents this information as a series of examples for specific species (including humans) spread over several volumes. He also produced tables of estimates for the lifespan of persons, but not for other organisms (Egerton (1967): 195).

These appear in Egerton's series on the history of ecology published by the Ecological Society of America Bulletin (http://esapubs.org/bulletin/current/history_links_list.htm).

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Nature which arose in reaction. The *Histoire Naturelle* resembles today's Wikipedia because of the exceptional number of resources he had access to. However, it differs in that it represents a system established by a single man who was in an exceptional position. Hence, Figure 3-3 is considered a snapshot of the usage of laws in a scientific context from one viewpoint, instead

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[45] See Egerton (1967), Hoquet (2010), Sloan (2014), and references therein.

[46] For example, J.F. Forster's (1729-1798) thinking about islands and latitudinal gradients in diversity. Forster and his son Georg accompanied Captain James Cook on his second voyage in the South Pacific (1772-1775). He published a synthesis in 1778 comparing island and mainland species and also suggests that temperature may be a factor in controlling their latitudinal distribution. His son later became a close friend of Alexander von Humboldt.

[47] Buffon's ideas also influenced Alexander von Humboldt's (1769 − 1859) seminal work written after his exploration of South America with Aimé Bonpland (1773 − 1858). As well as those of the biogeographer, P. Sclater (1829-1913) in the mid-19th century (Sclater 1858).

of a collective one. Compared with the laws shown on Figure 3-3a, there are only 18 possible statements that could occur on both plots (all in Physics and Mathematics); only six could be identified with some certainty in Buffon's text (the extent of overlap certainly deserves further investigation). In addition, Buffon is not presenting a scientific investigation (there are no discoveries here), but a means to organize knowledge. In the figure, phrases using the 1-gram 'loi' are distributed throughout the corpus, but mostly concentrated in the volumes issued prior to Buffon's death (notice that the y-axis is the number of pages on which the 1-gram appears, and not the actual count due to the way the corpus was structured). The exact phrases which appear are detailed by volume in Table 3-3 and by usage context in Table 3-4.

Table 3-3. Distribution of phrases with "loi" in Buffon's *Histoire Naturelle.*

Occurrences of terms in each volume of the corpus and the context associated with them. Ten volumes had no occurrence*
and any mentions in "*Table des Matières*" and indices are removed. Most scientific usage occurs between 1770 - 1780, whereas
the peak in "Cultural" usage is in volumes appearing prior to 1770.

Tome N°, Title, Title of first article	Year	Context	Associated terms
Tome I : Premier Discours - De la manière d'étudier et de traiter l'histoire naturelle -	1749	Physics	loi de la chûte des corps, loi de la pesanteur, loi de leur gravité spécifique
Tome II : Histoire générale des Animaux, Histoire Naturelle de l'Homme -	1749	Cultural	loi
		Mathematics	loi de la suite des nombres
		Natural History	loi, loix de la Nature
Tome III : Description du cabinet du Roi, Histoire Naturelle de l'Homme -	1749	Cultural	loi, loi Mahométane, loi de Mahomet
Tome IV (Quadrupèdes I) : Discours sur la nature des Animaux -	1753	Cultural	loi, loi de la Nature, loi divine, loi naturelle
		Natural History	loi commune, loi constante, loi réelle et générale du sentiment
Tome V (Quadrupèdes II) : La Brébis -	1755	Cultural	loi de Mahomet
Tome VI (Quadrupèdes III) : Avant-Propos; Le Chat -	1756	Cultural	loi des Juifs
Tome VII (Quadrupèdes IV) : Les Animaux carnassiers -	1758	Cultural	loi
		Natural History	loi de la mort naturelle
Tome IX (Quadrupèdes VI) : Le Lion -	1761	Natural History	loi générale
Tome XIII (Quadrupèdes X) : De la Nature Seconde Vue -	1765	Physics	loi, loi d'attraction, loi générale, loi d'affinité
Tome XIV (Quadrupèdes XI) : Nomenclature des Singes -	1766	Natural History	loi
Tome XV (Quadrupèdes XII) : Les Sapajous et les Sagoins -	1767	Cultural	loi de la Nature
		Natural History	loi de la mort naturelle
		Physics	loi d'affinité, loi d'attraction, loi générale
Tome XVI (Oiseaux I) : Discours sur la nature des Oiseaux -	1770	Natural History	loi
Tome XVII (Oiseaux II) : L'outarde -	1771	Cultural	loi
		Natural History	loi, loi du climat, loi générale du climat
Tome XVIII (Oiseaux III) : Le Crave ou Le Coracias -	1774	Natural History	loi de la Nature, loi du climat, loi déterminée
Tome XX (Oiseaux V) : L'Alouette -	1778	Natural History	loi de la Nature, loi générale
Tome XXI (Oiseaux VI) : L'Oiseau-mouche -	1779	Cultural	loi spéciale du Créateur
		Natural History	loi, loi génerale pour tout l'espèce, loi générale de la Nature
Tome XXII (Oiseaux VII) : Les Pics -	1780	Cultural	loi, loi de nourrir ses parens
		Natural History	loi commune, loi du climat
Tome XXIII (Oiseaux VIII) : L'Ibis -	1781	Natural History	loi du climat
Tome XXIV (Oiseaux IX) : Le Cygne	1783	Cultural	loi
		Natural History	loi, loi commune de migration
Tome XXV (Minéraux I) : De la figuration des Minéraux -	1783	Natural History	loi commune, loi générale
		Physics	loi, loi de l'équilibre, loi progressive de dureté et de densité
Tome XXVI (Minéraux II) : Du Bitume -	1783	Cultural	loi fiscale
		Physics	loi

Tome N°, Title, Title of first article	Year	Context	Associated terms
Tome XXVII (Minéraux III) : De l'Argent -	1785	Cultural	loi
		Physics	loi, loi de leur puissance attractive, loi d'affinité, loi générale de la cristallisation
Tome XXVIII (Minéraux IV) : Jaspes -	1786	Cultural	loi
		Physics	loi ordinaire
Tome XXIX (Minéraux V) : Des forces de la Nature en général, et en particulier de l'Électricité et du Magnétisme -	1788	Physics	loi, loi de la Nature, loi de progression ver l'ouest, loi d'attraction, loi générale qui port et dirige la marche de fluide électrique vers les poles de la terre
Tome XXX (Suppléments I) : De la Lumière, de la Chaleur et du Feu -	1774	Physics	loi, loi commune, loi de la Nature, loi générale de l'attraction, loi de l'attraction, loi de la raison inverse du quarré de la distance, loi de l'attraction universelle, loi des affinités, loi d'affinité, loi du progrès de la chaleur, loi du quarré des distances, loi d'attraction, loi de Képler, loi de la pesanteur, loi de l'attraction des particules, loi générale, loi générale de la pesanteur, loi physique, la loi générale de la gravitation
Tome XXXI (Suppléments II) : Servant de suite à la Théorie de la Terre, et de préliminaire à l'Histoire des Végétaux	1775	Physics	loi, loi du levier, loi générale de l'attraction universelle, loix du mouvement, loi de calcul
Tome XXXIII (Suppléments IV) : Servant de suite à l'Histoire Naturelle de l'Homme	1777	Cultural	loi, loi de Dieu
		Mathematics	loi, loi générale des suites
		Natural History	loi, loi commune, loi du climat, la loi commune de la Nature
		Physics	loi, loix de rigueur
Tome XXXIV (Suppléments V) : Des Époques de la nature -	1779	Physics	loi, loi de la force centrifuge, loi du refroidissement
Tome XXXVII (Reptiles I) : Histoire générale et particulière des Quadrupèdes ovipares.	1788	Cultural	loi divine
		Natural History	loi constante
Tome XXXX (Poissons II) : Discours sur la durée des espèces -	1800	Cultural	loi
		Physics	loi
Tome XXXXII (Poissons IV) : Troisième vue de la Nature -	1802	Natural History	loi fondamentale, loi suprême

*Volumes without the 1-gram are: 8, 10, 11, 12, HNO-4, HNP-3, HNP-5, S-3, S-6, S-7. These volumes are equally distributed across the publication interval (1760 - 1803).

Table 3-4. Distribution of 1-grams for the concept of law in Buffon's *Histoire Naturelle* curated corpus*.
The table lists all the terms returned by the 1-gram searches, including terms appearing in indexes and *Table de Matières*, according to the usage context. There are four terms (*loi, loi commune, loi de la Nature, loi générale*) that appear in multiple contexts: only one, "*loi*", occurs in all four. Two terms concerning topics in chemistry are grouped with Physics (*loi d'attraction, loi générale de la cristallisation*). The synonymy identified among these terms is given in Supplementary Data.

Context of usage	Terms assigned to each context	Number of terms in each context
Cultural	**loi**, loi de Dieu, **loi de la Nature**, loi de Mahomet, loi de nourrir ses parens, loi des Juifs, loi divine, loi fiscale, loi Mahométane loi naturelle, loi particulière du Créateur, loi spéciale du Créateur, loi suprême	13
Mathematics	**loi**, loi de calcul, loi de la suite des nombres, loi des combinaisons, loi générale des suites, loix de rigueur	6
Natural History	**loi**, **loi commune**, loi commune de la Nature, loi commune de migration, loi constante, loi de la mort naturelle, **loi de la Nature**, loi de la saison, loi déterminée, loi du climat, **loi générale**, loi générale de la Nature, loi générale du climat, loi réelle et générale du sentiment, loix de la Nature, lois secondaires	16
Physics	**loi**, **loi commune**, loi d'affinité, loi d'attraction, loi de Galilée, loi de Képler, loi de l'attraction, loi de l'attraction des particules, loi de l'attraction universelle, loi de l'équilibre, loi de la chûte des corps, loi de la force centrifuge, **loi de la Nature**, loi de la pesanteur, loi de la raison inverse du quarré de la distance, loi de leur gravité spécifique, loi de leur puissance attractive, loi de progression ver l'ouest, loi des affinités, loi du levier, loi du progrès de la chaleur, loi du quarré des distances, loi du refroidissement, **loi générale**, loi générale de l'attraction, loi générale de l'attraction universelle, loi générale de la cristallisation, loi générale de la gravitation, loi générale de la pesanteur, loi générale qui port et dirige la marche de fluide électrique vers les poles de la terre, loi ordinaire, loi physique, loi progressive de dureté et de densité, loix du mouvement, loi fondamentale	35

*Available at www.buffon.cnrs.fr (2007); viewed on June 2015 . This corpus contains 41 of the original 44 volumes in the series. The three volumes missing from this corpus were edited by de Lacépède after Buffon's death (volumes 38, 39, 44).

In the first three volumes from 1749, Buffon lays out his famous "*système*". The Buffon expert, French historian Thierry Hoquet in his exploration of this topic, translated the phrase which summarizes Buffon's reasoning:

> "In mathematics, one supposes; in physique, one poses and establishes; there, there are definitions; here, there are facts; one goes from definition to definition in the abstract sciences; one proceeds from observation to observation in the real sciences. In the first case one arrives at evidence, whereas we reach certitude in the latter. The word 'truth' includes those two meanings."[48]

For Buffon, Physics employs a method which most closely approaches objective truths; the most important use of law is associated with this category (Table 3-4), consistent with the meaning given to scientific laws as inseparable from universal qualities. Mathematics, he qualifies as an abstract science; that is those areas of knowledge that do not furnish facts, but rely on internally consistent definitions. In other words, mathematics cannot be completely objective for Buffon, whereas Physics with its method provides objective proof of facts. Thus, applying this logic, he places Natural History with the "real sciences" because it too is also

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[48] Translation appears in Hoquet (2010): 38, original citation from Buffon's *Histoire Naturelle, Premier discours* Vol. 1, p. 54.

concerned only by gathering facts which have "certitude". In contrast, Mathematics and socio-cultural knowledge (the Cultural category on the plots and tables) both rely on definitions that provide "evidence" of truth without certainty or generalization (similar to *ceteris paribus* conditions described earlier).

Buffon rejected the mathematics of Newton's mechanistic approach as a tool for describing the living world.[49] Examining his usage of phrases with laws in the four different contexts (Tables 3-3 and 3-4), only the 1-gram "*loi*" is used in all four contexts. "*Loi*" by itself is the term which appears most frequently in the corpus. The next three phrases appearing in more than one context, *loi de la Nature, loi générale* and *loi commune*, are associated with Physics, Natural History and Culture, but not in Mathematics. This usage is consistent with his wish to dissociate mathematics from his system of Nature.[50] Buffon has instead proposed an alternate path for natural history focused on describing the complexity of living organisms within particular environments and emphasizing where common patterns exist. Thus of the most frequently occurring phrases (in descending order, *loi, loi du climat, loi de l'attraction, loi de la Nature*), only "*loi du climat*" is associated exclusively with a Natural History context. The remaining two phrases are associated with either only Physics (*loi de l'attraction*) or all three (*loi de la Nature*).

The *loi du climat* in Buffon's work refers to his explanations for the distributions of organisms spread across several of the volumes.[51] Because of this usage, some consider Buffon as the first biogeographer.[52] This phrase underwent something of a revival in the 18th century by a contemporary of Buffon, the controversial lawyer and writer, Montesquieu in his political, proto-anthropological essays, especially *"De l'Esprit des Lois".[53]* For him the *loi du climat* explains how climate influences the prevalence of personality traits (stereotypes, *e.g.* persons from the south are hot-tempered, *etc.*) and thus the functioning of societies and cultures. Montesquieu used this law-like statement as the basis for a hierarchy of cultures and his political arguments about governance.[54] These themes probably originated much earlier in the work of Hippocrates who described how climatic conditions can have an influence on human health and including other qualities like behavior and intellectual curiosity. Later writers (Aristotle[55], Galen) integrated this idea into their own writings where it was transmitted through medieval Latin translations to subsequent generations of natural philosophers.

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[49] Buffon was an expert on Newton's work; he translated his works into French earlier. However, Buffon did not in any case reject mathematics because he did not understand the field, as appears to be so often communicated in recent decades (see EO Wilson's 2013 April 5 essay in the Wall Street Journal, "Great Scientist ≠ Good at Math" http://www.wsj.com/articles/SB10001424127887323611604578398943650327184).

[50] Hoquet (2010)

[51] Cox and Moore (2010): 6-7

[52] Egerton (1967)

[53] This work had a tremendous political impact at the time of its publication in 1748. The most famous citation of which was "*l'empire du climat est le premier de tous les empires*" that he used to promote his deterministic ideas about climate and human societies. Earlier, Francis Bacon had rejected this idea (after all the British did not fare well given their northerly location) as part of his wholesale dismissal of the domination of Greek and Roman philosophies in science (Pinna (1989).

[54] The consequences of declaring scientific "laws" with inadequate empirical testing creates a potential for misuse when transferred into other domains of society.

[55] Aristotle, Politics, Book VII, 7.

Buffon simply extends these arguments to explain the distribution of organisms. There is an inevitable quality about the association between climates and the types of organisms found in specific locations that fits well with Buffon's ideas about species having a point of origin from which individuals dispersed. Post-Darwin, Buffon's work is important for his remarks on climate for adaptation, as both biologists and biogeographers recognized, retrospectively.[56] Biogeographers focused on mapping distributions to be able to find back these points of origin as a result. By the mid 19th century, the *loi du climat* had become the biogeographer's primary theoretical framework under the name of "Buffon's Law".[57]

However, Buffon's system of knowledge was ignored by contemporaries like Laplace who preferred and promoted the work and style of Newton. Buffon reached an alternative conclusion. For him, there were limits to applying this method to the living world:

> "Mais cet abus n'est rien en comparaison des inconvéniens où l'on tombe lorsqu'on veut appliquer la Géométrie & le calcul à des sujets de Physique trop compliquez, à des objets dont nous ne connoissons pas assez les propriétés pour pouvoir les mesurer ; on est obligé dans tous ces cas de faire des suppositions toûjours contraires à la Nature, […]" —Buffon, 1749, Tome 1: 60-61.

While his contemporaries were engaged on another path inspired by Newton's mechanistic approach, Buffon employed law-like statements to characterize patterns he deduced from the facts he collected about the biosphere. Thus the *loi d'attraction* of Physics can be used to describe animal locomotion and the *loi du climat* to characterize their distribution. In addition, it has been overlooked that in Buffon the history of an organism became part of his method of induction.[58] Before Darwin[59], the history of an organism was mostly treated as irrelevant even if it was commonly admitted that durable change could be effected by breeding and hybridization, species were treated as immutable objects. Particularly interesting is the way Buffon hints at numerous ideas about the effect of the environment on species and his criticism of the Linnean system. Linneaus' prodigious works, especially the 10th edition (1754), launched the harmonization of classification and naming schemes, which Buffon did not use. Indeed, the two naturalists worked out rival concepts of the natural world, one based on morphological criteria of difference, and the other on criteria of reproduction which led him to propose a proto-theory of evolution based on *dégénérance*.

Buffon finally concludes that the laws of nature cannot be known or formulated as the laws of physics because the biological functioning is not understood well enough, and not like physics

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[56] In biogeography texts Buffon is commonly cited along with von Humboldt for his early influence on ideas about the distribution of organisms and his expedition to South America (1799-1804)). Alexander Von Humboldt and Aimé Bonpland spent nearly 5 years exploring parts of South America (1799-1804). Their important synthesis about the distribution of organisms relative to latitude and climate appears in "Essai sur la géographie des plantes [...]" published in 1805.

[57] The exact phrase seems to have originated in a later analysis of Buffon's work published in 1844 by Pierre Flourens in his chapter entitled "Lois de la Distribution" (Flourens, 1844).

[58] As Hoquet wrote: "In Buffon's Histoire naturelle, history was a method (induction from facts to laws) and a field for new inquiries (regarding ethological or behavioral matters)" Hoquet (2010): 37.

[59] Yet, Darwin's ideas about natural selection and adaptation didn't come out of nowhere. After more than a century of scholarship we now know that Darwin's insights emerged within a larger cultural and scientific debate about progress, modernization and demography.

or chemistry can understand their objects (whether atomistic particles or planets) at this time. Mathematical definitions then strip the living organism of its complexity; Buffon advocates for including complexity through descriptive observation first - until there are enough facts to deduce general rules (laws). Proposing laws is permitted by induction, but mathematical reasoning was unnecessary and could come later.

What about the impact on the scientific practice of the descendants of natural history, *i.e.* ecologists? If having laws provides a common framework for a discipline, then these laws themselves are also subject to being re-examined each time they are invoked. The effect is a continual re-testing of the limits of the theoretical framework; testing and verification of the original ideas are vital components of the law-based scientific practice. Scientific laws serve as a point of reference to which all reasoning and measurement can be referred to and compared, even centuries later. If a new explanation is made or discovered, then the phenomena remain exactly the same: it is only our understanding which changes. A new explanation can require new measurement(s) to be performed or even the object of study to be changed. These statements provide a fixed point of reference for hypotheses and empirical studies and an explanatory framework for reconstruction and prediction (Figure 3-2).[60] Hence, in this case, the word law is used to refer to a common agreement on the breadth of a statement's applicability.

Both ecology and evolution emerged from 18th century ideas about species, demography, economics, and, especially, biogeography.[61] These co-existing views on scientific laws had direct consequences on the 19th century trajectories for biology and ecology, which retained a mixed practice. In Figure 3-3c, which shows the distribution of phrases using the 1-gram "law" in the 1859 edition of the Origin of Species, Darwin makes liberal use of law-like statements. Darwin's work, while considered by some to be in Natural History, is limited to biological questions, unlike Buffon's usage. Like Buffon, he has not presented any mathematical arguments, but retained the liberal usage of 'laws' to convey the force of his conviction of the factual quality of his inductive statements. Indeed, none of Darwin's Natural History law statements appear in the Wikipedia list and they bear little resemblance to the same category of statements in Buffon. He retains only a handful of mentions to other categories of laws, namely those of Physics (two mentions of Newton's Law and one generic reference to laws of physics). We have, therefore, three different visions of the usage of scientific laws which suggest that while laws in Physics appear stable (in that they remain recognizable), law-like statements of Natural History are quiet malleable. This certainly merits further study.

In fact, law-like statements proliferate in ecology (see Table 3-5 for examples), but they are not widely acknowledged, like those in Physics or Chemistry. Scientific practice in ecology (and biology) has avoided the mechanistic approach and phenological methods have dominated. Both biology and ecology have resorted to the special case, the characteristics of a

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[60] Marc Lange asserts that laws provide stable descriptions for research practice Lange (2006): 365-366. Many other philosophers like Beebee, Ellis, Ruby, and Lehoux also state that governance is not conceptually necessary to lawhood in scientific laws.
[61] Egerton (1967), McIntosh (1985).

Table 3-5. Two centuries of statements of ecological laws, principles or rules.
A non-exhaustive list of concepts that have been described as generally applicable explanations for phenomena in natural history, ecology and biogeography over the past 200+ years.

Short name	Statement of	Author(s)	Date	Remarks
Law of mortality	All living things die	---	---	Often cited in ecological or biogeographic texts since Antiquity, treated as a general observation and fundamental difference between biotic and abiotic domains
Buffon's Law, or Climate law	Different regions are inhabited by different faunas, even if the climates are similar	Montesquieu / Buffon	1748 / 1753-1777	Probably much older idea popularized during Enlightenment. Fundamental to biogeographical studies and classification for definitions of biological zones or regions; some contemporaries and 19th C scientists suggest that this statement implies animals were "placed" in different regions and could not have migrated there
Leibig's Law of the Minimum	Suggests that the growth of a plant or the rate of a process is determined by the resource most limiting for that species. Or by the availability or rate of the slowest factor (the minimum)	von Leibig	1840	Led to single factor ecological reasoning according to Chase and Leibold (2003)
Law of substitution (and the theory of types)	"Law of Substitution" Originating in organic chemistry with the debate between Leibig (German) and Dumas (French) concerning how to interpret and represent the conservation of certain elements in chemical reactions. In biology it took the form that certain cations (Ca, Sr, Mg, K, Na, ...) can be replaced (substituted) in organisms by changing their food sources.	Dumas	1840	Debate about 'types' (elements as unreactive) vs 'radicals' (elements participate in reactions). There are many laws of substitution, in particular for economic theories of valuing (*e.g.* if the price is right (or low enough) the consumer will substitute one product or service for another to pay the least amount, even if there are differences between the services or objects).
Biogenetic/Biogenic law or rule	A restatement of Haeckel's phrase "ontogeny recapitulates phylogeny"; sometimes called recapitulation theory or embryological parallelism.	---	1824-1826; then 1867-1879	Preceded by a version called "Meckel-Serres Law" dating from the 1820s. Abandoned in the early 20th century.
Bergmann's rule	Larger size species will occur more in colder climates and smaller size species in warmer areas	Bergmann	1848	Concept limited to mammals and birds
Sanio's Law of Vertical Tapering	"…xylem conduit diameters and lengths in a coniferous tree increase from the apex down to a height below which they begin to decrease towards the tree base…"	Sanio	1872	
Allen's rule	Body shapes of endotherms will vary in such a way to optimize heat loss relative to the general climate conditions	Allen	1877	Similar reasoning with Bergmann's rule
Merriam's Law	Animal distribution is controlled by temperature	Merriam	1894	
Jordan's Law	"Jordan's Law (Jordan 1905) usually holds [that] the nearest related species to any given species population is found, not in the same area or in a very different on, but in an adjacent geographic region or in a far distant one with similar climatic and ecological conditions" Stebbins 1950: 238	Jordan	1905	Arose from marine dredging surveys, like the Challenger
Law of toleration or tolerance, Shelford's Law	Provided for a range of values for a factor as well as for identifying an optimal value for survival and growth	Shelford	1913	Added the possibility of a maximum to Leibig's Law. Hutchinson created his multidimensional niches in 1957 by reducing Shelford's relationship to linear relationships with environmental variables.
Law of succession	"all bare places give rise to new communities except those which present the most extreme conditions of water, temperature, light, or soil"	Clements	1916	His rules or laws exemplify a kind of ecological common sense

Short name	Statement of	Author(s)	Date	Remarks
Law of distribution frequency	If frequency numbers of a sample were grouped in five equal percentage classes, the resulting distribution is a reverse J-shaped curve	Raunkaier	1918	An artifact of sampling error, continued to be reproduced until the 1960s
Verhulst-Pearl law of population growth	Describes growth of human population with a logistic curve, in terms of birth, death, migration	Verhulst / Pearl & Reed	1838, 1920	
Hopkins's Law	Bioclimatic law, similar to Merriam's Law	Hopkins	1920	Lead to phenological work becoming part of ecology, see also Shelford 1929: 5
Vavilov's Law	Law of homologous variation: "held that the more similar species are, the more similar are their patterns of variation. This way of classification became very popular, and he was sometimes able to predict that a particular variant would be found"	Vavilov	1922	
Law of maximum energy, Maximum power principle	"It has been pointed out by Boltzmann that the fundamental object of contention in the life-struggle, in the evolution of the organic world, is available energy. In accord with this observation is the principle that, in the struggle for existence, the advantage must go to those organisms whose energy-capturing devices are most efficient in directing available energy into channels favorable to the preservation of the species." Lotka 1922: 147	Lotka	1922, 1925	From Lotka's ideas about "ecoenergetics". Later re-used in the energy-based re-conception of succession by Odum in 1971; who proposed as his 4th Law of thermodynamics, called it the maximum power principle, "Because designs with greater performance prevail, self-organization selects network connections that feedback transformed energy to increase inflow of resource or use them more efficiently."
Laws of Conditional Reflexes	Laws of Conditional Reflexes (formation, preservation, extinction of)	Pavlov	1923	Conceived of in opposition to the Automatic Reflexes ("elementary tasks of the nervous system") which are the unvarying physiological responses of the organism to the external world.
Murray's Law or principle	Relationship is optimized between amount of energy required to move fluids through diameters of main stem, (parent) conduits to daughter conduits or branches in a circulatory system	Murray	1926	
Law of periodic cycles	Fluctuations of 2 species populations are periodic and depend on the coefficients of increase and decrease and initial conditions	Volterra	1926	
Law of conservation of averages	Populations remain stable unless the coefficients of the equations change	Volterra	1926	
Law of disturbance of averages	In an attempt to destroy two species in proportion to their numbers, the prey species will increase and the predator will decrease	Volterra	1926	
Fisher's Principle	Conservation of parental expenditure (investment) justifies existence of a sex ratio of 1:1 in sexually reproducing species	Fisher	1930	
Kleiber's Law	"For the vast majority of animals, an animal's metabolic rate scales to the 3/4 power of the animal's mass."	Kleiber	1932	Part of the allometric laws in biology relating growth and production and the metabolic theory of ecology
Law of interspersion	"The potential density of game of low mobility requiring two or more types is, within ordinary limits, proportional to the sum of the type peripheries." Leopold, 1933: 132	Leopold	1933	
Gause's Law or axiom, Lotka-Volterra principle, Competitive exclusion principle	Essentially a reformulation of the Grinnellian niche, using a "Gaussian" curve : Logistic growth curve as a measure of the response of a population to particular environmental conditions	Gause	1932-1935	Lead to gradient analysis and description of continuums in ecological patterns. Use of these curves are central to much of niche theory

Short name	Statement of	Author(s)	Date	Remarks
Thorsen's Rule	"…there is a global-scale latitudinal gradient in the distribution of planktotrophic larvae…"	Thorsen	1936	
The Law of Necessary Progress	Lysenkoism proposed that by "training" one generation, the next generation would incorporate new, more desirable traits.	Lysenko?	1920s-1950s	Political and scientific ideas under Stalin's Five year Plans to remake the economy and production, especially agricultural production, of the USSR
Species-area relationship (Island Biogeography theory)	"that the number S of species of a given taxonomic group on an ''island'' (as far as creatures of that group are concerned) in a given ''archipelago'' increases, *ceteris paribus*, with the island's area A in accordance with a power function (or sometimes called a power law, S = cA^z)"	Wilson & MacArthur	1967	"… recent article in Nature (Pounds and Puschendorf 2004) refers to the species - area relationship as ''one of ecology's few ironclad laws'' Lange 2005: 398
Commoner's 1st Law	Everything Is Connected to Everything Else. There is one ecosphere for all living organisms and what affects one, affects all.	Commoner	1971	
Commoner's 2nd Law	Everything Must Go Somewhere. There is no "waste" in nature and there is no "away" to which things can be thrown.	Commoner	1971	
Commoner's 3rd Law	Nature Knows Best. Humankind has fashioned technology to improve upon nature, but such change in a natural system is, says Commoner, "likely to be detrimental to that system"	Commoner	1971	
Commoner's 4th Law	There Is No Such Thing as a Free Lunch. Exploitation of nature will inevitably involve the conversion of resources from useful to useless forms.	Commoner	1971	
Law of constant extinction also the Red Queen hypothesis	"The fossil record suggests that a species might disappear at any time, irrespective of how long it has already existed." Solé and Bascompte, 2006: 279	Van Valen	1973	An explanation for the linear relationship seen in taxonomic survivorship curves.
Rapoport's Rule	"…an apparent decline in the average sizes of species' ranges within comparable taxa, as one moves from higher to lower latitudes…" Lawton, 1996	Rapoport	1975-1982	
[Lawton-1]	*The first and second laws of thermodynamics*	*Lawton*	*1999*	*From physics and chemistry. These actually established by 1870s.*
[Lawton-2]	*The rules of stoichiometry, a particular application of the universal law that matter cannot be created or destroyed*	*Lawton*	*1999*	*From physics and chemistry. Established by early 1800s.*
Lawton-3	Darwin's law of natural selection as an explanation for evolution.	Lawton	1999	
Lawton-4	The set of general physical principles governing diffusion and transport of gasses and liquids, the mechanical properties that alone or in combination define limits to the performance of individual living organisms	Lawton	1999	Justification for study of organisms' physiologies in ecology
Lawton-5	Organisms interact with one another (no species. anywhere in nature, lives in isolation) and with their environment	Lawton	1999	"Trivial but important" -JHL
Latitudinal gradients in diversity	"that plots of a given area at lower latitude contain more species, ceteris paribus, than plots with that area at higher latitude." Lange, 2005: 400	?	?	Unclear origin, associated at various times with von Humboldt, Darwin, and Wallace

singularity, expressed by the fact that it refers to a particular locality or a particular time, as explanation for specific conditions. The emergence of new concepts is subject to an unanswerable criticism that each observation is unique and incomparable. Principles arise under *ceteris paribus sic stantibus* conditions. In consequence, one of the pillars of the scientific method - repeatability - has been neglected. The problem of comparability and trend analysis has been highlighted memorably in the writings of the fisheries scientist, Daniel Pauly.[62] Ecological studies rest largely on statistically tested inferences which have replaced a law-based practice. In statistics, the individual is the unit that carries the characteristic of the studied population. As in ecological populations, individual characteristics fluctuate; it became therefore straightforward to establish a parallel between objects of statistics and objects in Ecology, justifying the extensive use of statistics in ecology to validate conclusions.

In addition, the use of differential equations has shown their limits for prediction and was probably a factor that prevented the discovery of laws within ecology quite early. At the start of the 20th century, V. Volterra re-introduced mechanistic analogies with some success, inspiring G.F. Gause to use them in experimental studies with an openly assumed goal of finding laws for ecology. However, ultimately, Gause failed to find any laws for the very reasons that Buffon had expressed earlier: a group of living organisms is not a suitable "object" for a mechanistic approach because these analogies are inadequate to describe their possible dynamics (see Chapter 6 for details). But the persistent appeals for a renewed scientific practice closer to that of Physics and Chemistry continue to appear as new demands are made on ecology by society, like environmental impact, the protection of species, and responses to global change. Without specific scientific laws for ecological questions, ecologists have been unable to construct arguments in opposition to the social, economic and political "unscientific" assumptions which circulate in public debates.[63] There can be no Galileo's Defense possible.

To date, no viable alternative scientific practice has emerged.

Are there candidates for ecological laws? Elwick suggested that, already in the early 19th century, "analysis:synthesis"[64] was an imitation of the research practice in physics and chemistry created by natural historians hoping to replicate the successes and theoretical formulations of these disciplines. In point of fact, questions raised by studying the needs of organisms in controlled, manipulated environments like aquaria and at agricultural fields had by this time posed many problems about scientific research by natural historians. For example, throughout John Lawes' exhaustive descriptions of the results of decades of experimental work at the Rothamsted field station,[65] he clearly states and re-states the necessity not only of a long-term perspective, but also the need to integrate prior environmental conditions to understand and explain the rise and fall of plant populations on his twenty plots of grass. And

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[62] In particular his phrase "moving baselines" from his short essay Pauly (1995).
[63] Nadeau (2008)
[64] Elwick (2007)
[65] Lawes et al. (1882), but also as had Dureau de la Malle in 1825 (Dureau de la Malle, 1825).

at the other end of the spectrum, the fact-gathering of biogeographers had already failed to produce effective theoretical formulas.[66]

Unfortunately, recent work by ecologists, discussing the state of theory in ecology in which they propose a set of principles for ecology (Table 3-6)[67] have not advanced this topic much either. It is difficult to see how the types of statements in Table 3-5 or 3-6 can be used to respond to the question about laws in ecology at all. Then, instead of a generating discussion, subsequent papers that appeared[68] contained the beginnings of a rather acrid debate between groups about who understands theory better.[69]

Table 3-6. A list of fundamental principles proposed for a general theory of ecology from Scheiner & Willig in 2011 (after Table 1.3).
All principles are considered valid for all scales (individual to ecosystem).

Principle	Type
Organisms are distributed in space and time in a heterogeneous manner	property
Organisms interact with their abiotic and biotic environments (all interactions)	processes
Variation in the characteristics of organisms results in heterogeneity of ecological patterns and processes	processes
The distributions of organisms and their interactions depend on contingencies	processes
Environmental conditions as perceived by organisms are heterogeneous in space and time	mechanism
Resources as perceived by organisms are finite and heterogeneous in space and time	condition or resource
Birth rates and death rate are a consequence of interactions with the abiotic and biotic environments	characteristic
The ecological properties of species are the result of evolution	processes

Many scientists, and biologists in particular, hold Popper's views on science and his ideal of falsification as the line of demarcation between what is science and what is not (pseudo-science).[70] However, recently, the philosophy of science has moved away from Popper's ideals of Physics and Mathematics as their prime examples to be more inclusive; this has been the source of new ideas, such as the work of Lorraine Daston on the epistemic development of "objectivity" and "expertise".[71] The scientific method, as an *ensemble*, is a means to arrive at a description and understanding of the way things are, and work, independently of belief. In this picture, models are not pure mathematical constructions; they arise from a conceptualization of a problem within the framework of the scientific practice. They are a tool which we can use to probe the concepts, *i.e.* to explore their internal consistency, but without stating anything about their truthfulness. The scientific truth must be opposed to belief, even while the scientist may believe a hypothesis to be true. This is the essence of a dichotomous system which aims to achieve objectivity.

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[66] See Rehbock (1979), Table 2, p. 331, summary of the environmental factors attributed as controlling factors on marine fauna described by Forbes (1839) and Forbes (1843).
[67] Scheiner and Willig (2011)
[68] Scheiner (2013); Marquet *et al.* (2014); Houlahan *et al.* (2015)
[69] See the follow-up to Houlahan *et al.* 2015, also published in BioOne in 2015 by Marquet *et al.*
[70] Colyvan (2011): 11-12
[71] Daston and Galison (2010)

Thus far, the works of ecologists have overlooked a basic preliminary question, which Lange aptly points out: "what would an ecological relationship have to be like in order for it to qualify as an ecological law?".[72] Furthermore, he suggests another way of thinking about the problem as, "[…] ecological laws would differ from fundamental laws of physics in the range of counterfactual perturbations under which they are invariant."[73] And, he has proposed a series of statements (Table 3-7) which could fulfill these conditions, in his analysis.

Table 3-7. Candidates for ecological laws, after Marc Lange (2005).
The American philosopher, Marc Lange has contributed to the debate about scientific laws in ecological sciences by proposing a series of principles which could be good candidates for ecological laws according to his reasoning.

Principle	Supporting references given in Lange (2005)
Exponential population growth (Malthusian law)	Ginzburg (1986); Turchin (2001); Berryman (2003)
Allometries of macroecology	Colyvan and Ginzburg (2003); Ginzburg and Colyvan (2004)
Rules of stoichiometry and organism interactions with their environment	Lawton (1999)
Ecological succession occurs on open sites	Pickett *et al.* (1994)
Competitive exclusion principle	Vandermeer (1972); Murray (1979)
Impossibility of population increase without bounds	Murray (1986); Loehle (1988)
Population with constant age-specific rates of survival will eventually achieve steady-state	Murray (2000)

Whether or not we agree with these precise statements is not the question at this point, what is interesting is how he arrived at this juncture and could we as ecologists agree with this reasoning?

> "And yet, despite all these differences, science and the law share, at the deepest possible level, the same aspirations and many of the same methods. Both disciplines seek, in structured debate and using empirical evidence, to arrive at rational conclusions that transcend the prejudices and self-interest of individuals."[74]

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[72] Lange (2005): 394

[73] Lange (2005). In the introduction to this paper he also cites a series of publications by ecologists on the question of laws in ecology.

[74] Goodstein (2011): 52

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PART II. Revision and reconstruction

SUMMARY

After examining the preceding historiography of the objects of ecology and the discipline itself, the next section experiments with integrating some of these new perspectives into a theoretical framework. Armed with a historian's perspective on the epistemological trajectory of ecology, re-examination of earlier work becomes a means to revise some underlying assumptions in ecological practice today. Working at the confluence of two disciplines, in this case the epistemology and ecology, stresses the fundamental importance of precise, portable definitions.

Each of the next four chapters are manuscripts of articles written while exploring facets of challenges in historical ecology, namely: hindcasting population dynamics of single species over time-scales exceeding a century, reconstruction of a population density estimate from ancient traditional fishing techniques, experimenting with recursion using the work of G.F. Gause on competitive exclusion, and finally revising the historical notion of environmental impact in a quantitative framework, as was intended originally by Luna Leopold (1915-2006) when he wrote the first methodological description for the characterization of environmental impact in 1971.

From the preceding presentations of the early context of ecological studies, we can propose a new area of historical ecology studies: re-examination of earlier results in light of scientific and technological advances. If reconstructions of past conditions depend on historical observations made without instrumentation,[1] then it follows that the contextual dependency cannot be considered null. This is the premise of Lorraine Daston's "mechanical objectivity".[2] Thus historical ecology studies can furnish an expertise which encompasses the frontiers of modern ecology by evaluating its basic assumptions, and in doing so revises and suggests new means to test them.

The four perspectives considered are:

1. Observations of species presence and the composition of species assemblages in scientific literature are subject to expert fallibility and preconceptions

Hindcasting population dynamics of a single species at the scale of centuries using density and abundance from field observations as state variables, raises problems of observation bias and scarcity when reconstructing highly variable populations. The quality of observations in the scientific literature is rarely re-evaluated. Doubtful or uncertain species identifications can lead to estimates of population dynamics that adversely affect other types of studies downstream, such as those on global change or invasive species. This in turn may trigger unwarranted conservation measures or have a trickle-up effect when conclusions from a local scale are integrated into regional or global meta-analyses. When the dynamics of a population are estimated with demographic information extrapolated over an area of distribution using descriptive information about the species' resource requirements and compared with observations of presence from the scientific literature or field studies how is the bias detected? These dynamics are thus good candidates for recursive analysis using other conceptual frameworks.

Using a modeling approach to treat the dynamics of the NAO as a proxy for bottom conditions favorable for a small, short-lived polychaete (*Ditrupa arietina*) and observations of presence from the literature, I suggest an alternate scenario of the population dynamic of this

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[1] The history of instrumentation permits cross-calibration of early datasets with measurements made using modern instrumentation, such as what is done in historical climatology. The only means to achieve similar cross-calibration for ecological observations is through the study of specimen collections.

[2] Daston and Galison (2010), and specifically referring to underwater photography see Martinez (2014).

organism, and show how the role of their shell calcification on the carbon cycle may have been drastically over-estimated in earlier work because of scientific bias.

2. Species with long exploitation histories need quantitative methods to cross-calibrate ancient and modern harvesting techniques for effective hindcasting

Reconstruction of population estimates can be extended for species with long exploitation histories if there are means to cross-calibrate different fishing techniques. The second example considers how to reconstruct a population density estimate by first developing a robust statistical description of how an ancient artisanal fishing technique works.

A species of "Murex", *Hexaplex trunculus*, was used. This gastropod is well known among archeologists and historians as a source of the highly valued Tyrian Purple dye,[3] and the pigment production has been characterized as the earliest example of a chemical industry. *H. trunculus* were massively fished to collect a photosensitive molecule produced by the organism's hypobranchial gland. The period of intense production lasted from the late Bronze Age until about the 7th or 8th century AD, after which most large centers disappeared. A brief spark of interest in the 1850s[4] linked to the popular revival of Greek and Roman cultures in Victorian England, led a British organic chemist to attempt to replicate this color. Instead he produced the first synthetic coal-tar dye (the purple aniline dye, "mauve"), lowering the cost of fabric dying and which effectively ended 4000 years of natural pigment and dye production. In the intervening century, little attention was paid to these species, with the exception of local fisheries.

Surprisingly, few abundance estimates have been done for these gastropods and the information on their distribution is sparse. The statistical model combines individual behavior and a stochastic population model to produce population density estimates from a simple baited trap design.

3. Widely circulated truisms (tautologies) in ecology merit re-examination using new approaches to develop a body of fundamental principles or laws suitable for predictions

The discussion about the existence of a body of ecological laws and the nature of the scientific practice in ecology is ongoing. Nevertheless, data re-use and hindcasting depend on having a fixed framework in which to re-analyze earlier observations. One means of investigating the

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[3] Mostly this industry is associated with *H. trunculus*, and three other species, *Bolinus brandaris*, *Stramonita haemastoma*, and *Nucella lapillus* in European waters. Recent work has highlighted the global nature of the use of this natural pigment and centers of production are known from every continent (except Antarctica). Many muricid species produce the same family of photosensitive molecules which color in sunlight. See the seminal work on this topic by the French archeologist, Dominique Cardon (Cardon, 2003; Cardon, 2010).

[4] Due to a series of articles published by the French zoologist, Henri de Lacaze-Duthiers. Exceptionally, one was translated to English (de Lacaze-Duthiers, 1859).

applicability of earlier principles or declarations which are qualified as laws, or at least as strong principles, is to either repeat or apply a recursive analysis to the original studies.

In this example, a recursive study of the work done by G.F. Gause in the 1930s to study competition was done. This body of work is unique as he was one of the few ecologists to have specifically designed experiments and models with the goal of detecting or discovering a scientific law about species interactions. The outcomes of his work were variously described as a law or axiom or principle of competitive exclusion in later years (although never by himself). This 'rule' is widely applied in conservation planning today.

To explore the robustness of this application, we rebuild the original model of Gause and then two additional models to study how well they explain the experimental observations reported by Gause. Different approaches in population dynamics and individual based modelling were compared. In particular, this shows the interest of returning to a conception of the ecosystem in terms of interactions between individuals, instead of populations.

4. Baselines in ecological systems may not be well-represented by reconstructing trends of single variables, such as a particular species population dynamic.

The conception of how to detect an environmental impact depends on how the baseline, or reference conditions are defined. This is not a straightforward task for ecological systems which are dynamic and interconnected; thus impacts may not be limited to where projects actually take place or to specific receptors identified *a priori*. This situation presents a difficult theoretical problem for applying historical ecology studies, since ecological interactions are emergent properties arising from the continuous confrontation between two dynamic, deterministic systems: one driven by abiotic factor variability (environmental stochasticity) and a second driven by biological growth (demographic stochasticity).

Environmental impact assessment (EIA) is an area where ecological concepts could be applied and tested, but it has undergone almost no theoretical development and no theoretical transfer in the past. I have explored the possibility to build a framework for environmental impact assessment reconciling the statistical and probabilistic definition of impact and ecosystem modelling using the idea that a minimal ecosystem formulation can grasp impact of project implementation on a set of interconnected receptors. The baseline concept is explicitly described by the simulated state before impact, and the impact becomes predictable in terms of both amplitude and variance. Socio-economic components are not described as classical feedbacks, but as drivers of change instead. This emphasizes the place of populations and individuals as receptors in a network of interactions, including socio-economic drivers of the impact scenario.

<p style="text-align:center">***</p>

Copies of the articles developed in each perspective are included here. Chapters 4 and 6 are in draft formats. Chapter 5 is submitted. Chapter 7 is accepted with major revisions by the ICES Journal of Marine Sciences (the final publication is available in volume 74, issue 1 of this journal).

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CHAPTER 4

RECONSTRUCTING POPULATION DYNAMICS

"Every event has had its cause, and nothing, not the least wind that blows, is accident or causeless. To understand what happens now one must find the cause, which may be very long ago in its beginning, but is surely there, and therefore a knowledge of history as detailed as possible is essential if we are to comprehend the present and be prepared for the future."

-- Pearl S. Buck, My Several Worlds: A Personal Record (1954), p. 52 - 53

Toward a comprehensive approach to quantify the long-term dynamics of *Ditrupa arietina* (O.F. Müller) metapopulation, and their impact on the carbon cycle, in the coastal areas of the Gulf of Lions.

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Running head: Linking metapopulation dynamics and carbon cycle

Keywords: Ditrupa arietina, Metapopulation dynamics, carbon cycle, Mediterranean Sea

ABSTRACT

The serpulid polychaete *Ditrupa arietina* is found in very high densities (compared to other benthic invertebrate species) in the northwestern Mediterranean Sea. With a life cycle defined by a pelagic dispersive larval stage, and a benthic sedentary phase (when individuals are juvenile or adult), *Ditrupa arietina* local populations can be seen to be part of a large metapopulation. Estimating the effect that a metapopulation may have on the carbon cycle in coastal ecosystems remains a significant challenge since data series become both scarcer and sparser as temporal and spatial scales enlarge. We explore here the dynamic properties inferred from a size-structured population model calibrated at one locality in the Gulf of Lions (Bay of Banyuls-sur-Mer). Processes governing the population dynamics were quantified by minimal formulations using a 10-year spatio-temporal survey from the bay. A deterministic model filled data gaps and provided extrapolated observations. The dynamic model was designed to simulate a population with auto-regenerating capacities. The mathematical properties were studied to investigate conditions of persistence for the population within the theoretical framework of a metapopulation. Two extrapolations were made: the first one simulates the population dynamics over 180 years using NAO indices to force recruitment variability, and the second one calculates the steady-state population densities for the entire Gulf of Lions from a connectivity matrix. The connectivity matrix quantified exchange rates between sites in the metapopulation. Our modelling results are consistent with observations, but ancillary information are required to make accurate predictive estimates if we want to quantify the impact of marine benthic metapopulations on carbon cycles.

INTRODUCTION

Coastal ecosystems of the Mediterranean Sea are strongly influenced by a many global and local changes, mainly due to human activities (Williams 2008). The Bay of Banyuls-sur-Mer is a small open bay situated in the northwestern basin of the Mediterranean Sea near the French-Spanish border. It is a typical bay of the Mediterranean coastal regions hosting a high benthic species diversity (Labrune *et al.* 2006) but with low population densities. Population densities of dominant species rarely exceed 50 ind.m^{-2}. During a species survey of local benthic macrofauna in the early 1990s, one annelid species, *Ditrupa arietina* (O.F. Müller, 1776), was found at very high densities (several thousands of individuals par square meters; Gremare *et al.* 1998) and has captured the attention of researchers because it was not identified during a similar inventory carried out in the late 1960s (Guille 1971). This species occurs in many other coastal ecosystems in the western Mediterranean Sea and in North Atlantic (from Norway to the Canary Islands). As such, the local population of *Ditrupa arietina* in the Bay of Banyuls-sur-Mer should be considered as part of a large, spatially distributed population (Grimm *et al.* 2003). Besides, the larval stage is pelagic and hydrodynamic transport ensures dispersion and mixing at regional scale.

Ditrupa arietina individuals have the particularity to build and inhabit an external tube made of $CaCO_3$. Calcification of external structures during the growth of marine organisms is a process that modifies significantly the carbon cycle in ecosystems (Gattuso *et al.* 1996), and organisms producing these calcium carbonate structures may be affected by the carbon cycle in return. During a survey in the Bay of Banyuls carried out in 1994, *Ditrupa arietina* was discovered at abundances of more than 20000 ind.m^{-2}, and Medernach *et al.* (2000) estimated that the population was able to produce up to 12000 g.m^{-2} of calcium carbonate per year, which is four times higher than the maximum estimated production of calcium carbonate by coral reefs (Gattuso *et al.*, 1996).

If the initial estimates published by Medernach *et al.* (2000) are correct, the retroaction between the dynamics of the population and the calcification processes (*sensu lato*) should be very strong when the population peaks (Martin *et al.* 2007). However, when the spatio-temporal distributions of species' abundances are highly variable, the production of calcium carbonate remains very difficult to estimate accurately for the entire ecosystem. Therefore, a quantitative approach is required to explicit the links between the carbon cycle and population dynamics. Population dynamics, as considered in ecology, originated in the 18th century with the writings of Buffon, Euler and Malthus; however, they have been developed in several contexts and has never been formulated as a single set of commonly admitted rules (Bacaër, 2011). We have therefore, many modelling techniques developed to simulate population dynamics, each emphasizing specific features (size distribution, fecundity, spatial distribution - continuous or discrete -, interactions ...) to the detriment of general aspects.

Our objective is to quantify comprehensively and from all information available, the population dynamics of *Ditrupa arietina* in the Bay of Banyuls-sur-Mer, emphasizing its role in the carbon cycle. For this, we formulate several mathematical models: (1) to simulate the dynamics of the size structured population of *D. arietina* in the Bay of Banyuls-sur-Mer, (2) to quantify the mass of calcium carbonate precipitated during the growth of their tubes, and (3) to hindcast the dynamics of the population at a timescale of two centuries and at the spatial scale of the Gulf of Lions. Mathematical properties of the models were studied to investigate conditions of persistence (or extinction) of the local population, and different hypotheses are discussed for local and regional scales by comparing simulations and observations from the study site and from other scarcer data collected throughout the Gulf of Lions (Labrune *et al.* 2007).

MATERIALS AND METHODS

Description of the study site. The Bay of Banyuls-sur-Mer (Figure 1) is located in the Gulf of Lions (42°30.00' N; 003°08.50' E). Water renewal depends strongly on the local water circulation which is influenced by a specific wind regime (Guizien *et al.* 2010). The main water circulation outside the bay is oriented north-south. The water depth in the bay increases from west to east; the isobath at 38 m was taken as a boundary for the bay at the eastern end. The surface of the bay is about 6 km², corresponding to a volume of *ca.* 0.15 km³, and *Ditrupa arietina* individuals were found over most of this area.

Conceptual development. The primary model was designed to simulate the dynamics of the abundance of *Ditrupa arietina* in the Bay of Banyuls-sur-Mer. The population is structured by the size, s (in mm), representing the length of the straight axis between the opening and the opposite end of the tube. The state variable, n(s,t) (in number of individuals), represents the abundance of the population in the Bay of Banyuls-sur-Mer, distributed according to the size, s (Gros 1992). The dynamics are governed by the processes of growth, mortality and recruitment and was formulated in a minimal way as:

$$\begin{cases} \dfrac{\partial n(s,t)}{\partial t} + \dfrac{\partial g(s)n(s,t)}{\partial s} = -m(s)n(s,t) \\ n(s_0,t) = r(t,n,s) \end{cases} \quad [1]$$

where g(s) is a growth function (in mm.day^{-1}), m(s) is a mortality function (in day^{-1}) et r(t) is a recruitment function, (in number of recruited individuals). The function g(s) is described by a linear ordinary differential equation:

$$g(s) = \dfrac{ds}{dt} = \gamma(s_{max} - s) \quad [2]$$

where s_{max} is the mean asymptotic maximum size of individuals (in mm) and γ is a mean individual growth rate (in day^{-1}). The mortality function is expressed by m(s) = μ, where μ is a

constant mortality rate, (in day^{-1}). The recruitment at s_0 was simulated by the following continuous function:

$$r(t) = \rho \frac{1}{\sigma\sqrt{2\pi}} \exp\left\{ -\frac{(t-t_c)^2}{2\sigma^2} \right\} \left(\int_{srep}^{+\infty} n(s, t-t_r)ds \right)$$ [3]

where ρ is the number of recruits per reproductive individuals and σ is a dispersion of recruits around the central date of the recruitment period, t_c. σ is set to represent the duration of the recruitment phase, that is *ca.* 1 month. s_{rep} is the average length at which an individual becomes a potential reproducer. t_r represents the duration of the larval stage, equal to *ca.* 1 month (Charles *et al.* 2003).

Steady-state estimate of the number of recruits per reproducers. The number of recruits per reproducer, ρ, cannot be estimated directly from the data series, because samples of individuals at the recruitment size ($s_0 = 1$ mm) were too variable. ρ^* was estimated in order to maintain the population of *Ditrupa arietina* in a state of equilibrium between two periods of recruitments. The model [1] was simplified to a two state variables model, one representing the subpopulation of juveniles, J (in number of individuals) and the other, the subpopulation of adults, A (in number of individuals). Introducing $N = J+A$, the model became:

$$\begin{cases} \dot{N} = -\mu N \\ \dot{A} = +c(N-A) - \mu A \end{cases}$$ [4]

where c is a transfer rate, which is the growth function, g(s), integrated from s_0 and s_{rep}. s_{rep} is equivalent to 18 mm according to Charles *et al.* (2003).

The system [4] has an analytical solution calculated on a time interval T ($T \in R^{+*}$) between 2 recruitments:

$$\begin{cases} N_{t+T} = \alpha N_t \\ A_{t+T} = \alpha A_t \beta + \alpha N_t (1-\beta) \end{cases}$$ [5]

where $\alpha = \exp\{-\mu T\}$ and $\beta = \exp\{-cT\}$.

The transition between two periods, which represents the recruitment, was calculated at the end of the period T, as:

$$N_{t+T} = N_{t+T} + \rho A_{t+T} = \alpha N_t + \rho A_{t+T}$$ [6]

where ρ is the number of recruits per reproducer at t+T. This model assumes that the duration of the peak of the recruitment phase is so short compared to the time between two recruitment periods that recruitment can be considered as instantaneous at the scale of the overall dynamics of the population. The equilibrium is expressed by $N_t = N_{t+T} = N^*$. Therefore,

as $(\alpha\beta)<1$ the time series $A_{t+T}=f(A_t,N^*)$, equation [5], converges to the solution $A^*=\alpha N^*(1-\beta)/(1-\alpha\beta)$, and ρ^* can be estimated from this steady-state solution as:

$$\rho* = \frac{(1-\alpha\beta)(1-\alpha)}{\alpha(1-\beta)} \qquad [7]$$

which does not depend on the steady-state biomasses, A^* and N^*. In addition, with the order of magnitude of parameters estimates, $\alpha\beta$ appeared to be very small compared to α when $\Delta t > 365$ days. Therefore, the calculation of ρ^* can be simplified as $\rho* = (1-\alpha)/\alpha$. $\rho*$ depends on the estimated value of the mortality rate and on the value of T (Figure 2). When the periods between two recruitments changes, steady-state can only be calculated between the first and the last recruitment periods of the time series. Using the approximation $\{\alpha\beta << \alpha\}$ to describe the dynamics of N_t, and introducing $\{T_i, i=1,I\}$, a series of fluctuating periods between two recruitments, ρ_T* can be approximated by:

$$\rho_T * = \sqrt[n]{e^{-m\sum_{i=1}^{I}T_i}} -1 \qquad [8]$$

Calcification calculation. The calcification rate was calculated from the growth rate of individuals. An allometry function links the size, s (in mm), with the individual mass of $CaCO_3$, w (in mg). This function ($w = as^b$) predicts that the mass of $CaCO_3$ increases with the size of individuals. The mean individual rate of calcification (in mg $CaCO_3$.ind^{-1}.day^{-1}) was calculated, for each size s, as a temporal variation of the individual mass, w:

$$\frac{dw}{dt} = \frac{dw}{ds} \times \frac{ds}{dt} = abs^{b-1}g(s) \qquad [9]$$

The calcification in the Bay of Banyuls-sur-Mer (mg $CaCO_3$) was calculated by integrating over time intervals ΔT and over the size range of the population, the mean individual rate of calcification, multiplied by the corresponding abundance, n(s,t):

$$Cal(\Delta t) = \int_{t}^{t+\Delta t}\left(\int_{s_0}^{+\infty} abs^{b-1}g(s)n(s,t)ds\right)dt \qquad [10]$$

Numerical integration of the dynamic model. The equation [1] was solved by numerical integration according to an implicit finite difference method ensuring the numerical stability.

$$n_s^t = -\frac{\Delta t}{2\Delta s}g_{s-\Delta s}n_{s-\Delta s}^{t+\Delta t} + n_s^{t+\Delta t}(1+\mu\Delta t) + \frac{\Delta t}{2\Delta s}g_{s+\Delta s}n_{s+\Delta s}^{t+\Delta t} \qquad [11]$$

The numerical scheme is presented Figure 3. The size, s, is defined between s_0 (recruitment size) and s_{lim} (limit size of the population chosen to respect $s_{lim} >> s_{max}$), and t is defined

between t_0 and $+\infty$. Δt and Δs are the size and time steps respectively. The resulting tridiagonal matrices were computed using Thomas's algorithm (Hirsch 1989).

Data collection and analysis. A 9 year-long series (between June 1994 and June 2003) of *Ditrupa arietina* population densities were recorded every two weeks at the SOLA station (located at 18 m water depth from 1994 to 1996, and relocated to 27 m afterwards, see Figure 1). At both locations, tube size (length of the straight axis between the opening and the opposite end of the tube), biomass (flesh dry weight) and the $CaCO_3$ biomass, were measured for individuals. The tube was assumed to be 100% calcite.

In addition to the biweekly sampling at SOLA, synoptic spatial samplings of the population densities were performed every year for a grid of 78 stations (Figure 1). The spatial distributions of *Ditrupa arietina* density in the Bay of Banyuls were inferred by a geostatistical analysis based on an intrinsic hypothesis of stationarity (Guarini *et al.* 1998). This was then used to estimate the frequency distribution of individuals as a function of water depth, z. The probability density model that represents the frequency distribution is a skew-normal distribution:

$$f(z) = \frac{1}{\omega\pi} e^{-\frac{(z-\xi)^2}{2\omega^2}} \int_{-\infty}^{\alpha\left(\frac{z-\xi}{\omega}\right)} e^{-\frac{x^2}{2}} dx \qquad [12]$$

where ξ is the location ω is the scale factor, and α is the skew parameter. When α equals zero, the normal distribution is unskewed, when $\alpha > 0$, it is left-skewed and when $\alpha < 0$, it right-skewed. These parameters were estimated using a direct search algorithm (simplex) and a Pearson χ^2 test for the goodness-of-fit (Gupta and Chen 2001).

Hindcasting the long-term trend. Assuming that the storm regime is a predominant factor to explain recruitment variability, an indicator of storm occurrences was defined using the North Atlantic Oscillation index (NAOi). NAOi is a global index, and even if it was designed to characterize climate variations in the North Atlantic basin, it is also a good indicator of the meteorological disturbances in the north of Europe (Kutzbach, 1970). Values of the index are calculated as a deviation from the average difference of pressure between the anticyclone of Azores (measured in Lisbon) and the depression of Iceland (measured in Reykjavik). They are used to determine the storm trajectory on the European coast; when they are positive, storms are pushed northwards, and when they are negative, storms move along more southerly tracks, hence impacting directly the north-west coast of the Mediterranean Sea. The advantage of using the NAOi is that it can be calculated every month since 1821, providing a long time series to explore variations of recruitment success and population dynamics of *Ditrupa arietina* in the region. An averaged NAOi was calculated each year, from 1821 to 2004, in three different cases: for the full year, for the first half of the year (January to the end of June) when most of the reproduction and recruitment occur and for the four months when most of the

larval dispersal and recruitment occur in March, April, May and June. Thus, it was considered that recruitment was possible in the Bay of Banyuls only when the NAOi was positive.

Metapopulation approach. Finally, because the study area is open to exchange, the link between subpopulations in a metapopulation of *Ditrupa arietina* at the level of the Gulf of Lions was estimated. To achieve this, a system that dispatches the contribution to the recruitment among S connected sites was developed. This system is based on equation [9], and is formulated as:

$$N_s(t + \Delta t) = \alpha N_s(t) + \rho \sum_{v=1}^{S} \kappa_v A_v(t) \qquad [13]$$

where κ_v is the exchange rate of recruits between sites (*i.e.* the proportion of adults A in site v producing each ρ recruits at time t). At steady state:

$$N_s^* = \alpha N_s^* + \rho^* \sum_{v=1}^{S} \kappa_v A_v^* \qquad [14]$$

Using the local result $A_s^* = \alpha N_s^*(1-\beta)/(1-\alpha\beta)$ and equation [10], equation [13] become

$$(1 - \kappa_s)N_s^* = \sum_{\substack{v=1 \\ v \neq s}}^{S} \kappa_v N_v^* \qquad [15]$$

Only one value for N_s^*, characterizing the reference site (*i.e.* the Bay of Banyuls sur Mer), is available and the other ones are estimated solving the system Kx=b, where b is a vector of size (S,1) containing the values for the reference site, and K, is a matrix of size (S,S-1) containing the y values of the exchange rates of recruits between sites, and x is the vector of size (S-1,1) of the values of population densities that need to be estimated. Estimates of rates of connectivity performed by Guizien *et al.* (2006) were used to calculate the vector x for 11 sectors in the Gulf of Lions, from Marseille to the Spanish border.

All calculations and simulations were done with SciLab (version 5.5.2).

RESULTS

Estimating the spatial structure of the population densities of Ditrupa arietina in the Bay of Banyuls-sur-Mer. The empirical semi-variogram was calculated to model the spatial distribution structure of densities. Three models - spheric, exponential and Gaussian - were fitted to the empirical semi-variogram data. The Gaussian model (nugget = 0.26 × sill, effective range = 635 m) minimized the sum of square residuals between observations and predictions, and was set aside for kriging. A cross-validation of the interpolation was performed by comparing predictions *vs.* observations: the regression slope was 0.990 ± 0.114 (SE), and the intercept was not significantly different from zero.

The resulting skew-normal frequency distribution of individual abundances as a function of depth, z, is shown in Figure 4. Parameter estimates led to $\xi = 29.4$, $\omega = 8.0$, and $\alpha = -4.1$, hence the mean of the distribution is 23.2 (m) and the variance is equal to 25.6 (standard deviation = 5.06 m). These results signify that the maximum density is expected at about 28 m water depth, that the minimum depth at which *D. arietina* can be observed is 2 m, and that the maximum depth is expected to be 36 m. This distribution was used in the population dynamic model to estimate the spatial distribution of the *D. arietina* population (and hence, the total abundance).

Estimates of the demographic parameters. The parameters of the growth function, γ and s_{max}, were estimated from 5 separate cohorts (1998 to 2003). The averaged growth rate, γ and maximum size (s_{max}) were respectively 0.0035 ± 0.0006 (SE) day^{-1} and 32 ± 2 (SE) mm. The mortality rate, μ (day^{-1}), was estimated from the exponential decrease of densities during two long periods with no recruitment (06/1994 to 11/1996 and 11/2001 to 06/2004). It was found to be equal to 0.0045 ± 0.0020 (SE) day^{-1}. These estimates imply that the P/B was equal to 1.640 ± 0.002 (SE) year^{-1} (Allen 1971).

Steady-state estimates of number of recruits per reproducer. With $\mu=0.0045$ d^{-1} and $\Delta\tau = 365$ days, $\rho*$ is equivalent to 4.16 recruits per reproducer. In other words, with a constant annual recruitment, the population of *Ditrupa arietina* in the Bay of Banyuls-sur-Mer can be maintained at steady state if a reproducer generates on average *ca.* 4 reliable recruits. If they produce more, the total abundance (N_t) increases and diverges to infinite (the model does not represent density-dependent limitations). If they produce less, the total abundance decreases asymptotically to zero (corresponding to the local extinction of the population). The general form of the series is then $\{\rho=\delta\rho*, \delta\in P^{+*}, N_{\tau+\Delta\tau}=N_\tau(\delta+\alpha(1-\delta))\}$.

Simulating the temporal variations. Next, was to simulate the dynamics of the *D. arietina* population in the Bay of Banyuls-sur-Mer, and to compare results with the data series recorded at the SOLA station (Figure 5). The transition due to the relocation of the SOLA station occurred around day 1000 of the simulation, when the number of individuals in the bay was low. No 'step' effect was detected at this time, but the data series from 1994 to 1996 were re-aligned to fit with the new 27 m SOLA station where the 1997-2003 data series were collected. This re-alignment was done using the estimated frequency distribution of abundances (Figure 4), which provided a conversion factor of 3.2 between average densities. Recruitment events occurred in 1998, 1999 and 2001. Using Equation [11], the estimated recruitment rate at equilibrium was $\rho*=7.9$ recruits per reproducer, respectively. $\rho*(0)$ was set arbitrarily to 4.16 recruits per reproducer (we assumed that a recruitment occurred in 1993), and the initial condition of the simulation, N(0), that minimized the square distance between observations and simulations was equal to 12 ind.m^{-2} (all individuals considered as adults in the initial population). While filtering a part of the variability, the model simulates correctly

both the observed pattern of total abundances and the amplitude of recruitment peaks. However, ranges of fluctuations were large; the maximum estimated abundance value was reached in 1994 (51 ind.m^{-2}). The minimum estimated value was reached in 1998 (520 ind.m^{-2}).

The relationship between the sizes of individuals (s, the maximum straight length of the tube in mm) and their biomass (w, in mg dry weight of flesh), was established by Medernach *et al.* (2000), as w = 0.00017s$^{2.87}$. The transformation of size structure abundances in mean individual weight (mg.ind^{-1}) was compared to an independent data series collected at the SOLA site (Figure 5). The orders of magnitude and trends were respected but the model over-estimates by up to 30% the higher values of the flesh dry weight for individuals.

Extrapolating the population dynamics in time and space. Population density variations were calculated over 180 years, using Equation 11 applied to the estimated series of T_i successive periods between two recruitments from 1824 to 2004. A sensitivity analysis was done by applying a jack-knife to the data and then reconstructing the time series for each case. The initial condition (for all cases) was determined for the optimal simulation fitting with the 10-year survey and was equal to 120 ind.m^{-2} (Figure 6).

For a yearly-averaged NAO index, the best estimate for ρ^*_T is 19.3 recruits per reproducer. The mean value after 50 jack-knife re-samplings is 18.3 ± 2.15 (SE) recruits per reproducer. The maximum density was reach in 1930 (1926 among all jack-knife pseudo-replicates), with 6.10^8 ind.m^{-2} and the minimum density was reached in 1881 (same date among all jack-knife pseudo-replicates), with 50.10^{-5} ind.m^{-2} or about 2632 individuals in the entire bay of Banyuls-sur-Mer. For an averaged NAO index calculated for the 6 first months of the year, the best estimate for ρ^*_T is 13.7 recruits per reproducer (mean value after 50 jack-knife re-samplings equals 14.51 ± 1.32 (SE) recruits per reproducer. The maximum density was reach in 1928 (same date among all jack-knife pseudo-replicates), with 10253 ind.m^{-2} and the minimum density was reach in 1874 (1868 among all jack-knife pseudo-replicates), with 60.10^{-5} ind.m^{-2} or about 3158 individuals in the entire bay of Banyuls-sur-Mer. For the last case, the NAO index was averaged for the months concerned by larval dispersal and recruitment, the best estimate for ρ^*_T is 39.7 recruits per reproducer (mean value after 50 jack-knife re-samplings equals 37.17 ± 6.67 (SE) recruits per reproducer). The maximum density was reached in 1847 (1859 among all jack-knife pseudo-replicates), with 97.10^3 ind.m^{-2} and the minimum density was reached in 1943 (1951 among all jack-knife pseudo-replicates), with 28.10^{-7} ind.m^{-2} or about 15 individuals in the entire bay.

Concerning the *D. arietina* metapopulation approach, Figure 7 shows the estimates of the densities for the sub-populations at the regional scale of the Gulf of Lions. The region was divided in 11 sub-populations with similar surfaces. The steady-state estimates of densities were compared with the averaged measured densities for each local population. Even if the

order of magnitude is respected (around 200 ind.m^{-2}), the model as formulated does not represent well the variations as they were observed by Labrune *et al.* (2007).

Calcification and potential influence on the carbon cycle. The third step in the modeling was to estimate the $CaCO_3$ production and determine if this has the potential to influence the carbon cycle in the Bay of Banyuls-sur-Mer. The allometric relationship between the size of individuals (maximum straight length of the tube) and the weight of calcium carbonate was established by Medernach *et al.* (2000). The values used in the calcification calculation are a=0.0076 mg and b=2.84 (dimensionless).

Figure 8 represents the mean individual weight of the tube of $CaCO_3$ (which has similar dynamics as the mean individual weight of the flesh, with a scaling factor equal to *ca.* 40) and the daily quantity of calcium carbonate ($CaCO_3$) produced by the calcification of tubes of *D. arietina* both at the SOLA station and in the entire Bay of Banyuls-sur-Mer. Values were averaged to provide estimates per square meter. The production at the SOLA station varies from 0.003 to 4.69 mg $CaCO_3$.m^{-2}.day^{-1}, which corresponds to a range of 0.03 to 46.9 mmole CO_2 trapped in the $CaCO_3$ per square meter per day. The peak of $CaCO_3$ production is observed at the end of November 1994, 145 days after the recruitment peak. Integrated over each year (Figure 9), the production of $CaCO_3$ reached its maximum value in 1995, with *ca.* 835 g $CaCO_3$.m^{-2}.day^{-1}, or 8.35 moles of CO_2 trapped in the $CaCO_3$ per square meter per day. The minimum is in 1998, with *ca.* 1.2 g $CaCO_3$.m^{-2}.day^{-1}. Variations of production depend on the variations of population density (Figures 5 and 8), but the maximum $CaCO_3$ is delayed by 3-months relative to the peak of recruitment. Following the same trend, the production estimate at the scale of the bay drops to a range between 0.0003 to 0.45 mg $CaCO_3$.m^{-2}.day^{-1}. The yearly production varied over the 10 year period, between 0.10 to 80 g $CaCO_3$.m^{-2}.year^{-1}, or *ca.* 1 to 800.10^{-3} mole CO_2.m^{-2}.year^{-1} trapped in the calcium carbonate tubes built by the population.

DISCUSSION

The approximately decade long spatial and temporal survey of the *Ditrupa arietina* population in the Bay of Banyuls-sur-Mer constitutes a unique data series to explore population dynamics in a Mediterranean ecosystem. Because it is one of the most abundant populations in the bay and because individuals build rapidly external tubes of $CaCO_3$, *D. arietina* was considered to regulate the carbon cycle in this ecosystem (Medernach *et al.* 2000).

Characteristics of the population dynamics. The apparent lack of competition with other species (Gremare *et al.* 1998) justified studying the population dynamics independently from other species in the benthic invertebrate community. First, simulations of the variability pattern of both the population abundances and biomasses were done. The model represents the size distribution of individuals; in this population, the crucial step in the life cycle is when

juveniles become reproductive adults at an average size of 18 mm (s_{rep}, Charles *et al.* 2003). Our deterministic model was designed to simulate the trend of the entire Bay of Banyuls-sur-Mer, hence filtering most of the random variability. Direct comparison with the observed size structure distribution at the SOLA station was not possible because: (1) the variability has two components, spatial and temporal, and (2) the parameters of growth, mortality and recruitment were not known *a priori*. Instead, the integrated density data were used to estimate these parameters for the model and conversions between density and weight (dry weights of flesh and shell) were done using relationships published in Merdernach *et al.* (2000). Comparisons between the simulations and observations were then made using independent data series of individuals' weights.

Ditrupa arietina is not a well-documented species, but its demographic characteristics suggest that it is a pioneer species with a strong ability to colonize suitable habitats (McHugh and Fong 2002). The population of *D. arietina* is composed of small size organisms (the average maximum size is *ca.* 30 mm) with a fast growth (the maximum size is reached in *ca.* 1 year), and a short life time (4 years). With 9000 eggs per female in average, the fecundity is moderately high for a polychaete species (McHugh & Fong 2002). Growth and mortality do not appear to be influenced by changes in environmental conditions (presence or absence of recruitment) or by the state of the population itself (low *vs.* high abundances). No seasonal trend was detected and the survival curve is a decreasing exponential function with a constant mortality rate.

A large part of the inter-annual variability in the population abundance was assumed to be due to variations in the recruitment success (*i.e.* settlement of juveniles at the size $s_0=1$ mm). This is a common property of sedentary marine invertebrates which have a pelagic larval dispersion phase (Botsford 2001, Ripley and Caswell 2006). Several factors may influence the success of the recruitment, mainly: the larval and post-larval mortality, physical disturbance of the habitat and competition for resources. The larval and post-larval mortality due to predation is probably the factor that controls recruitment (Dekshenieks *et al.,* 1997; Hiddink *et al.* 2002; Weissberger and Grassle, 2003). Larvae can even be consumed by adults of the same species because they filter particles in the water column without active sorting (Takasuka *et al.,* 2004). In addition, the Bay of Banyuls-sur-Mer as an open bay with hydrodynamic forces which increase during storms, inducing stress at the sediment surface, preventing recruitment from happening (Guizien *et al.,* 2010). Intensity and frequency of storms are therefore assumed to explain a large part of the success or the failure of the recruitment. In this situation, a storm may have two effects, to increase the larval dispersion (Guizien *et al.,* 2006) and to increase mortality of juveniles that have just settled. Even if some population dynamics models take into account explicitly larval and post-larval mortality (Thiebaut, 1994; Dekshenieks *et al.,* 1997; Ellien *et al.,* 2004), we have chosen not to do so here because the sensitivity of recruitment to small uncertainties in these processes is too high to allow

comparisons between observations and simulations in an optimization context (Rippley and Caswell, 2006).

The parameter ρ^*, which represents the number of recruits per reproducer, is a steady-state estimated value that can is interpreted in terms of demography. This value depends only on the duration between two recruitments and on the mortality rate (Figure 2). In addition, the lowest value of ρ^*, is small (less than 1 %) compared to the average number of eggs produced by females. This characteristic means the species has a high potential for proliferation: when ρ is greater than ρ^*, the average biomass increases. A proliferation can induce a density-dependent process of recruitment (Marshall and Keough, 2003), but this was not observed during the 10-year survey. The recruitment event of 1994 had the highest density values, nonetheless this does not provide any information on potential limitations since the density before this recruitment is unknown.

Influence of the NAO on the occurrence of the recruitment. The results showed that the choice of the time window inside which the NAO index is averaged, conditions the pattern of density variations. Nonetheless, the results of the jack-knife re-sampling, performed after the time window was chosen, showed that there is a strong consistency in the simulated pattern. In Figure 6, which summarizes the 3 choices of time windows, the largest differences between population densities estimates can be found between 1920 and 1970. But deciding which window is the most relevant remains difficult if no ancillary information is available. However, the fact that *D. arietina* was not found in the inventory completed in 1967 and 1968 (Guille, 1971) and that the order of magnitude of the density values remained in the range of the last 10 years of observations, suggested that the calculation of the averaged NAO index for the 4-month period corresponding to the larval dispersion and recruitment could be more relevant than for the other cases.

Is the population of Ditrupa arietina, a subpopulation in a metapopulation? Results of our simulations suggest that with the observed mortality and growth rates, the population of *D. arietina* in the Bay of Banyuls-sur-Mer is able to self-regenerate. A small number of recruits per reproducer are enough to maintain the population in steady-state over long periods of time. However, in order to fully understand the dynamics of the population of *D. arietina* in the ecosystem of the Bay of Banyuls, it is necessary to consider and quantify what could be the contribution of other populations (in terms of recruitment) and how, in return the Bay of Banyuls can contribute to other sub-populations, within a larger metapopulation defined at the regional scale of the coast of the northwestern Mediterranean Sea.

A successful recruitment is also a successful larvae development (Perkins and King 2006), and during the dispersion phase (which may vary from days to months) larvae of marine invertebrates are transported passively by currents. Larvae can also choose their substrate. For example, *Capitella sp.* (Grassle *et al.*, 1992) prefers to colonize fine, muddy sediments enriched

with organic matter, and *Spisula solidissima* and *Mulinia lateralis* inhabit coarse sand sediments preferentially (Snelgrove *et al.* 1993, Weissberger and Grassle 2003). These organisms are known to sink and then swim actively near the bottom where the current is weak until they find suitable conditions (Butman and Grassle 1992) or they settle and then leave if conditions are not favorable. For instance, juveniles of *Pectinaria korenii* develop first a tube made of mucus, which is partly abandoned to permit their resuspension if the conditions of post-larval development are not suitable (Olivier *et al.,* 1996; Thiebault *et al.,* 1996). In our case, juveniles of *D. arietina* build a tube made of mucus first and do not colonize muddy sediments, which appear not to be favorable for their development; however, no process of sediment selection seems to occur (Charles *et al.,* 2003). Therefore, the only criteria used to explain the spatial distribution is depth, even if it is partly related to sediment and hydrodynamic characteristics.

The question of the meta-population leads to another: is the local population in the Bay of Banyuls-sur-Mer a source (self-regenerating) or a sink (*i.e.* local persistence is due to imports from other connected sites; Runge *et al.,* 2006; Doncaster *et al.,* 1997)? Model results were compared with the data collected during an extensive sampling in Autumn 1998 in the Gulf of Lions (Labrune *et al.,* 2007). The averaged density estimated by the model in the bay at this period (*ca.* 230 ind.m^{-2}) was used as a reference point. The estimates of x coordinates do not match with what was found on average for all sectors during the 1998 sampling, even if the orders of magnitude are consistent (Figure 7). These large discrepancies show the limits of this approach. In order to specify the level of interactions of the studied population with other local populations in a region, a genetic marker study to trace fluxes of genes between groups of individuals will be necessary (Grimm *et al.,* 2003; Jolly *et al.* 2003).

Calcification and carbon cycle. And finally, we re-consider the link between calcification at the level of the metapopulation and the carbon cycle in the meta-ecosystem. Clearly, our results contradict the previous results obtained by Medernach *et al.* (2000). The quantity of calcium carbonate produced by calcification varies according to abundance and the age of the individuals that make up the population of *D. arietina*. After recruitment, a rapid increase of $CaCO_3$ production is expected, because both abundances and individual growth rates are high. The maximum $CaCO_3$ production is calculated when individuals reach 20 mm long and this is what accounts for the time lag of 145 days between peaks of recruitment and maximum production of $CaCO_3$. When no spring recruitment occurs, the production and mass of $CaCO_3$ decreases strongly. The maximum value of $CaCO_3$ production for the entire Bay of Banyuls-sur-Mer occurred in 1995 (and not in 1994) and was estimated to be only 80 g $CaCO_3$.m^{-2}.year^{-1}. Our estimate is considerably lower than the value in Medernach *et al.* (2000) for the same period and the same ecosystem (2180 g.m^{-2}.year^{-1}). The maximum value estimated at 27 m water depth was equal to 835 g CaCO3.m^{-2}.year^{-1}, which is close to the maximum values classically estimated for temperate climate ecosystems (Migné *et al.,* 1998; Chauvaud *et al.,* 2003; Martin *et al.,* 2006), and lower than the estimated value for coral reef ecosystems (1000 to 4000 g.m^{-2}.year^{-1}) The model only represents a trend and filters the day-to-day

variability, however, to be able to observe a peak of production of $CaCO_3$ equal to ca. 12000 $g.m^{-2}.year^{-1}$, it would be necessary to have ca. 740,000 individuals per square meter recruited in 1994 (instead of 51,200 individuals per square meter), and this, everywhere in the bay.

The increase of pCO_2 in the seawater (*i.e.* increase of the concentration of dissolved CO_2) during calcification (Ridgwell and Zeebe, 2005), induces a decrease of pH (Bates *et al.*, 1995) because of the shift in total alkalinity and total carbon equilibriums. Calcification modifies the equilibrium of total inorganic carbon in the sea water (SW), symbolized as CT (in $\mu mol.(kg\ SW)^{-1}$), and total alkalinity, AT ($\mu mol.(kg\ SW)^{-1}$) as follows (Bates *et al.*, 1995):

$$\begin{cases} CT = CT - Cal(\Delta t) \\ AT = AT - 2Cal(\Delta t) \end{cases} \qquad [16]$$

where $Cal(\Delta t)$ is expressed in $\mu mol\ CaCO_3.(kg\ seawater)^{-1}$. CT is the sum of the concentrations of the different forms of inorganic carbon in the seawater:

$$CT = [CO_2] + [HCO_3^-] + [CO_3^{2-}]$$

and AT is equal to the sum of the active ions concentrations:

$$AT = [HCO_3^-] + [CO_3^{2-}] + [B(OH)_4] + [OH] - [H^+]$$

Calculation of equation system [16] should provide an estimate of deviation from total inorganic carbon and total alkalinity equilibrium due to calcification. However, as deviations depend strongly on the state of the chemical variables at each time step, to be able to apply this calculation to the influence of the calcification of *D. arietina* on the carbon cycle in the Bay of Banyuls-sur-Mer, it will be necessary to calculate an accurate budget of exchanges between Ocean and Atmosphere, and a renewal of water mass in the bay, as well as an estimate of other calcifying species present.

CONCLUSIONS

Our study provided a context for testing the metapopulation concept as a means to integrate ecosystem – scale processes with studies of geochemical cycles at both local to regional spatial scales, and short and historical time scales. Our study investigated the possibility to infer, from a quantitative estimate of the dynamics of the metapopulation of *Ditrupa arietina* over a 10-year period at one single site (Bay of Banyuls-sur-Mer), patterns of densities variations over the past 200 years, and patterns of abundance distributions at the scale of the Gulf of Lions. We feel that such tasks are required to understand effects of global changes on the dynamics of most of the marine populations, communities and ecosystems. The present increasing effort to monitor environmental variables will not help in hindcasting past trends. Even if these tasks are technically possible, results suggested that ancillary data sets are required to perform predictions with a better accuracy. Some of these data may be found by mining historical

archives, which appear recently to be quite fruitful (Cardinale *et al.* 2009) and are attracting more and more research attention (*e.g.* History of Marine Animal Populations project) among ecologists. Nonetheless, the relevance of past observations can be difficult to assess; here for example empty shells of *D. arietina* in benthic sediments can be cited as presence in the literature (Pruvot 1895).

Our study describes how estimates of the calcification production rates during the growth of the population may be achieved. These estimates are more theoretically sound than previous estimates for the same population, and our values are consistent with the range of values reported for temperate ecosystems. Our analysis does not suggest that the calcification by this population can change significantly the chemical properties of the water column, nor that the recent changes in carbon content could alter the construction of the $CaCO_3$ structures, as has been suggested by Gazeau *et al.* (2007). These kinds of assessments can only be performed if complete carbon budgets are done at the scale of the (meta-)ecosystems inhabited by the (meta-)population of the organism of interest.

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FIGURE LEGENDS

Figure 1. Study site of Bay of Banyuls-sur-Mer, in the Gulf of Lions, Western Mediterranean Sea, France. The bay is wide open on the rest of the coastal zone and the 38m isobath between *cape Béar* and *cape La Belle* is a boundary. The polygon is the area with soft sediments colonized by the local *Ditrupa arietina* population. The symbol x shows the location of the stations sampled each year, and the symbol ♦ indicates the location of the SOLA station sampled each week since 1997. The same unfilled symbol shows the location of the station SOLA sampled between 1994 and 1997.

Figure 2. The steady-state recruitment rate as a function of the mortality rate, μ, and the time period between two recruitments, T. When the mortality rate and the time period between two recruitments increase, the number of recruits per reproducer must be higher to maintain the population around equilibrium. This steady-state value for the recruitment rate increases twice as fast when T increases than when μ increases.

Figure 3. Numerical grid used to solve the size-structured population dynamic model (Equation [1]). The grid shows the different sizes used to frame the dynamics, s_0, which is the minimum size of recruits (1mm), s_{max}, which is the maximum average size for the growth, and s_{lim}, which is an arbitrary size limit for individual. This limit cannot be reached even if numerical diffusion allows individuals to be longer than s_{max} (no growth occurs above the maximum size). Δs and Δt are the size and time steps respectively. The numerical integration scheme is implicit (hence, unconditionally stable) and centered (minimizing the numerical error) except for the boundaries (s_0 and s_{lim}).

Figure 4. Skew-normal frequency distribution of *Ditrupa arietina* population as a function of the depth (solid line) fitted to the empiric distribution (o). Parameter estimates are $\xi = 29.4$, $\omega = 8.0$, and $\alpha = -4.1$. The mean of the distribution is equal to 23.2 m and the standard deviation is equal to 5.06. A maximum density is expected at z $\approx$ 28 m. The minimum and maximum depths at which *Ditrupa arietina* can be observed are 2 m and 36 m respectively.

Figure 5. Simulations of the population dynamics of *Ditrupa arietina* in the Bay of Banyuls-sur-Mer, and comparison with observations performed weekly at the SOLA station. The upper figure shows the variations of densities at the SOLA station (the solid line represents the simulation and the symbol ♦ indicates data); the corresponding unfilled symbols between 1994 and 1996 represent the observations at the former SOLA station, which were converted to match with the new location. The lower figure represents the variations of the mean individual flesh dry weight, simulated (solid bold line) and observed (solid thin line and empty squares) with an independent data series collected at the SOLA site. The model over-estimates the mean individual flesh dry weight by up to 30%.

Figure 6. Hindcast scenarios of the population density variations in the Bay of Banyuls-sur-Mer over 180 years. Three scenarios were compared : the first (o−) rests on the calculation of the NAO index averaged over the year as an indicator of the yearly recruitment of the population of *Ditrupa arietina*, the second one (+−) limits the averaging period to the first six months of the year (when most of the reproduction and larval dispersal occur), and the third one (•−) restricts it to 4 months, March to June (when most of the larval dispersal occurs).

Figure 7. Estimates of the contributing densities to the recruitment of the subpopulation of the Bay of Banyuls-sur-Mer in a context of a *Ditrupa arietina* metapopulation at the regional scale of the Gulf of Lions. The region was divided in 11 sub-systems (upper figure) with similar surfaces. The first region contained the Bay of Banyuls-sur-Mer and was used as the "reference" site for the calculation of the distribution at the regional scale (lower figure). The simulation (continuous line) was compared with the averaged measured density (dashed line) for each local population.

Figure 8. Simulations of dynamics of $CaCO_3$ production by the population dynamics of *Ditrupa arietina* in the Bay of Banyuls-sur-Mer, and comparison with observations performed weekly at the SOLA station. The upper figure shows the variations of mean individual weight of $CaCO_3$ simulated (solid bold line) and recorded at the SOLA stations (solid thin line and empty squares). Variations of the mean individual $CaCO_3$ weight follow a similar pattern as the variations of the mean individual flesh dry weight. The lower figure represents the production of $CaCO_3$ per unit of surface at the SOLA station. The solid line represents the simulation while the empty symbol "o" represents the production estimates by numerical differentiations between two observations. It varied from 0.003 to 4.69 mg $CaCO_3.m^{-2}.day^{-1}$, with a maximum occurring 145 days after recruitment peaks.

Figure 9. Yearly-integrated production of $CaCO_3$ at the SOLA station (unfilled bars) and for the entire Bay of Banyuls-sur-Mer (filled bars). The maximum production occurred in 1995, even if the peak of recruitment was in 1994. The production estimated at the scale of the bay (per unit of area) is more than 8 times lower than the production estimated at the SOLA station.

Figure 1.
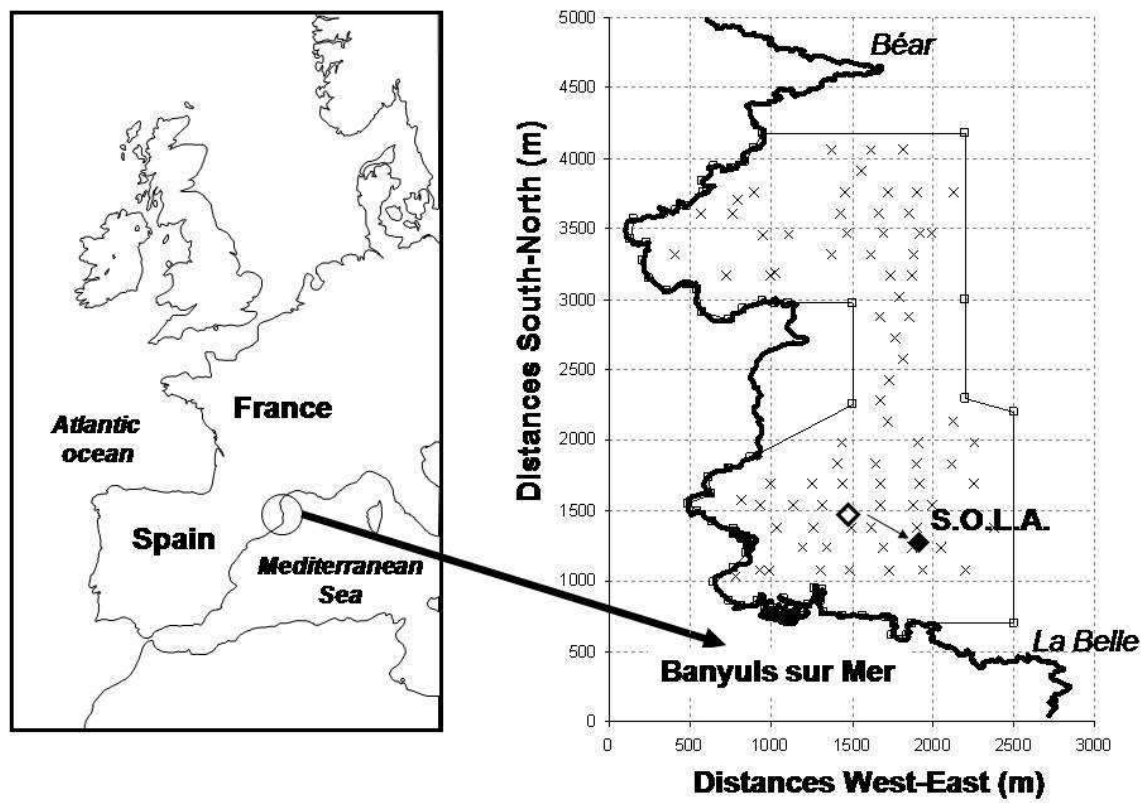
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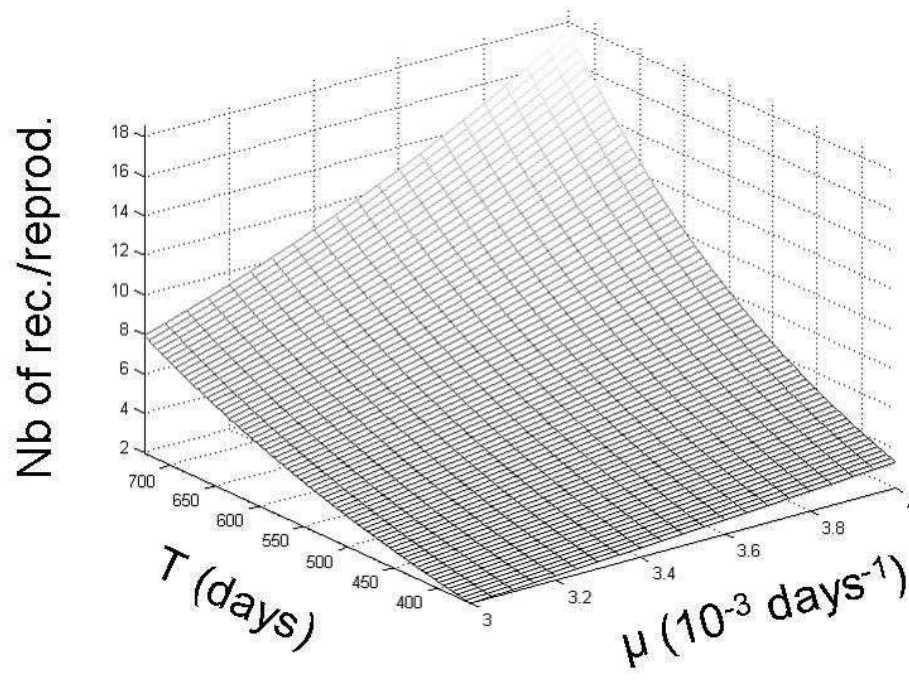
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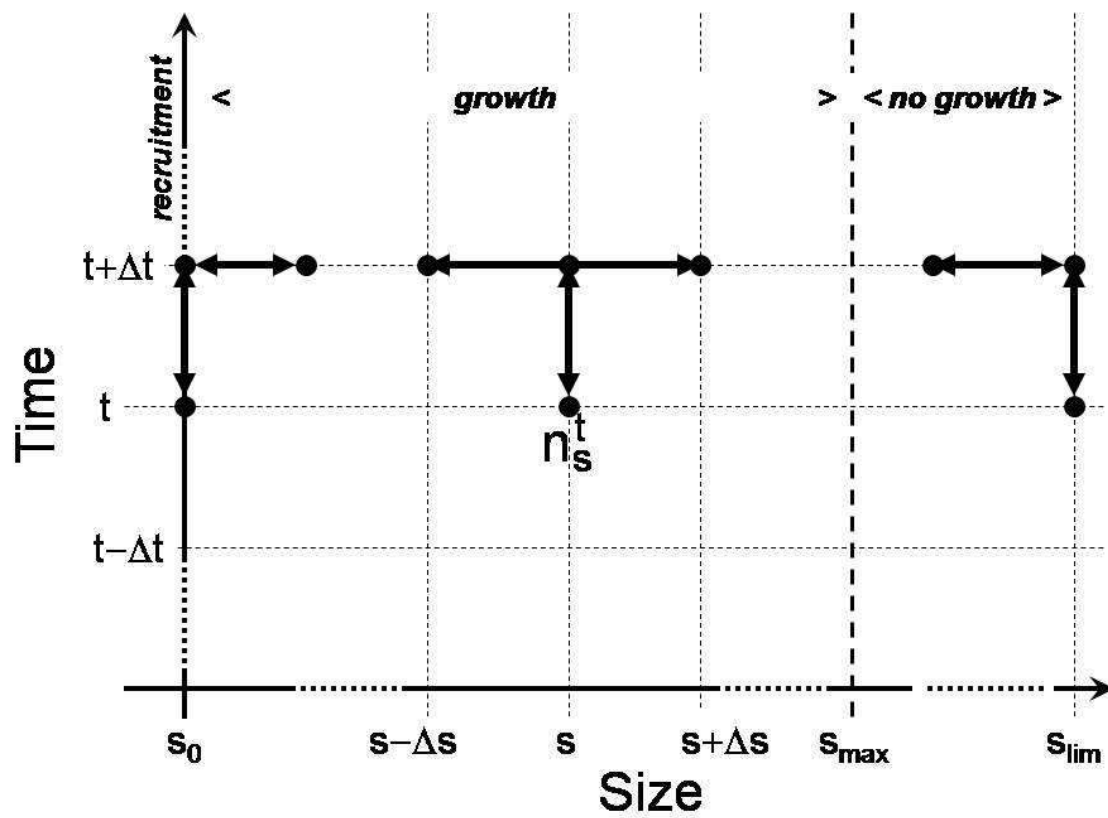
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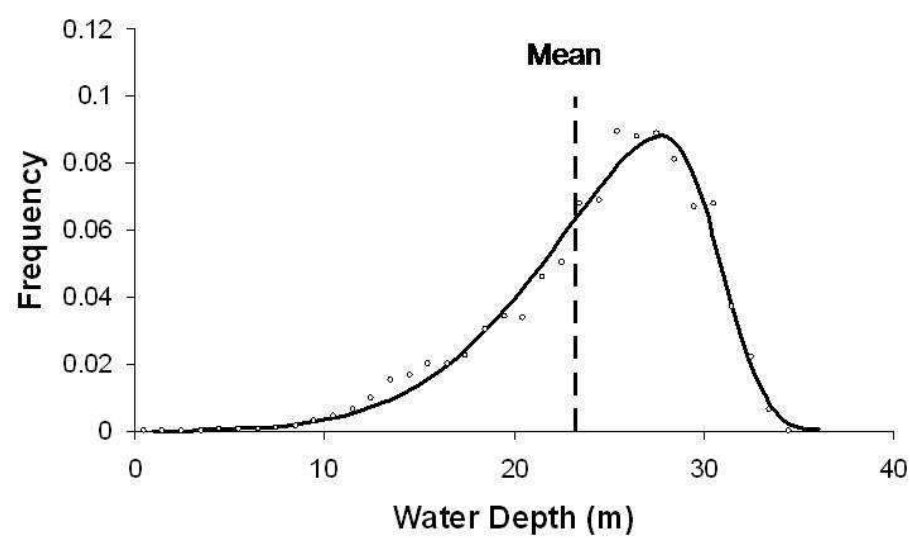
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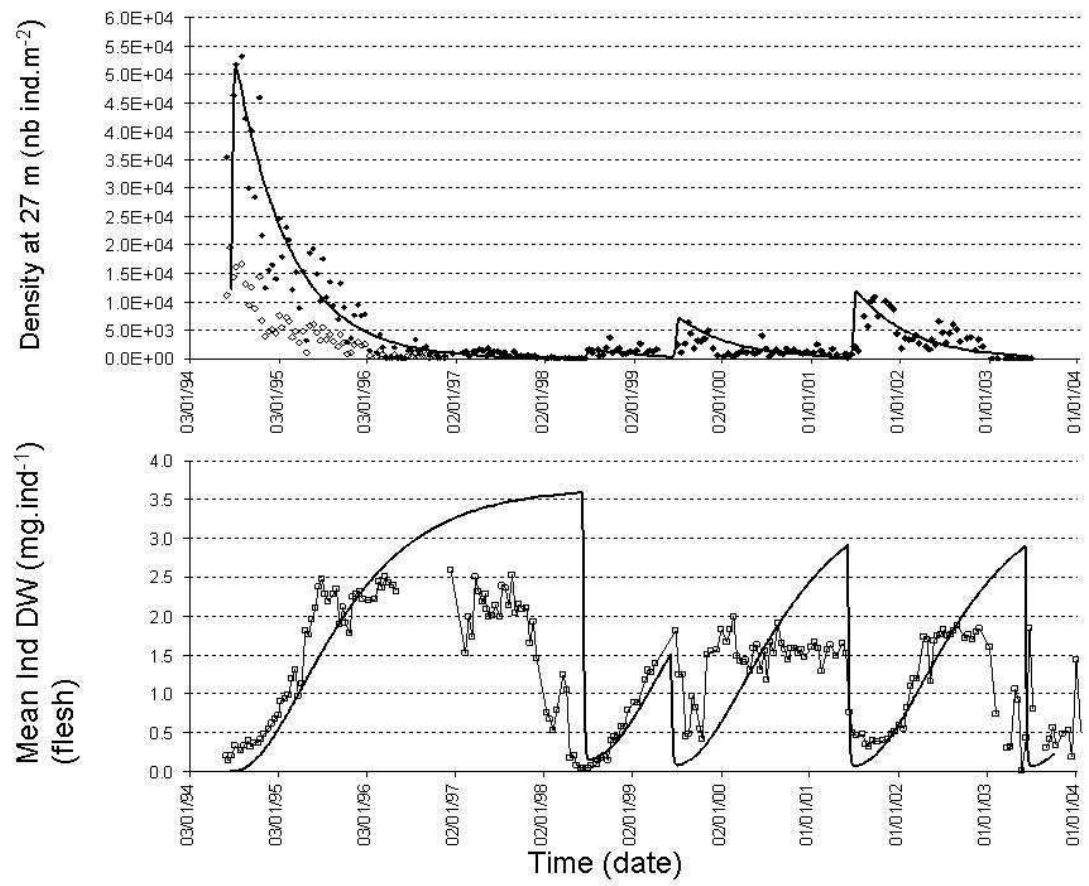
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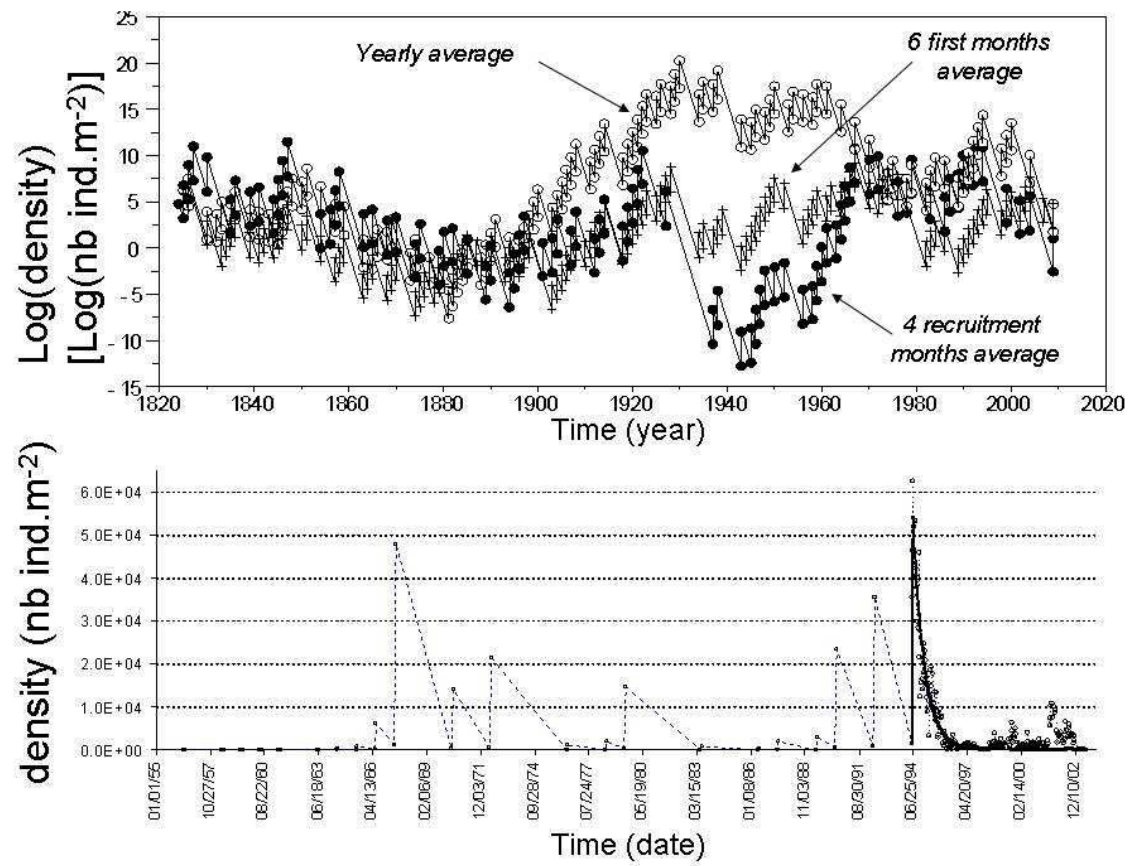
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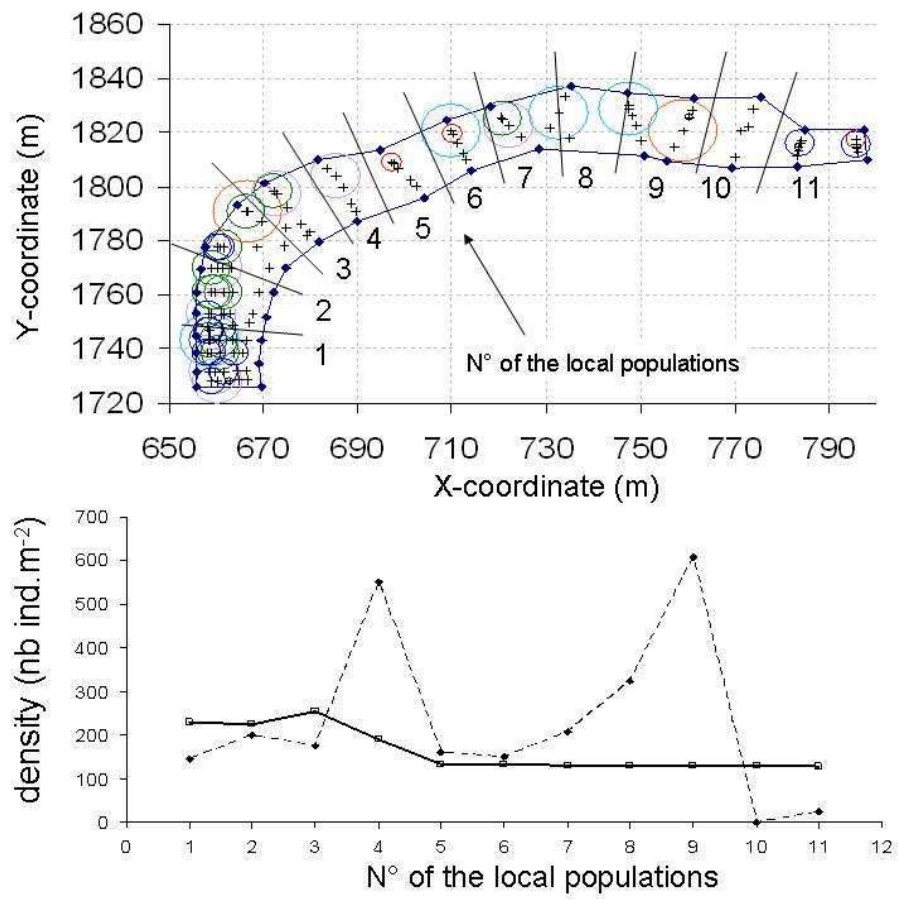
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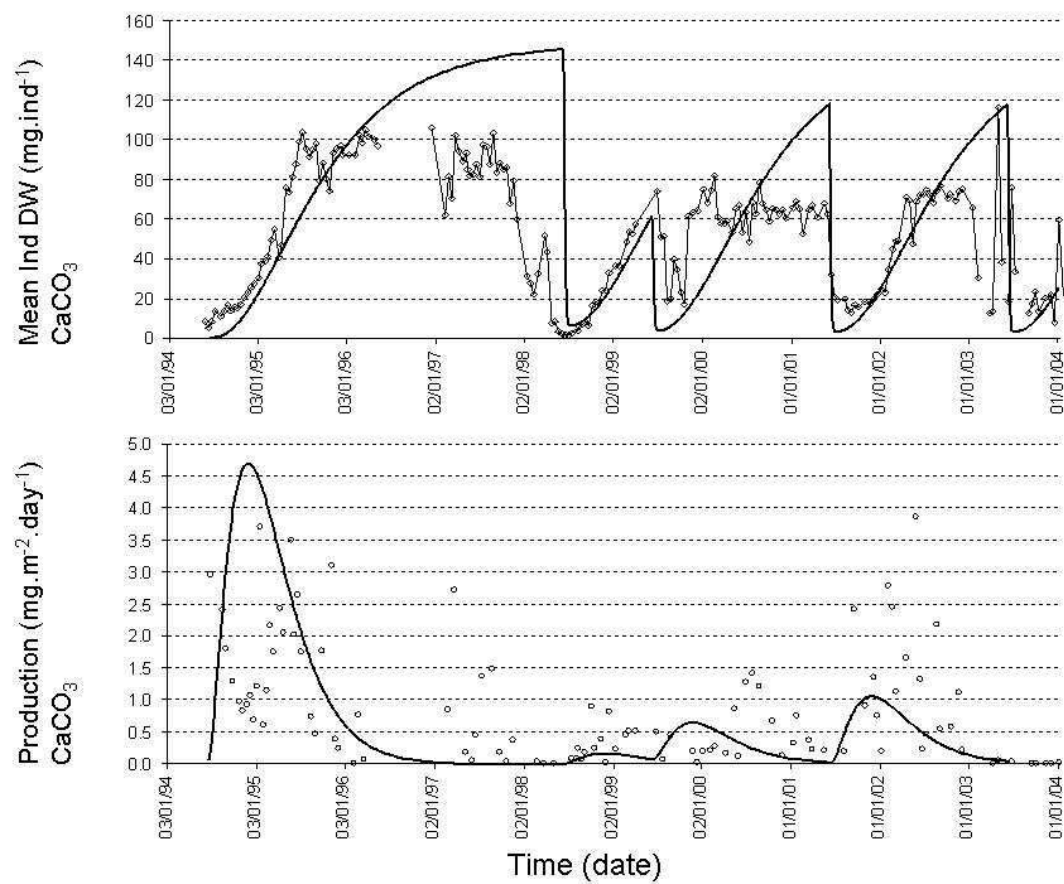
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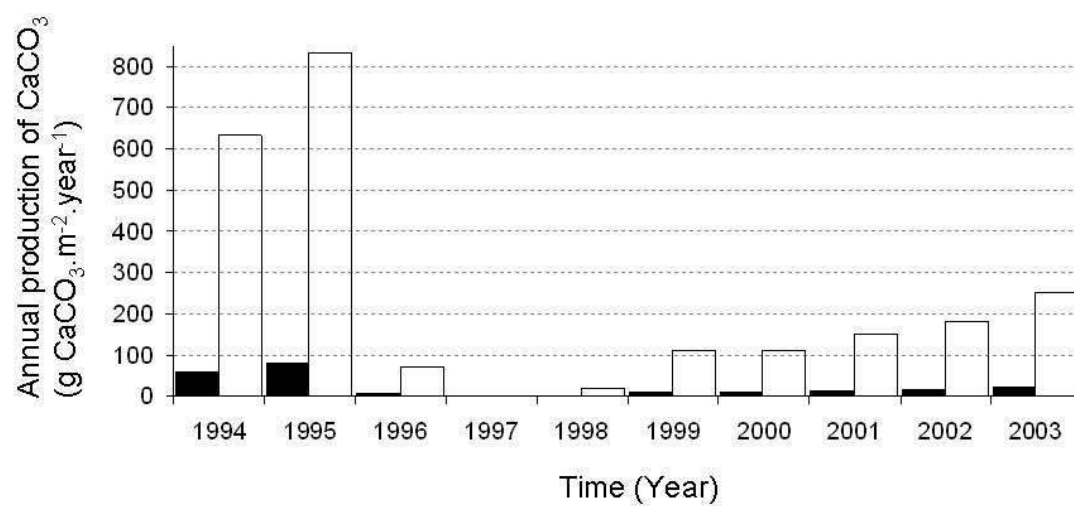
CHAPTER 5

RECONSTRUCTING POPULATION ESTIMATES

"How many fish *are* there in the sea?"

-- Anonymous

Running head: Low density population abundance estimates

Title: **A probabilistic approach to estimate low density population abundances applicable to ancient 'Murex' fisheries**

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Version: 12 Oct 2016

ABSTRACT

We describe a statistical method to assess population abundances of neogastropods at scales relevant to artisanal, coastal fisheries. Our approach is inspired by an ancient capture technique employed for millennia in the purple dye industry of the Mediterranean. The objective was to use successive captures with baited traps to estimate the density of the banded dye-murex, *Hexaplex trunculus* (Linnaeus, 1758) in the nearshore environment by applying a cumulative capture stochastic model taking into account the low densities of the populations. The theoretical design was validated by comparison with data acquired during a field experiment conducted on Crete Island, near Heraklion. Sampling devices were deployed in two shallow water habitats over a one-week period. The catchability and the Effective Area of Attraction of the traps were estimated using the individual speed and behavioral response toward the bait in independent laboratory experiments. We report here the first modern population density estimates for *H. trunculus* on the island of 6.7 individuals per square meter, ranging from 6 to 8 individuals per square meter, in seagrass and rocky habitats, respectively. This original method using ancient principles should be relevant to hindcasting neogastropod population abundances in most coastal environments.

KEYWORDS

INTRODUCTION

Population sizes and distributions are fundamental information in ecology (Pielou, 1977), yet with rare exceptions, absolute values cannot be measured directly. This is a long-standing difficulty for ecological studies, particularly for marine environments. Many marine animal populations are estimated based on depletion methods that rely on catch reports combining Catch per Unit of Effort indices (CPUE; Serchuk, 1978) and other biological parameters (*e.g.* recruitment, growth, mortality; Cadima, 2003). However, in fishery science, to fulfill the management objective of tracking relative changes of stock exploitation, absolute abundances have been considered unnecessary (Gulland, 1969) and relative measures, like the CPUE, have prevailed. When population densities are not available, other indirect information may be used instead which are still related to fishing and its ancillary commercial activities (*e.g.* total catches over specified periods, transaction amounts).

To understand how past conditions affect population dynamics, we would have a long series of observations that constrains reconstructed trends. But long time series in marine ecology are rare (Edwards *et al.*, 2010), and this situation has led to research activities aimed at recovering data from non-traditional and traditional historical sources (de Vooys and van der Meer, 1998; McClenachan *et al.*, 2012). Qualification and re-integration of data from sources outside the scientific literature has become a central challenge of "historical" ecology as well as conservation biology. While integrating these data can improve our understanding of, and ability to predict environmental change, we should not overlook the methodological problems associated with these disparate data sources. Data validation issues must be addressed through experimentation, reconstruction and re-analysis of not only recovered data, but their original epistemological context as well (Taylor, 2013; Kjer *et al.*, 2016).

There is thus an important need for the development of methods before the impact of earlier economic activities on coastal populations can be characterized in socio-economic contexts going back several millennia. We focus on gastropods because they (and other invertebrates) are subject to increasing exploitation (Valentinsson *et al.*, 1999; Eddy *et al.*, 2015) on modern coasts (Appendix S1: Fig S1, Table S1) and have also been harvested for thousands of years on nearly every inhabited coast (Alvarez *et al.* 2011; Klein and Steele, 2013).

Our goal is to develop approaches to estimate both the population densities of exploited gastropod species and characterize a fishing process that would be used in shallow, nearshore environments accessible to both ancient (Nielsen-Bekker, 2009) and modern fishing communities (Vasconcelos *et al.*, 2008). For all these reasons, we selected the banded dye-murex, *Hexaplex trunculus* (Linnaeus, 1758) as a representative case. This marine gastropod species occurs throughout the Mediterranean Sea basin, and extending as far north as the Gallican coast and south to Morocco (Bañón *et al.*, 2008; Vasconcelos *et al.*, 2008). Currently it is considered a minor commercial species ("Murex spp." FAO category, about 1% of non-abalone captures reported worldwide, Appendix S1). But in the Mediterranean region, it is

known as a common food and bait species (Vasconcelos *et al.*, 2008; Sawyer *et al.*, 2009) harvested using artisanal methods (Peharda and Morton, 2006; Vasconcelos *et al.*, 2008) and by trawling (Elhasni *et al.*, 2013). Some exploited populations exhibit a low genetic variability associated with 'bottleneck' effects (González-Tizó *et al.*, 2008). In addition, this species is collected for imposex monitoring programs since the mid-1990s (Axiak *et al.*, 1995; Terlizzi *et al.*, 1998; Terlizzi *et al.*, 2004).

In the past, *H. trunculus* was exploited intensively (*ca.* 4000 until about 1350 BP), along with *Bolinus brandaris,* as a source for the famous indelible purple dye, 'Royal Purple' or 'Tyrian Purple' throughout the Mediterranean basin (Cardon, 2003, Forstenpointner *et al.*, 2007). Today, dye production from muricid species, once believed to be exclusive to Mediterranean cultures, is known from archeological sites distributed across the globe (Cardon, 2003; Haubrichs, 2004; Giner, 2009). The dye, produced from precursor molecules present in the gastropod's hypobranchial gland (Cooksey, 2001), was time-consuming and labor intensive to collect, making this pigment a valuable trade commodity during classical Antiquity (Burke, 1999; Ruscillo, 2005; Giner, 2009). It remains unexplained how an industry which required such high numbers of individual organisms (*ca.* 1.4 g of pigment per 12 000 individuals, Friedländer, 1909) should exploit species that could be assumed to exist in relatively low densities.

In this study we propose a statistical method based on a stochastic cumulative capture model that integrates behavioral observations made in the laboratory and field observations to estimate population densities with their uncertainties. This method uses a sampling technique that strongly resembles what is known of ancient and modern methods of murex fishing (Ruscillo, 2005; Vasconcelos *et al.*, 2008), thus providing a means to hindcast population states for the murex fisheries of Antiquity in addition to making modern population estimates.

MATERIALS AND METHODS

The methodology employed is based on a depletion method (Serchuk, 1978) where individuals are removed from the targeted population at each sampling, instead of mark-and-recapture techniques used to make stock estimates. This approach was selected because the population density is hypothesized to be low, the animals are relatively slow-moving, and thus the mixing of marked individuals with non-marked individuals in a population would require a long time period. The study design (Figure 1) combines analytical calculations and numerical simulations with data from behavioral and field experiments using baited traps (Figure 2) installed in the shallow coastal study area on Crete Island near the Heraklion Marine Research Center (HCMR; Figure 2, inset). Crete Island is also where some of the earliest centers of Mediterranean purple dye production are found (Stieglitz, 1994).

Concepts underpinning fluctuating captures. The trend of the successive catches from traps placed and replaced at the same location is a cumulative curve (Serchuk, 1978). The average number of catches per unit of effort decreases while the number of total individuals collected at time t, n(t), tends to a maximum value:

$$n(t) = N_{\infty}\left(1 - e^{\{-\alpha t\}}\right) \tag{1}$$

where N_{∞} being the abundance (in nb of individuals) of a subpopulation distributed on a surface defined as the Effective Area of Attraction (EAA), which is also the initial subpopulation size that is being estimated here), and α (time^{-1}) is the catchability rate; the catchability rate being the rate at which the targeted sub-population is susceptible to be caught. The beginning of the experiment is set to $t_0 = 0$ and the number of individuals caught per unit of time decreases according to the following function:

$$\frac{dn(t)}{dt} = \alpha\left(N_{\infty} - n(t)\right) \tag{2}$$

Assuming that no other process occurs during the time interval of the capture experiment, the abundance of the targeted sub-population N(t) decreases by:

$$\frac{dN(t)}{dt} = -\alpha N(t) \tag{3}$$

leading to, $N(t) = N_{\infty}\exp\{-\alpha\ t\}$. N(t) is defined as N(t) + n(t) = N_{∞}.

In our study, the EAA depends on both the speed of displacement of the organisms and on their behavior toward the bait (depending on the bait attractiveness), hence it is linked to the estimate of α. Essentially, the baited trap creates an abrupt and external discontinuity in one environmental factor (the food resource) and the model exploits the organism's response (the numbers of organisms reaching the trap) to this anomaly to estimate the local population abundance.

For small populations, captures are assumed to fluctuate strongly. In other words, stochastic effects (like variability of individual behavior) are likely to predominate in the captures, hence the deterministic model representing the variations of the subpopulation abundances Equation [3] must be reformulated as:

$$N(t+h) = N(t)(1 - \alpha h) \tag{4}$$

where h is a continuous random variable (h $\in$ R^{+}*) representing the fluctuating time-step between two events of capture (assuming that one organism is trapped at a time). In this stochastic model, the probability that the population has the size N at time-step t+h is the probability that the population had a size N+1 at t, multiplied by the probability that an

individual is captured between t and t+h, that is given by the rate, α hN(t). Therefore, the probability that the population has a size N at any time t follows a Binomial Law $\mathcal{B}(n,p)$:

$$Proba\{N,t\} = \begin{pmatrix} N_\infty \\ N \end{pmatrix} p^N q^{N_\infty - N} \qquad [5]$$

where p is the probability to capture one individual, equal to $e^{\{-\alpha\,t\}}$, and q is the complementary probability to capture no individuals, which is equal to $(1 - e^{\{-\alpha\,t\}})$. The clearing time, T_e (in the same units of time as for α), is the time for reaching N = 0 in the EAA and has an expectation and variance equal to:

$$E(T_e) = \sum_{N=1}^{N_\infty} \left(\frac{1}{\alpha N} \right) \qquad [6a]$$

$$Var\left(T_e \right) = \sum_{N=1}^{N_\infty} \left(\frac{1}{\alpha N} \right)^2 \qquad [6b]$$

Estimating the asymptotic value of abundance of the targeted subpopulation (N_∞).
Our problem is actually the reverse of the reasoning developed in Equations [5] and [6]. In fact, we wish to estimate N_∞ (which then becomes a random variable) from a series of n_T fixed catches (realization of T > 1 successive capture experiments) instead of N. Theoretically, N_∞ follows the reciprocal law of that which describes N, and is then described by a Negative Binomial Law, $\mathcal{B}_N(n,p)$:

$$Proba\{N_\infty\} = \begin{pmatrix} N_\infty - 1 \\ N_\infty - n_T \end{pmatrix} \left(e^{-\alpha t} \right)^{N_\infty - n_T} \left(1 - e^{-\alpha t} \right)^{n_T} \qquad [7]$$

which determines what is the size of the population (N_∞) that permits trapping a cumulated number of n_T organisms after a series of T successive captures. This reasoning is obviously circular because it requires knowing the value of N_∞ to calculate the distribution law. However, a solution is to estimate this distribution law by means of simulation, using successive capture experiment data. To achieve this, a range of possible values for N_∞ is defined, starting from the total number of organisms captured per successive experiments and increasing up to values for which the realization of the stochastic process is no longer compatible (considered as the maximum of N_∞). Then, for each value of $N_\infty \in [\min(N_\infty)$ $\max(N_\infty)]$, the stochastic model Equation [4] is simulated numerically for each experimental run (Step 3, Figure 1) until the final time of the successive experiments is reached. The simulation is done X = 500 times; the probability that the targeted subpopulation size has size

N_∞ was calculated as the number of times the simulated catches n_T matched with the actual successive observations, divided by 500.

Successive capture experiments. The experimental method used baited, cost-effective "wallet-line" traps (Vasconcelos *et al.*, 2008). Two different habitats were investigated in July 2013: a rocky substrate consisting of both loose boulders and exposed bedrock substrate, and a seagrass (*Posidonia oceanica,* (Linnaeus) Delile, 1813) meadow. Water depths were less than 5 m.

Each "wallet" is constructed from rigid plastic netting (mesh size 1.5 x 1.5 cm) and had a finished surface area equal to 225 cm². Thus an installation consisted of five "wallets" total (Figure 2), arranged as a squared cross: one trap at the center (trap 0) and additional traps attached at the extremity of each four, one-meter long branches. This arrangement differs from the long lines (more than 100 meters) described in Vasconcelos *et al.* (2008) and is better suited to making observations on a single substrate patch. Individual wallet-traps were lested to prevent any movement over the duration of each capture experiment and baited with squid and sardine flesh. Traps were installed on each substrate by diving. Throughout the remainder of the presentation, "trap" will be used to refer to the individual "wallet-traps".

Traps retrieved after a preliminary experiment lasting overnight were either completely emptied of their bait or untouched, hence, the experimental time was determined to be too long relative to the size of the traps and the bait attractiveness for consumers in the attraction area. For the actual experiments, the duration was shortened to between 3 and 4 hours (Table 1), which permitted the installation and removal of traps in daylight hours on multiple sites. Each trap was collected and placed separately in a labelled plastic bag, and then transported to the laboratory where *H. trunculus* individuals could be identified, counted and their length measured (in mm). Data were reported for each trap and from each habitat. This was repeated for three series of two successive capture experiments in sea grass meadows and two series of three successive captures on the rocky substrate. The traps are not exclusive for this species (this is detailed in Vasconcelos *et al.* 2008) and during the experiments other secondary consumers caught were also identified.

Estimating α and the Effective Area of Attraction from behavioral experiments. Ten organisms collected on the traps, then depurated for 72 hours, were placed individually in experimental, flat-bottomed tanks and their movements were observed and photographed (every 30 seconds) over a period of ten minutes. For each individual, the total distance (in cm) covered and the direction followed (in radial degrees) for each time interval of 30 s were recorded. For each individual specimen, four replicates were done: twice without food and twice with food placed at the center of the container. The average speed (in m/h) was calculated from the total distance travelled by each individual during the observation period. In order to take into account both the configuration of the sampling installation and the behavior of the organisms, a correlated random-walk simulation model was formulated

(Renshaw and Hendersen, 1981). Speed was considered as constant (the average speed calculated above was used), and the direction considered as a random variable with a probability distribution depending on the bait's attraction properties.

To define the dimensions of the Effective Area of Attraction (EAA) around each wallet-trap installation, simulations were done for 100 virtual snails placed in a random position in a 4 X 4 m^2 area at the center of which is placed the trap installation, and then running 500 iterations for a maximum of three hours of movement, or until the virtual snail is trapped, as determined by the correlated random walk parameter defined above. The number of times that a virtual snail falls in one of the five traps was counted to determine the probability that one individual will be captured; this estimate was linked to the minimum distance between the initial position of the individual and the trap. This can be understood as the inverse of the protocol used to estimate α. To estimate α, 500 individuals were withdrawn randomly in the EAA and each one realized one movement for the duration of the experiment according to the rules (speed and direction) determined by the observed behavior of the organisms. α (in h^{-1}) is determined as the proportion of individuals reaching a particular trap per unit of time. This procedure was repeated 100 times to permit the calculation of the statistical distribution (mean and variance).

All calculations and simulations were done with SciLab (version 5.5.2). Codes are included as Supplementary Information (Data S1).

RESULTS

Determination of the Effective Area of Attraction and α estimates. Both the EAA value and catchability rate were measures made on members of the population being studied (Figure 1, step 3). During the behavior experiments, movements of the individuals are not oriented in one particular direction, neither with, nor without bait. The percentage of immobility was high, 63% and 52% of the time, with and without bait, respectively. Average speed estimates were done for moving individuals only (0.92 ± 0.75 SD $m.h^{-1}$ and 1.16 ± 1.10 SD $m.h^{-1}$, with and without bait, respectively). Thus, given the precision of the measurements, 1.00 $m.h^{-1}$ was used to estimate the trap depletion area with the correlated random-walk numerical simulations.

From the behavior experiment, the correlated random walk model was defined as first consisting of performing a movement or not (animal remains in the same position as from the previous step). Movement to adjacent cells is done by selecting among only 7 possible directions, and no backtracking movements were allowed. No specific attraction for traps was simulated since no specific orientation was detected by the behavior experiment. The direction followed was chosen from a Gaussian distribution centered on the last direction followed. This implies that individuals avoid making frequent sharp changes in direction in their tracks:

a behavior which was not observed during the experiments. Speed was fixed as a constant, with the exception that organisms were allowed to stop moving along their individual tracks. Under these conditions, the maximum significant average radius of attraction around each trap is 60 cm (Figure 3, inset). This value is then used to determine the Effective Area of Attraction (EAA), which defines the total surface sampled by each set of five traps. The EAA was estimated as 5.47 m². The average value of α (the catchability rate, or the rate at which we expect to catch a snail on one of the five traps) was calculated as 0.043 h^{-1} (Figure 3) with a standard error (as an estimate of the uncertainty) of 0.005 h^{-1}. The statistical distribution appeared to be Gaussian (Chi-sq test with a significance level of 0.05), permitting a confidence interval of 0.010 h^{-1} to be calculated around the average.

Capture experiments. Results for all of the successive capture experiments from the field site are given in Table 1. The average numbers of individuals captured were 8 in seagrass (SG), and 17 on the rocky (RK) substrates, and for an average immersion time of 3.4 hours. Captures for three of the five experiments (SG-B; RK-A, RK-B) do not show any decreasing trend. And, as expected, there is no difference between the rocky substrate and seagrass meadow after only two consecutive capture experiments. The variability appears slightly higher on the rocky substrate than the seagrass meadow, and had a smaller number of replications due to high wind conditions during the field experiment. There is also no difference for the relative position of the individual traps, neither for the center nor for a specific axis (26 individuals on the North-South axis and 26 individuals on the East-West axis).

The traps were not selective for size. Individuals with a wide range of sizes were trapped (distribution not shown). For example, very small individuals (0.7 to 0.8 cm) were found within the traps, while larger ones fed on the bait from the outside. The largest individual snail caught was 5.2 cm long during these experiments. In addition, this type of trap is not exclusive for *H. trunculus*. Several other species were attracted to or captured by the traps: fish (including *Thalassoma pavo*, *Scorpaena* sp., *Muraena helena*) were visually identified in the area when recovering the traps, and other gastropods (including *Nassarius unifasciatus*), crustaceans (hermit crabs, crabs (including *Xantho poressa*)), brittle stars and polychaetes (*Hermodice carunculata*) were found in or on the traps after recovery. By-catch was not quantified in this study.

Density estimates and expected time of extinction for successive captures. Results of the density estimates and the frequency distributions of calculated abundances are presented in Table 2 and Figure 5, respectively. Estimated abundances fluctuated from 21 ± 8 (SE) and 46 ± 12 (SE) individuals in the seagrass meadows, and 19 ± 6 (SE) and 74 ± 12 (SE) individuals on the rocky substrate, yielding overall average densities of between 6 (SG) and 8 (RK) individuals per square meter. Both empirical and theoretical probability distributions are remarkably consistent for all experimental conditions (Figure 4).

An expected time of extinction for successive captures was calculated from the density estimates using the stochastic model. The depletion estimated by the model should be complete in all cases between 80 (for the lowest abundance estimate) and 113 hours (for the higher abundance estimate), with a near constant standard error estimate of about 30 hours (Table 2). Because the process is identical for each of the five cases, there is a trivial increase of the extinction time with respect to the abundance estimates.

DISCUSSION

Passive, baited traps are common fishing gears in benthic coastal invertebrate fisheries. The approach presented here was selected because the population density of these relatively slow-moving animals was hypothesized to be low, and therefore the mixing of marked individuals with non-marked individuals in a population would require a long time. Techniques using baiting experiments are also very different from other approaches which describe depletions but are based on bottom trawling and dredging data where the population decreases as the scraped surface increases (Hennen *et al.*, 2012). Quantitative descriptions of how baited traps methods work have focused on characterizations of the CPUE index for targeted species and estimates of areas of attraction (Eggers *et al.*, 1982; Gros and Santarelli, 1986). But establishing a relationship between absolute population abundances and other variables measured in fisheries research (*i.e.* catch numbers/biomass, gear/species selectivity, the "catchability" of a particular species and estimates of effort) remains problematic (Eggers *et al.*, 1982; Kideys, 1993; Harley *et al.*, 2001; Petrere Jr. *et al.*, 2010).

Serchuk (1978) states that with a depletion method the size of the initial population can be estimated by the relationahips either between catch per unit effort and cumulative effort or between catch per unit of effort and a cumulative catch model. Cumulative catch estimates have been employed for large-scale methods like repeated dredging or trawling of sites (*e.g.* Hennen *et al.*, 2012) and smaller scale successive capture techniques, like baited traps or hooks (Eggers *et al.*, 1982; Valentinsson *et al.*, 1999) described here. In all cases, the primary assumptions are that the population is closed and all losses are accounted for. Thus, to estimate a population size, successive catches should be done in the same area until the catch begins to decline for the targeted species (Leslie and Davis, 1939). This necessity can create absurd situations like that described in (Valentinsson *et al.*, 1999) where repeated trapping reduces a population to the point where population recovery is not observed in site revisits.

Depletion methods are based on the fact that catches per unit of effort decreases when cumulative catch or cumulative effort increases (Serchuk, 1978; Rago *et al.*, 2006; Hennen *et al.*, 2012). This is not the case when populations are small, and in our application to *Hexaplex trunculus* population, we did not expect to observe a deterministic decline in catch (Table 1) because the process described is stochastic as a consequence of the low population densities.

This problem inspired us to estimate Murex population density as an asymptotic abundance (N_∞) within a calculated "area of attraction" using the rebuilt distribution of a stochastic model (Equation [4]). Our theoretical development expands on earlier ideas about depletion methods and benthic population estimates (Eggers *et al.*, 1982; Gros and Santarelli, 1986; Valentinsson *et al.*, 1999; Hennen *et al.*, 2012). We have not included patchiness in our model like Hennen *et al.* (2012), instead we assume that the only anomaly in an otherwise homogeneous environment is that created by the bait in the traps. Catchability (α) is expressed as a normalized rate (in units of time^{-1}), hence is a constant and therefore differs from the catchability given in both Rago et al. (2006) and Hennen *et al.* (2012). Both these studies rely on making a link between fishing performance and properties of the particular targeted population. Our α (which is scaled to the population, since it is a "number of individuals caught per catchable individuals per time") serves to convert the catches into population density.

The stochastic nature of the process is interpreted as the individual variability been much higher than variations at the scale of the population. Observations in the literature, such as Vasconcelos *et al.* (2008: 296) remark about the, "frequent occurrence of very dissimilar fishing yields between adjacent lines" in their experiments, support this inference. Moreover, it suggests that ancillary information is needed to fully describe the interaction(s) between the organisms and the traps, but this is, however, a weak point in the study since there was little experimental information available on the targeted species, as discussed below.

Distributions. "Fishermen", Eggers *et al.* (1982: 451) wrote, "target the placement of gear in areas that traditionally yield the highest catches", thus estimates of abundance would be biased relying only CPUE data. Our target species, *H. trunculus* has been described as a ubiquitous species present on soft (Poppe and Goto, 1991; Vasconcelos *et al.*, 2008), hard substrates (Rilov *et al.*, 2004) and mixed substrates (Peharda and Morton, 2006) with a macroscale homogeneous distribution (unpublished Ph.D thesis by Wurzian (1982), cited in Sawyer *et al.*, 2009).

The estimates reported in Table 2 are, to the best of our knowledge, the first modern population density estimates for *H. trunculus* on Crete Island (average for both substrates was 6.7 ind/m^2 $\pm$ 1.7) and these values compare favorably with other published data (5 ind/m^2 on a sand bottom, < 10m depth) reported for *B. brandaris* and *H. trunculus*, by Mutlu and Ergev (2008); about 6 ind/m^2 as estimated from the data in Vasconcelos *et al.* (2008) whose trap design we used. The wide range in CPUE values reported in Vasconcelos *et al.* (2008) where traps were set monthly over a year-long study, suggests that seasonal variations are large, in addition to a heterogeneous distribution. It seems reasonable to assume their distribution is strongly structured by food resources: within an oyster bed, densities as high as 120 ind/m^2 have been reported (values cited in Peharda and Morton (2006), and in Sawyer *et al.*, (2009) from Zavodnik and Simunović, 1997).

Activity patterns. In contrast with earlier studies, periods of inactivity are allowed, which accounts for our relatively small EAA value (*Buccin* "pots" studies cite 372 m^2 from Gros and Santarelli (1986). Anecdotal observations are given in the literature about resting times and seasonal variations in mobility for gastropods, like: *B. undatum* and *Busycon carica* "may spend a large proportion of its time quiescent" (Kideys, 1993: 44) ; *Nucella lapillus* which moved less than 20 cm during a 12-hour foraging period (Hughes and Drewett, 1985); and *H. trunculus* individuals on mussel beds were immobile for 7.3 hours (out of 22.9 h), on average (Sawyer *et al.*, 2009).

A simple correlated random walk model was used to simulate the crawl path of the individual snails, which implies that the attractiveness of the bait was low. Behavior was studied for individuals isolated from each other, however, a report of group foraging for this species (Peharda and Morton, 2006) suggests some kind of communication exists, and this would subvert our assumption of randomness. When the laboratory experiments were done a small amount of sand covered the bottom to permit the passage of the snail. At the end of each experiment, the sand was mixed and partially replaced to minimize any potential effect from a mucus trail, and this could have created a confused signal for the next animal. In addition, new technologies, such as accelerometers and bio-sensor tags, will offer better descriptions of the range of gastropod activities with individual-level observations (Lyons *et al.*, 2012; Brownscombe *et al.*, 2015; Mooney *et al.*, 2015).

Trade-offs between feeding preferences, bait selection and immersion time. This species' feeding has been described as "highly" facultative (Sawyer *et al.*, 2009) and both its predatory and scavenging behaviors have been exploited in traditional fisheries for harvesting this species. Its diet includes: sponges, tube worms, a variety of bivalves, limpets, barnacles, tunicates, other gastropods, fish carrion and even conspecifics (Spight *et al.*, 1974; Rilov *et al.*, 2004; Peharda and Morton, 2006; Book IX, Pliny the Elder, 1601; Sawyer *et al.*, 2009). Several reports mention live bivalves being used by fishermen to collect *H. trunculus* (Pliny the Elder, 1601; Morton *et al.*, 2007; Vasconcelos *et al.*, 2008).

We used a generic raw bait, but their predatory behavior could be exploited with live bait instead. Vasconcelos *et al.* (2008) used live bait also, but had a longer trapping time (24 to 36 hours) because live bait means the prey is less accessible. Muricids attack live bivalve prey by drilling or chipping the shell, a process which may last from 12 hours to up to 7 days (Peharda and Morton, 2006; Sawyer *et al.*, 2009). While longer immersion times may increase the number of individuals caught, there is also an increased risk for predation. Known predators of muricids were observed in the vicinity of the traps (moray eels, fish (e.g. *Sparus aurata*)) during the experiments; Vasconcelos *et al.*, (2008) listed 39 other taxa besides the banded-dye murex (*H. trunculus*) and the purple-dye murex (*B. brandaris*) on their traps in a Portuguese lagoon. In our case, a preliminary trapping experiment (conducted overnight in a small port

where *H. trunculus* could be observed on the walls) led to catching three small individuals and all the bait disappearing, or no visible bait consumption and zero catch.

Finally, the time spent feeding and feeding frequency for *H. trunculus* are unknown. Laboratory observations indicate individuals can survive starvation periods of up to 6 months (Sawyer *et al.*, 2009). This is consistent with descriptions in ancient sources that "purples" (assumed to be *H. trunculus* and *B. brandaris*) may be held for many weeks before pigment is extracted (Book IX, Ch. 36, Pliny the Elder, 1601).

Use of method for determining baselines and distribution patterns. Depletion experiments for estimating population sizes of benthic invertebrates with low densities appear more practical and reliable than direct observation and point sampling (Rago *et al.*, 2006). Earlier surveys of the macrobenthos on Crete, did not indicate the presence of *H. trunculus*, or other muricid species (Karakassis and Eleitheriou, 1997, Tselepides *et al.*, 2000). Both studies sampled much deeper areas (40 m to 1570 m depth, extending downslope toward the Cretan Basin), using transects, box corers and grab samples. These methods were not designed to sample low density populations, so an absence of muricids is not surprising. In the subtidal zone where data are often insufficient for evaluating anthropogenic pressures on these populations, and there is often a mix of hard and soft substrates, this method is well-suited to a systematic sampling effort or monitoring program of small or larger areas. The wallet-line traps are extremely easy to construct and use, which are significant practical advantages in coastal areas where artisanal invertebrate fisheries operate. Once the initial installation of anchor points was completed, it only took about 20 minutes to install and arrange, or collect, the traps on the different substrates for each sampling.

This method could be used to study what the impact of earlier activities on coastal populations and test scenarios of fishing practices. For example, is aquaculture necessary to sustain the development of an industry based on this species? Gastropod fisheries may be developed in the near future around the Mediterranean basin and elsewhere (Morton *et al.*, 2007; Elhasni *et al.*, 2013; Cheour *et al.*, 2014; Appendix S1), and, as noted in the introduction, they have existed for many millennia already. Moreover, the depletion method modeled here strongly resembles ancient harvesting techniques (Ruscillo, 2005) for *H. trunculus* (and other species like *B. brandaris* and *Stramonita haemastoma*). Since for each baited trap, we replace "effort" with an estimate of the species "catchability" rate and our catchability was estimated using the speed and behavioral response toward the bait source it is consistent with a metapopulation approach that seeks to establish reference points, not with respect to a particular fishing technique, but with respect to a particular population in an environment. This enables impact scenarios to be explored for much earlier time periods, by combining archeological evidence with our method. For example, the potential impact of the industrial-scale harvesting and transport of muricids for purple dye production organized throughout

the Mediterranean some 4000 years ago (Stieglitz, 1994; Watrous, 1998; Burke, 1999; Ruscillo, 2005) can now be explored.

CONCLUSIONS

Our results are promising, and the general statistical method to reconstruct estimates of population density is proposed as a tool for studying low density marine scavenger or predator populations, relevant for estimating natural (*i.e.* uncultivated) populations targeted by artisanal invertebrate fisheries. Many challenges remain. Focusing the problem on the catchability of a population relative to the methods employed should provide a relevant reference condition. In other words, the abundance or population density observed should be independent of the method used, otherwise this may lead to aberrant conclusions about the population. The comparison between the theoretical and empirical distributions (Figure 4) provides an important link between the fishing technique and the population size estimate necessary for building testable scenarios about ancient practices of harvesting.

The depletion-type experiment is an ecologically relevant version of a description of a commercial harvesting tool, reconciling fundamental ecology with conservation. Ecosystem-based management has for objective to enable informed conservation and management decisions and reduce reliance on presumptions and ballpark figures (Caddy and Mahon, 1995). In another invertebrate coastal fishery, a study using catch-and-release established that the population abundance variability was tied to environmental factors, such as loss of habitat, and not fishing pressure (Diele *et al.*, 2005). This was attributed to the traditional practices still in use and emphasizes the importance of developing a full, quantitative description of existing harvest methods to understand how both past and future management policies impact exploited populations.

Data are needed about marine biological diversity, whether or not species are exploited (Caddy and Mahon, 1995; Lester *et al.*, 2009; Halpern *et al.*, 2010), but the methods used must be adapted to the problem. To understand the impact of past conditions on a particular population in any ecosystem, requires being able to reconstruct past results with modern approaches. But, we caution that even with a long history of commercial interest and their use in biological monitoring, fundamental behavioral parameters about many 'common', targeted gastropod species necessary for statistical and modeling approaches are lacking and cannot be fulfilled with present resources.

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TABLES

Table 1.

Records of *H. trunculus* individuals trapped in each of the successive capture experiments series, for the seagrass meadow (SG) and rocky substrate (RK). Replicate placements within a substrate are designated as A, B, ... and replicate samplings of the same placement are numbered (*e.g.* "A1", "A2"). The relative position of each trap is indicated as C, center, S, south, W, west, N, north, and E, east (Figure 2). Each row contains data from one installation of 5 traps at one particular placement. Total number of individuals captured per experiment, and for each sampling device are in the last column and the total number captured per trap (in a specific configuration) is in the last row.

Table 2.

Abundance estimates for *H. trunculus* for the 5 cumulative capture experiments on two different shallow substrates. SG = "seagrass" and RK = "rocky". Abundances and their standard errors in the Effective Area of Attraction (5.47 m²) were calculated from the simulated probability distribution Equation [4]. Densities were calculated from the surface of the Effective Area of Attraction; the time of extinction and their standard deviation were calculated with Equations [6a, 6b]. The frequency distributions for the "Abundance" estimated by the model are plotted in Figure 4 for comparison.

Table 1.

Records of *H. trunculus* individuals trapped in each of the successive capture experiments series, for the seagrass meadow (SG) and rocky substrate (RK).

Experiment	Duration, *(hours)*	Trap 0 - C	Trap 1 - S	Trap 2 - W	Trap 3 - N	Trap 4 - E	Total (ind/experiment)
SG - A1	3.50	0	0	5	0	1	6
SG - A2	3.50	0	1	0	0	0	1
SG - B1	3.50	1	1	1	0	0	3
SG - B2	3.40	0	1	0	1	1	3
SG - C1	3.50	0	3	1	4	2	10
SG - C2	3.25	0	0	0	0	2	2
RK - A1	3.25	2	0	0	1	3	6
RK - A2	3.40	2	7	5	0	0	14
RK - A3	3.70	1	3	1	1	1	7
RK - B1	3.15	0	0	0	2	0	2
RK - B2	3.10	0	0	0	0	0	0
RK - B3	3.50	1	1	2	0	1	5

Table 2.

Abundance estimates for *H. trunculus* from the 5 cumulative capture experiments on two different shallow substrates.

Substrate	Mean Abundance, *nb ind*	*Std Err, nb ind*	Mean Density, *nb ind /m²*	*Std Err, nb ind /m²*	Mean Extinction time (T_E), *hours*	*Std Err, hours*
SG A	24.6	8.7	4.5	1.6	87.9	29.5
SG B	21.3	8.3	3.9	1.5	84.6	29.4
SG C	45.7	11.6	8.3	2.1	102	29.6
RK A	73.7	11.8	13.5	2.2	113	29.7
RK B	18.6	6.4	3.4	1.2	81.4	29.4

FIGURE LEGENDS

Figure 1. The study design.

The objective was to fuse theoretical and experimental information. Our treatment of the problem takes the unknown population size of *H. trunculus* as an object of inquiry that is represented with a population sampling concept for the study. Outcomes calculated analytically (1) can then be compared with those simulated from the experimental observations (2). To achieve this, two mathematical representations of the concept [Eq. 4; Eqs. 6a,b] are parameterized with data from experiments (3), and the stochastic model is further constrained with the results of the successive capture experiments (4). $\hat{N}_\infty$ is the true population abundance and $\hat{S}_{\bar{N}_\infty}$ is the empirically derived population abundance. Mathematical symbols are defined fully in the text.

Figure 2. Depletion experiments and study site.

(a) Arrangement of wallet-traps used on seagrass meadow and rocky substrate sites. Five artisanal wallet-type traps (Vasconcelos *et al.*, 2008, 15 cm square), baited with squid and sardines were used. One at the center (0) and four at each of the cardinal points (clockwise) at a distance of 1 m from the center trap. The image is not drawn to scale. (b) Traps were set on the north coast of Crete, near the Heraklion Centre for Marine Research (HCMR, 35°20'05.5"N 25°16'50.1"E). On the northern coast, the shallow (<50 m depth) shelf extends up to 2 km offshore. Important centers of purple dye production known from archeological evidence on the island are also indicated.

Figure 3. Parameterization and statistical distribution of alpha.

The statistical distribution of alpha estimates calculated from 100 random simulations from 500 randomly distributed individuals. The average was estimated as 0.043 h^{-1}, with a standard error of 0.005 h^{-1}. Inset: calculation of the Effective Area of Attraction (EAA) performed from 100 virtual snails placed in a random position around the trap installation, and then simulated 500 times for 3 hours of movement, or until the virtual snail is trapped. The probability to reach a trap is calculated as the proportion of trajectories ending up in one of the 5 traps arranged as in Figure 2. The minimum distance from any of the 5 traps is taken into account to determine the average radius around each trap. The radius of effectiveness for each trap was set to 60 cm which is where the threshold probability to be trapped descends to 5% (indicated by arrow on inset). The calculations take into account the period of immobility estimated from experiments (individuals were immobile for two consecutive minutes 52 % of the time when bait was not present, and for 63 % of the time when bait was present).

Figure 4. Comparison of empirical and theoretical distributions.

Plots show the frequency distributions of the estimated abundances per unit of effective area of attraction for the five successive capture experiments (Tables 1 and 2). The left column shows the empirical distribution calculated from the stochastic model [Eq. 4], constrained by the observed data, *i.e.* this is the frequency at which the model matches the observations. The corresponding graphs for each experiment on the right were calculated from the analytical solution [Eq. 7] of [Eqs. 6a, 6b], *a posteriori.*
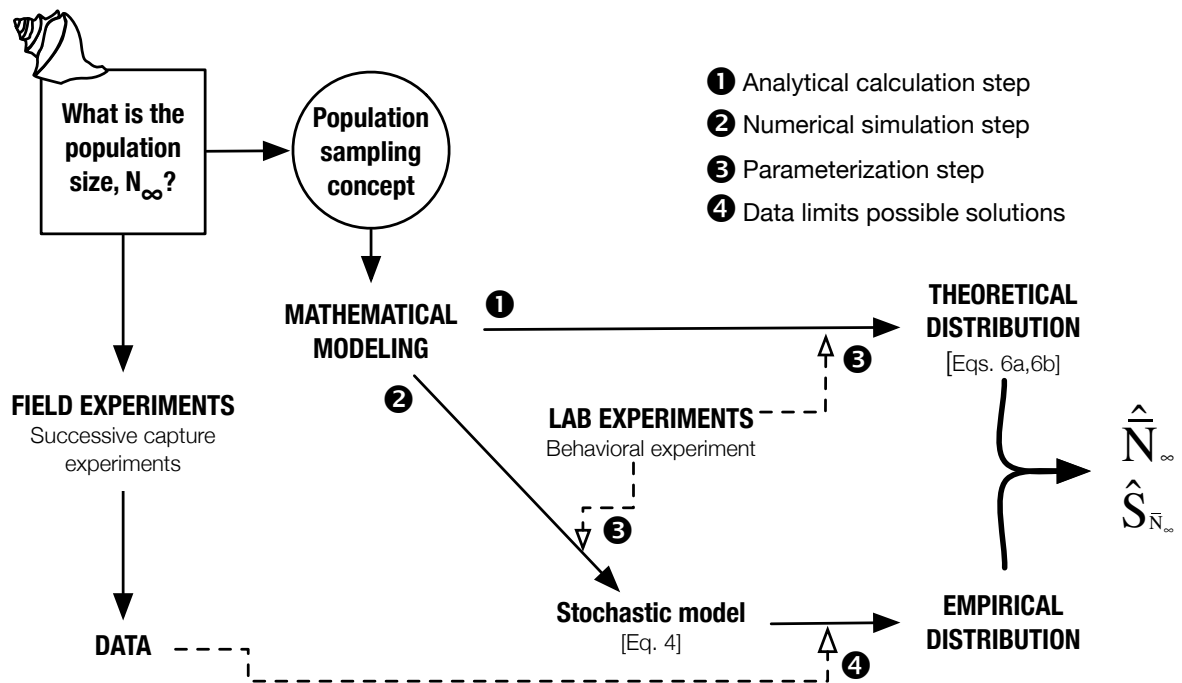
FIGURE 1.

Coston-Guarini, J. et al. "A probabilistic approach to estimate low density population abundances applicable to ancient 'Murex' fisheries"

submitted Ecology, 2016

(a)

(b)

3

2   **0**   **4**

1 m

1 m

1   0.15 m

0.15 m

N

HCMR
STUDY SITE

Knossos   Mallia   Petras

Palaikastro

CRETE

Aghia Eirene   Kouphonisi (island)

Kastri

Kommos
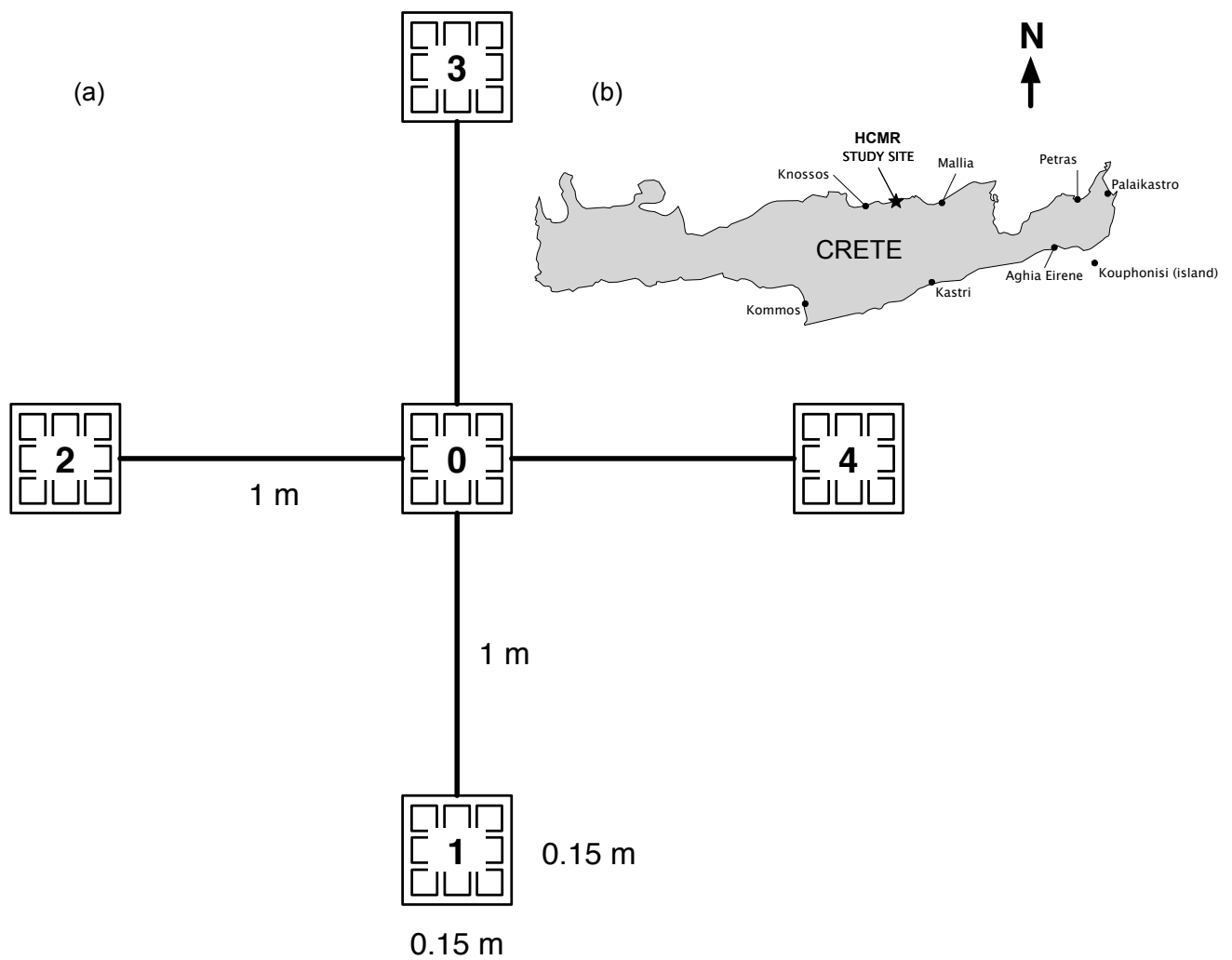
FIGURE 2.

Coston-Guarini, J. et al. "A probabilistic approach to estimate low density population abundances applicable to ancient 'Murex' fisheries"

submitted Ecology, 2016
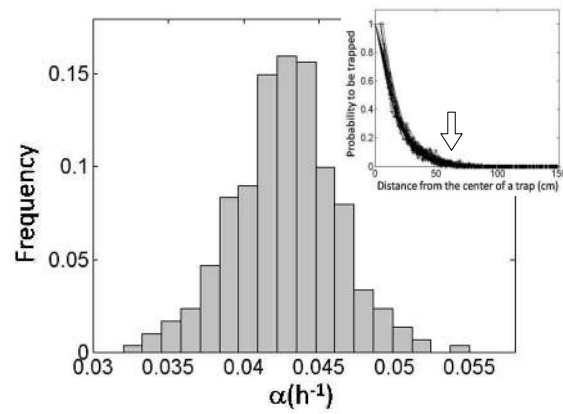
FIGURE 3.

Coston-Guarini, J. et al. "A probabilistic approach to estimate low density population abundances applicable to ancient 'Murex' fisheries"

submitted Ecology, 2016
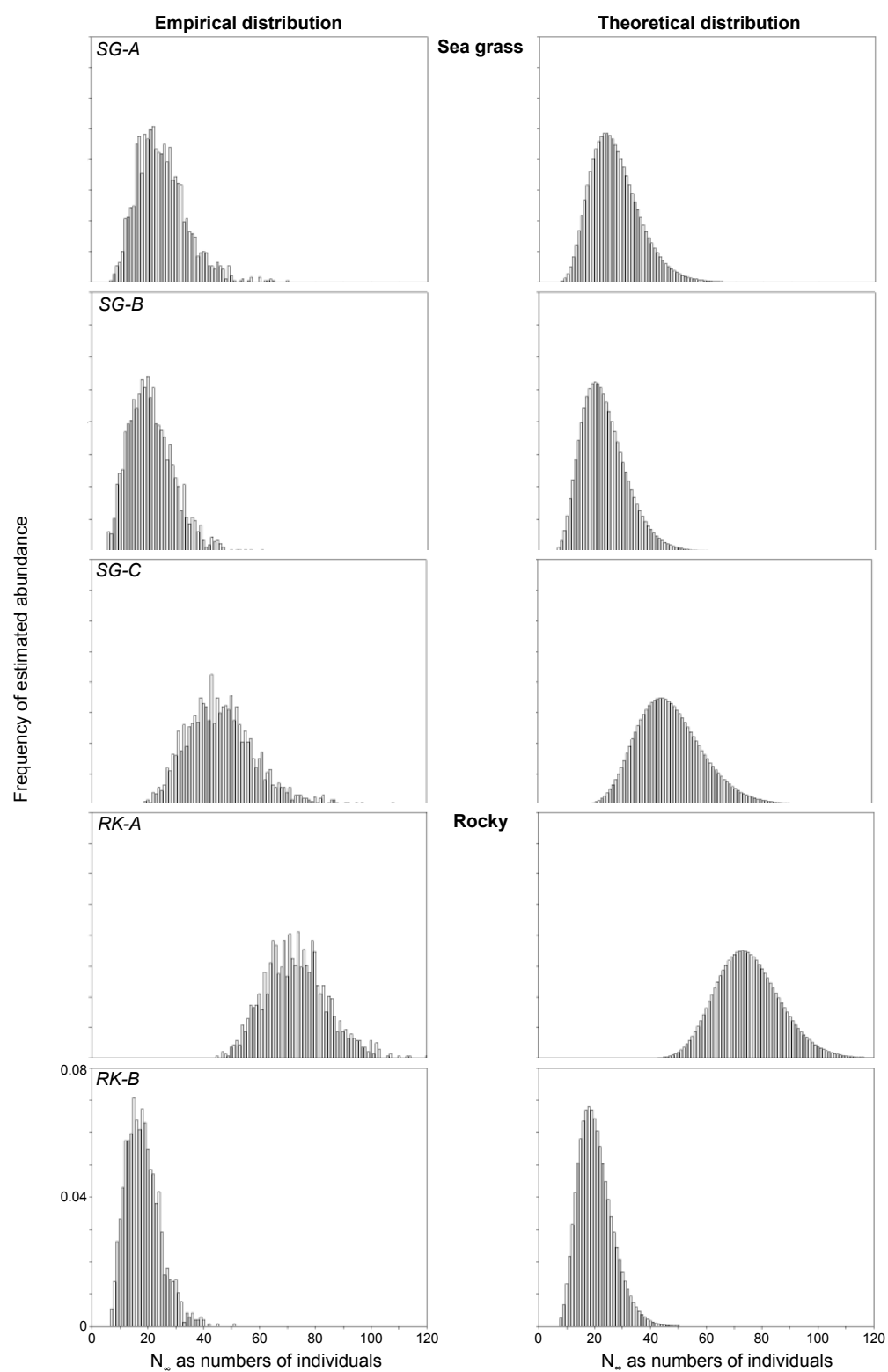
FIGURE 4.
Coston-Guarini, J. et al. "A probabilistic approach to estimate low density population abundances applicable to ancient 'Murex' fisheries"

submitted Ecology, 2016

SUPPORTING INFORMATION (*Not included here)*

APPENDIX S1

FAO data on non-abalone gastropod captures reported world-wide, 1950-2014.

Figure S1 and Table S1.

DATA S1

Codes used to make the calculations described. Codes are made to run in SciLab, version 5.5.2.

CHAPTER 6

RECURSIVE ANALYSIS TO INFER LAWS

"By studying the influence of
ecological factors on organic
systems we shall be able to
recognise the laws governing the
structure of the biosphere, this
peculiar envelope of our planet
saturated with life."

-- Gause (1932): 44

When the struggle for existence became a struggle for concepts: 80 years of Gause's Legacy

J. Coston - Guarini

J-M Guarini

L Chauvaud

ABSTRACT

Eighty years after G.F. Gause (1910-1986) published a series of experiments about competitive exclusion, this concept is still used as he defined it. Interspecific competition is seen as the appropriation of resources of one population (*i.e.* a group of individuals of one species) by another one, leading to the exclusion of one species when the interspecific competition is 'strong' (*i.e.* is greater than the intraspecific competition within each of the populations). We have re-examined Gause's work and fit three different models to his experimental data on competitive exclusion of two species of Paramecium (*P. aurelia* and *P. caudatum*). The first model is the one he used in his study, but we have re-estimated parameters with a modern optimization procedure. The second model is a hybrid population dynamic model that takes into account the resource as a third variable and which simulates as a discrete event the renewal of resources each day, according to Gause's protocol. This model was fit to Gause's data with the same optimization procedure as before. The third and final model is a hybrid, individual-based dynamic model, which represents at the organism level, food intake, consumption of energy, cell division and mortality. We found that all three models represent with similar degrees of accuracy, the observations reported by Gause. The two models that took into account resources suggested that starvation governs the dynamics more than actual competition. The individual-based dynamic model, which explicits a lack of competition and has a very limited set of parameters to describe all individuals of all species, produced interesting properties that need to be tested experimentally. We conclude from this recursive analysis that an individual-based study shows more promise for exploring the possibility of fundamental laws in ecology. Furthermore, our results suggest concepts like "competition" and "niche" have not been adequately defined and will need to be revised as new technological solutions for observing individual organisms in populations are adopted by ecologists.

INTRODUCTION

Ecology, like biology, relies on a scientific practice of testing hypotheses formulated according to common principles, rather than fundamental scientific laws (Lange, 2005). As a consequence, many ecologists have criticized the diversity of frameworks in the discipline, citing most recently the absence of prediction as a scientific goal (Houlahan *et al.* 2016). For more than a century, ecological principles have arisen under counterfactual and *ceteris paribus sic stantibus* conditions, which limits in return their applicability. An unfortunate effect of this practice is that Ecology is not able to construct a scientific argument in opposition to social, economic and political "unscientific" assumptions that circulate in public debates (Nadeau, 2008).

Lange (2002, 2005) has analyzed the absence of fundamental laws in ecology, reminding us that many theoretical ecologists have advocated for upgrading their favorite candidates to the rank of laws in past decades (*i.e.* see compilations in Lawton, 1999; Scheiner and Willig, 2008, 2011; Coston-Guarini 2016). These lists raise the thorny problem of what exactly a scientific law is and their standards of proof. Cartwright (1983) has proposed that two different kinds of scientific laws can be distinguished: fundamental laws, which are derived from theories and validated by experiments, and phenological (or phenomenological) laws, which are scientific statements established from replicable experiments. In both cases, laws can be qualitative statements, but if they account for principles that can be numerically described, then they should be expressed mathematically by canonical equations with constant parameters.

In ecology, laws, whether they are fundamental or phenological, should address a basic concept in the discipline: the conditions of (co-)existence of organisms in their environment. The principle of competitive exclusion, in the frame of the struggle for existence, has been declared a good candidate for a law in ecology (Murray 1979; Lange 2005), as well as being heavily criticized for its reliance on describing growth with the logistic curve (Mallet 2012). This principle arose out G.F. Gause's (1910-1986) studies he initiated in the 1930s after learning of the work of Vito Volterra (1860-1940), Alfred Lotka (1880-1949) and Raymond Pearl (1879-1940) on competition and population growth, respectively (Kingsland 1995). Gause, who had already completed several field studies attempting to correlate environmental conditions with observed densities of insect populations, was convinced that ecological studies would not progress without experiments in controlled conditions (McIntosh 1985). He began a sustained effort to discover an ecological law of competition between species (*i.e.* a mathematical statement of Darwin's "struggle") under the direction of V.V. Alpatov (1898-?) in Moscow. From 1932 to 1934, Gause worked meticulously to link sets of experiments using yeast and paramecia with mathematical expressions of the processes of competition he wished to study. These results were regrouped and published in a monography entitled "The Struggle for Existence" which appeared in 1934.

Eighty years later, what has been retained from this work? Evidently not the conclusions of Gause himself, who never described his results as fulfilling the requirements of a law. He expressed a more nuanced view that the predictions he had made were proof that his approach would eventually transform ecology into an exact science. He wrote in the preface: *"It became evident that the processes of competition between different species of protozoa and yeast cells are sometimes subject to perfectly definite quantitative laws. But it has also been found that these processes are extremely complicated and that their trends often do not harmonize with the predictions of the relatively simple mathematical theory"* (Gause 1934: vii). It was others, namely the ecologist, G.E. Hutchinson (1903-1991) and the evolutionary biologist, D. L. Lack (1910-1973) who several decades later promoted Gause's results and elevated his ideas to the level of a general rule, declaring it a "principle of competitive exclusion" (Kinsgsland 1995) and sometimes even calling it "Gause's Law".

The purpose of our study is to evaluate the ecological theory of competitive exclusion using a recursive approach. We postulate that to investigate the question of epistemological progress in ecology, it is necessary to critically re-examine studies on which concepts declared as fundamental are built. To achieve this, we first re-analyze Gause's competitive exclusion experiments on *Paramecium caudatum* and *Paramecium aurelia*, and his associated mathematical developments based on logistic equations. In a second step, two new and original models are introduced; the first, inspired by Herbert *et al.* (1956), is a population dynamic model linking the variations of the food source to the variations of the interacting consumer species. The second new model, motivated by the work of Jansen and Sevenster (1997), is an individual-based model that represents basic physiological processes of food assimilation, energy consumption and cell division. Our study seeks to explain why Gause's experimental work, as rigourous as it was, did not lead to establishing a fundamental law and to propose new directions for ecological research on scientific laws.

MATERIALS AND METHODS

Experimental data were taken from figures and appendices published in the 1934 edition of Gause's "The Struggle for Existence". The data shown on Figures 21 to 25 (pages 101 to 112) were recovered from digitized versions of the figures; and actual values are reported in Tables 3, 4 and 5, which are part of Appendix 1 in the monograph. Details of the experimental protocols are described by Gause in Chapter 5 of his work; these are summarized in Table 1 and in the following paragraphs.

Gause did his experiments in small microcosms. These consisted of 10 cm^3 graduated centrifugation tubes that were filled with 5 cm^3 of nutritive medium, then closed with cotton wool stoppers, and incubated in a moist thermostat at 26° C for the duration of a given growth experiment. The prey he used was a gram negative pathogenic bacterium, *Bacillus*

pyocyaneus (now synonymized with *Pseudomonas aeruginosa* (Schröter 1872) Migula 1900), cultured separately and added to the microcosms in the growth medium. Two different media used: Buffered Medium (BM, which is a pH buffered version of Osterhout's medium) with two different prey concentrations, and Osterhout's unbuffered medium (for composition, see Table VIII in Gause 1934).

Briefly the protocol for these experiments was as follows (Gause 1934, Part 2, Section 2, p. 97-98:

> 1. From pure lines of infusoria of each species, individuals were added to each tube as:
>
>> a) "Separate" conditions, that is 20 individuals of the corresponding species in every tube (n=20);
>
>> b) "Mixed" conditions, that is 20 plus 20 individuals of each species in every tube (n_{Tot}= 40).
>
> 2. Before the medium was changed (see step 3) each tube was carefully stirred, and 0.5 cm^3 of the liquid was removed to count the number of infusoria present daily. After counting the sample was destroyed.
>
> 3. Next the growth medium was changed. First each tube was centrifuged two minutes at 3500 rpm. Liquid supernatant is removed by a pipette, then freshly made nutritive medium is added back. Prey are pre-mixed into the growth medium at two different relative concentrations (see Table 1).
>
> 4. Every other day, each culture was also washed with a volume of bacteria-free Osterhout's salt solution to prevent the accumulation of waste products in liquid remaining at the bottom of the tube with the Paramecia when the medium was refreshed.
>
> 5. After pouring off the old medium, the tubes were filled with this salt solution, centrifuged and the liquid removed a second time. After this 'washing', fresh nutritive medium was added back (step 3).

For Gause, this procedure will enable him to achieve a constant level of "energy" in the microcosm: *"Such a standard and convenient technique of cultivation enables us to approach the experimental investigation of an important problem: the course of the process of competition for a source of energy kept continually at a certain level"* (Gause 1934: 97). However, this assumption overlooked the description he gives of replacing the prey each day. Thus, the "energy" or food source is actually being added by pulses and could not be considered constant as he has characterized it.

Concepts

Three different models were investigated: the orginal model developed by Gause, a hybrid population dynamic model including a discrete periodic renewal of resources, as defined by

the conditions of Gause's experiments, and a discrete individual-based model representing a periodic renewal of resources and their partitioning among the populations of organisms. For the population models (1 and 2, see below), parameters were identified by minimizing an ordinary least-squares criterion, using a Simplex algorithm (Nelder and Mead, 1965). Initial conditions are fixed (in agreement to the experimental protocol that controls the initial input of organisms and resource). The mean square error (MSE) matrix was used to estimate the accuracy of the parameter estimates and was computed by resampling the centered residuals with replacements, according to the bootstrap method applied in the context of regression (Efron and Tibshirani 1993). They are described in detail in the following pages.

1. G.F. Gause's original model. G.F. Gause based his study on the logistic model:

$$\begin{cases} \dfrac{dN}{dt} = rN\left(1 - \dfrac{N}{K}\right) \\ N(t_0) = N_0 \end{cases} \qquad [1]$$

where N is the number of individuals (of the Paramecium species), r is a growth rate (in Time^{-1}) and K is called carrying capacity (*i.e.* the maximum number of individuals that the environment can sustain). Gause points out that N can also be considered in terms of density (number of individuals per 0.5 cm^3), and in terms of concentration (L^3.[0.5 cm^{-3}]), by converting the abundance in volume from the average estimates of cells volumes. Gause estimates cells volumes by considering that their shape is an ellipsoid (values in Table 1). Gause expressed the data he collected neither in density, nor in volume, but on a volume-equivalent density, multiplying the density of *Paramecia aurelia* by the volume ratio between *Paramecia aurelia* (V_a) and *Paramecia caudatum* (V_c).

From system [1], he determined a certain number of indexes, mainly what he called the "intensity of the struggle for existence":

$$I_{SE} = \frac{rN - dN/dt}{dN/dt} = \frac{(N/K)}{(1 - N/K)} \qquad [2]$$

which is dimensionless, and diverges to infinite when N converges to K, the maximum value that the environment can sustain (then N/K converges to 1 and (1-1/K) to 0). System [1] also has an analytical solution:

$$N(t) = \frac{KN_0}{N_0\left(1 - \exp\{r(t - t_0)\}\right) + K\exp\{r(t - t_0)\}} \qquad [3]$$

From system [1], the system of equations for the competition between two populations is:

$$\begin{cases} \dfrac{dN_1}{dt} = r_1 N_1 \left(1 - \dfrac{(N_1 + \alpha N_2)}{K_1}\right) \\[3mm] \dfrac{dN_2}{dt} = r_2 N_2 \left(1 - \dfrac{(N_2 + \beta N_1)}{K_2}\right) \\[3mm] \{N_1(t_0) = N_{10}, N_2(t_0) = N_{20}\} \end{cases} \qquad [4]$$

where r_1 and r_2 are net growth rates (in Time^{-1}), K_1 and K_2 are maximum sustainable values for N_1 and N_2 respectively (abundance or volume or density or concentration, or volume-equivalent density or concentration), and β and α are interspecific competition factors (dimensionless), of species 1 on 2, and of species 2 on 1, respectively. Implicitly, the values for the intra-specific competition factors is 1, hence if β or α are greater than 1, then the interspecific competition is strong, otherwise, it's weak. The steady-state solutions are multiple in the domain of definition of N_1 and N_2, being [R*$^+$x R*$^+$].

Trivial solutions are: $\{N_1=0, N_2=0\}, \{N_1=K_1, N_2=0\}, \{N_1=0, N_2=K_2\}$. The general non trivial solution is:

$$\left\{ N_1 = \frac{\alpha K_2 - K_1}{\beta \alpha - 1}, N_2 = \frac{\beta K_1 - K_2}{\beta \alpha - 1} \right\} \qquad [5]$$

The domain of validity for the non trivial solution is $N_1 > 0$ and $N_2 > 0$. This is achieved if both numerators and denominators - and for each species - are of the same sign. In other words, if α is lower than K_1/K_2, then β must be lower than K_2/K_1, and *vice versa* (in this case, the equilibrium is stable). On the contrary, if α is greater than K_1/K_2, then β must be greater than K_2/K_1, and *vice versa* (in this case, the equilibrium is unstable). This is not in agreement with Gause's first statements (page 48) "*the mathematical considerations show that with usual α and β, there cannot simultaneously exist positive values for both $N_{1\alpha}$ and $N_{2\alpha}$*", since one set of conditions allows coexistence of two species in "competition". Gause corrected this statement in a later work (Gause and Witt 1935), however, assuming that the "condition of coexistence" can also be considered a situation of niche segregation, they stated that: "*the disturbance of the stable combination of species leads automatically to the re-establishment of stable combination, in which each of the species is driven into its niche*". The definition of the quantitative link beween the niche and the factor of competition are not consistent with the conditions of coexistence he provided. In particular, Gause points out in 1934 (page 45) that "*the coefficient α is the coefficient reducing the number of the individuals of the second species to the number of places of the first species which they occupy [...] But if the species lay claim to the very same "niche", and are more or less equivalent as concerns the utilization of the medium, then the coefficient α will approach unity*". Indeed, the condition for the coexistence (stable non trivial equilibrium) is not dependent on the absolute value of the competition factors, but depends on the ratio between K_1 and K_2.

Equation [3] is used to estimate demographic parameters (r_i and K_i, i=1,2) for both species cultivated separately. For the sake of generalization, N_{i0} was first estimated as well, but for the final optimisation N_{i0} was fixed as the initial number of individuals added by Gause. Estimated demographic parameters were then used to estimate competition factors α and β.

2. Hybrid dynamic model including resources. The experiment of Gause can be seen as continous dynamics (multiplication and death of the organisms), interrupted by discrete events of resource renewal, which is imposed by the protocol that Gause used. The continuous dynamics for one population, between two resource renewal events, are represented by the following equations:

$$
\begin{cases}
\dfrac{dN}{dt} = gN \dfrac{R}{k+R} - mN \\[2mm]
\dfrac{dR}{dt} = -\gamma N \dfrac{R}{k+R} \\[2mm]
\{N(t_0) = N_0, R(t_0) = R_0\}
\end{cases}
\qquad [6]
$$

where N is the population abundance (or volume or density or concentration, or volume-equivalent density or concentration), R is the resource (in units of R), g is the growth rate (in Time^{-1}) , m is the mortality rate (in Time^{-1}), γ is the assimilation rate (in units of R . unit of N^{-1}. Time^{-1}), and k is a half saturation coefficient (in units of R). The discrete events are triggered by the fact that at the end of each time period T (that is, every day in this case), R is reset to $R(T)=R_0$. $N(T)$ should be maintained during this step. However, the protocol of measurement (the enumeration step, step 2) imposes that a fraction of 10% of the total amount of individuals is sampled, and hence removed from the experimental populations: therefore $N(T) = 0.9N(T)$.

The steady state of the continuous model, with $\{N_0,R_0\} \in R^{*+}$x R^{*+}, without renewal of resources, is $\{N^*=0$ and $R^*=0\}$. Therefore, the moment at which the resource is renewed is always situated in a transitory phase. When all resources are consumed, the populations start to decline down to zero. The mathematical behaviour of a hybrid model can be studied by integrating analytically the system [4] between 2 discrete events of resource renewals, t and t+T. As system [4] cannot be integrated analytically, the system can be simplified by splitting the dynamics in two phases: the growing phase and decreasing phase. The growing phase is defined when dN/dt > 0, or when:

$$
R(t) > \frac{mk}{(g-m)}
$$

In this phase, as long as k is small (individuals have a strong affinity for the resource), the system [4] simplifies as:

$$\begin{cases} \dfrac{dN}{dt} = gN - mN \\[2mm] \dfrac{dR}{dt} = -\gamma N \\[2mm] \{N(t_0) = N_0, R(t_0) = R_0\} \end{cases}$$ [7]

and has the following analytical solution:

$$\begin{cases} N(t + T_R) = N(t)\exp\{(g-m)T_R\} \\[2mm] R(t + T_R) = R(t) + \dfrac{\gamma N(t)}{(g-m)}\left(1 - \exp\{(g-m)T_R\}\right) \\[2mm] \left\{N(t_0) = N_0, R(t) = R_0, T_R = \dfrac{1}{(g-m)}\ln\left(\dfrac{\gamma N(t) - mk + R_0(g-m)}{\rho N(t)}\right)\right\} \end{cases}$$ [8]

which exists as long as $g \neq m$ and $N(t) \neq 0$ (in its domain of definition R^+). Therefore, stating that T_E, the time at which Paramecium individuals are "exposed" to the resource, is equal to $\min\{T_R, T\}$, and the population dynamics are represented by the following geometric progression:

$$N(t + T) = N(t)\exp\{gT_E - mT + \ln(a)\}, \text{ with } N(t_0) = N_0$$ [9]

with a (dimensionless) being the fraction of cells remaining after having collected the volume used for counting (here, a = 0.9). $N(t)$ converges to the asymptotic value:

$$N^* = \frac{mk - R_0(g-m)}{\rho\left(1 - \exp\left\{\dfrac{(g-m)}{g}(mT - \ln(a))\right\}\right)}$$ [10]

which is strictly positive as long as $g > m$ (since mk is a negligible term).

Again, from system [4], the system of equations for the competition is:

$$\begin{cases} \dfrac{dN_1}{dt} = g_1 N_1 \dfrac{R}{k_1 + R} - m_1 N_1 \\[3mm] \dfrac{dN_2}{dt} = g_2 N_2 \dfrac{R}{k_2 + R} - m_2 N_2 \\[3mm] \dfrac{dR}{dt} = -\gamma_1 N_1 \dfrac{R}{k_1 + R} - \gamma_2 N_2 \dfrac{R}{k_2 + R} \\[2mm] \{N_1(t_0) = N_{10}, N_2(t_0) = N_{20}, R(t_0) = R_0\} \end{cases}$$ [11]

where N_1 and N_2 are abundances (or volumes or densities or concentrations, or volume-equivalent densities or concentrations). R is the resource (in units of R_1). g_1 and g_2 are growth rates (in Time^{-1}), m_1 and m_2 are mortality rates (in Time^{-1}), γ_1 and γ_2 are assimilation rates (in units of R_i.units of N^{-1}.Time^{-1}), and k_1 and k_2 are half saturation coefficients (in units of R_i).

The proposed model has introduced a new state variable (the resource, R) but does not contain any parameters accounting for the "competition factors" *per se*; the "competition" is performed by the use of the resource, which links the dynamics of the two *Paramecium* populations. The number of parameters is equal to eight in this conceptualization. Morevoer, g_1 and g_2 differ respectively from γ_1 and γ_2, which encompass both a unit and efficiency conversion factors of the resource to the *Paramecium* individuals. As no information is available to quantify the resource in Gause's work (he reported only the '1-loop' and '1/2-loop' pseudo concentrations), the unit of R is expressed in percent here.

At the end of each time period T, R is reset to $R(T)=R_0$ and a fraction of 10% of each population is sampled: $N_1(T) = 0.9N_1(T)$ and $N_2(T)=0.9N_2(T)$. The study of the mathematical properties can be generalized from the study on the 1-population case. The growing phase of each population is defined by $dN_1/dt > 0$ and $dN_2/dt > 0$, or when:

$$R(t) > \frac{m_1 k_1}{(g_1 - m_1)} \text{ for population 1 and } R(t) > \frac{m_2 k_2}{(g_2 - m_2)} \text{ for population 2}$$

In these phases, as long as k_1 and k_2 are small (individuals have strong affinity for the resource), the system [5] simplifies as:

$$\begin{cases} \dfrac{dN_1}{dt} = g_1 N_1 - m_1 N_1 \\[2mm] \dfrac{dN_2}{dt} = g_2 N_2 - m_2 N_2 \\[2mm] \dfrac{dR}{dt} = -\gamma_1 N_1 - \gamma_2 N_2 \\[2mm] \{N_1(t_0) = N_{10}, N_2(t_0) = N_{20}, R(t_0) = R_0\} \end{cases}$$

and has the following analytical solutions (for $m_1 k_1/(g_1\text{-}m_1) \geq m_2 k_2/(g_2\text{-}m_2)$):

$$\begin{cases} N_1(t+T_1) = N_1(t)\exp\{(g_1 - m_1)T_1\} \\ N_2(t+T_1) = N_2(t)\exp\{(g_2 - m_2)T_2\} \\ R(t+T_1) = R(t)+ \dfrac{\rho_1 N_1(t)}{(g_1 - m_1)}(1 - \exp\{(g_1 - m_1)T_1\}) + \dfrac{\rho_2 N_2(t)}{(g_2 - m_2)}(1 - \exp\{(g_2 - m_2)T_1\}) \\ \begin{cases} N_1(t_0) = N_{10}, N_2(t_0) = N_{20}, R(t) = R_0, \\ T_1 \to \dfrac{m_1 k_1}{(g_1 - m_1)} = -\dfrac{\rho_1 N_1(t)}{(g_1 - m_1)}(1 - \exp\{(g_1 - m_1)T_1\}) - \dfrac{\rho_2 N_2(t)}{(g_2 - m_2)}(1 - \exp\{(g_2 - m_2)T_1\}) - R_0 \end{cases} \end{cases}$$

then,

$$
\begin{cases}
N_1(T_1 + T_2) = N_1(T_1)\exp\{-m_1 T_2\} \\
N_2(T_1 + T_2) = N_2(T_1)\exp\{(g_2 - m_2)T_2\} \\
R(T_1 + T_2) = R(T_1) + \dfrac{\rho_2 N_2(t)}{(g_2 - m_2)}(1 - \exp\{(g_2 - m_2)T_2\}) \\
\begin{cases}
N(T_1) = N(t + T_1), R(T_1) = m_1 k_1 / (g_1 - m_1), \\
T_2 = \dfrac{1}{(g_2 - m_2)}\ln\left(\dfrac{m_1 k_1 (g_2 - m_2) + (\rho_2 N_2(t) - m_2 k_2)(g_1 - m_1)}{\rho_2 N_2(t)(g_1 - m_1)}\right)
\end{cases}
\end{cases}
$$

which exists as long as $g_1 \neq m_1$ and $g_2 \neq m_2$, and $N_1(t) \neq 0$ and $N_2(t) \neq 0$ (in their domain of definition $R^+ \times R^+$). Therefore, stating that T_{E1}, the time at which Paramecium individuals of species 1 are "exposed" to the resource, equal to $\min\{T_1, T\}$ and T_{E2}, the time at which Paramecium individuals of species 2 are "exposed" to the resource, equal to $\min\{T_2, T\}$, the populations dynamics are represented by the two following geometric progressions:

$$
\begin{cases}
N_1(t + T) = N_1(t)\exp\{g_1 T_{E1} - m_1 T + \ln(\alpha)\} \\
N_2(t + T) = N_2(t)\exp\{g_2(T_{E1} + T_{E2}) - m_1 T + \ln(\alpha)\}
\end{cases}, \text{ with } N_1(t_0) = N_{10} \text{ and } N_2(t_0) = N_{20}
$$

with α (dimensionless) being the fraction of cells remaining after having collected each volume used for enumeration ($\alpha = 0.9$, see Table 1).

3. Individual-Based model of food resource splitting. The individual-based (IB) model is completely discrete. Figure 1 summarizes the steps in this model. Each of the individuals is performing different activities at defined time steps. Three activities are considered in the model: feeding (*i.e.* assimilating a part of the overall resource), reproducing (asexually by simple cell division), and dying (when resources are depleted in the cell). The state of a cell i (i=1,N) is governed by its intra-cellular resource quota (θ_i). The activities are rules as described below:

a) The quota (θ_i) varies as a function of the assimilation q_a and global consumption q_c (including respiration, excretion ...):

$$
\begin{cases}
\theta_i(t + h) = \theta_i(t) + (q_a - q_c)h \\
R(t + h) = R(t) - q_a h N
\end{cases}
\tag{6a}
$$

b) When a nominal quota (θ_{nom}) is reached, the cell divides. During the division (which is considered to be instantaneous, *i.e.* happening within one time step), two cells are generated and the initial intra-cellular quota is divided in two equal quotas:

$$\begin{cases} if \;\; \theta_i(t) = \theta_{nom} \\ \Rightarrow \theta_i(t) = \theta_j(t) = \theta_i(t)/2 \\ \Rightarrow N = N + 1 \end{cases} \qquad \text{[6b]}$$

c) Cells die if the intra-cellular quota becomes lower than a minimum quota θ_{min}. The minimum quota was set to zero in order to simplify the parameterization.

$$\{ if \;\; \theta_i(t) \le \theta_{min} \Rightarrow N = N - 1 \qquad \text{[6c]}$$

In Gause's experiments, there is no spatial structure since the medium is assumed to be well mixed. In the model, the remaining resource R is split among N individuals at each time step. A probability that one cell cannot access any resource is calculated as:

$$proba\{ \theta_i(t) = \theta_i(t) - q_c h \} = \frac{q_a N h}{(q_a N h + R)} \qquad \text{[6d]}$$

In such a way, if $q_a N h$ (the food requirement of the population) is small and/or R (the food availability) is large, then the probability that one cell does not get any food is close to zero, although never null. On the contrary, if $q_a N h$ is large and/or R is small, then the probability increases and tends to 1. This probability is used as a deviate of the discrete uniform distribution of food among the population. This deviate corresponds to a Binomial distribution $\mathscr{B}(n, p)$, with n being the size of the population and p, the complementary probability of [6b].

The competition model is transposed from equations [6a, 6b, 6c, 6d]:

The quotas (θ_{i1} or θ_{t2}) vary as a function of the assimilation q_{a1} or q_{a2} (*resp.*) and global consumption q_{c1} or q_{c2} (*resp.*, including respiration, excretion, ...)	$\begin{cases} \theta_{i1}(t+h) = \theta_{i1}(t) + (q_{a1} - q_{c1})h \\ \theta_{i2}(t+h) = \theta_{i2}(t) + (q_{a2} - q_{c2})h \\ R(t+h) = R(t) - q_{a1}hN_1 - q_{a2}hN_2 \end{cases}$
When a nominal quota (θ_{nom1} or θ_{nom2}) is reached, the cell (*i* or *j*) divides: a new cell is created for species 1 or 2 (*resp.*)	$\begin{cases} if \;\; \theta_{i1}(t) = \theta_{nom1} \\ \Rightarrow \theta_{i1}(t) = \theta_{j1}(t) = \theta_{i1}(t)/2 \\ \Rightarrow N_1 = N_1 + 1 \\ if \;\; \theta_{i2}(t) = \theta_{nom2} \\ \Rightarrow \theta_{i2}(t) = \theta_{j2}(t) = \theta_{i2}(t)/2 \\ \Rightarrow N_2 = N_2 + 1 \end{cases}$
Cells die if the intra-cellular quotas (of species 1 or 2) get lower than a minimum quota θ_{min1} and θ_{min2} (*resp.*)	$\begin{cases} if \;\; \theta_{i1}(t) \le \theta_{min1} \Rightarrow N_1 = N_1 - 1 \\ if \;\; \theta_{i2}(t) \le \theta_{min2} \Rightarrow N_2 = N_2 - 1 \end{cases}$

And there is a probability that any of the cells of species 1 and 2 cannot access any resource

$$proba\{\theta_i(t) = \theta_i(t) - q_c h\} = \frac{(q_{a1}N_1 + q_{a2}N_2)h}{(q_{a1}N_1 h + q_{a2}N_2 h + R)}$$

This model does not require any specific calibration since it re-uses parameters of the model for isolated species, assuming that, at the individual level, properties remain the same.

RESULTS AND DISCUSSION

New optimization of Gause's original model. The results of the new optimization (summarized in Table 2A, "Isolated") showed that for mono-specific cultures, the *per capita* growth rates fluctuated from one culture condition to another. The lowest net growth values were found for the experiments realized with Osterhout unbuffered medium (0.78 day^{-1} for *P. aurelia* and 0.69 day^{-1} for *P. caudatum*). The highest values were found with half loop BM for *P. aurelia* (1.40 day^{-1}) and with one loop BM for *P. caudatum* (1.18 day^{-1}), suggesting that the average performances of individuals differ among culture media. Estimates of the maximum number of individuals supported by the media (that is, its carrying capacity, K) showed the opposite pattern: higher values were found for Osherhout unbuffered medium (*ca.* 200 volume equivalent individuals for both species) and lower values were found for buffered medium, half loop (ca. 100. volume equivalent individuals for *P. aurelia* and ca. 60 volume equivalent individuals for *P. caudatum*). According to Gause's description, the ratio of the carrying capacities between experiments using the one loop and half loop media should be equal to two for both species. Instead the ratios were 1.81 ± 0.21 SD for *P. aurelia*, and 2.18 ± 0.46 SD for *P. caudatum*.

Estimates of competition factors fluctuate between experiments, from ca. 0.9 to 1.5 for the competition factor of *P. caudatum* on *P. aurelia*, and from 0.75 to 1.2 for the competition factor of *P. aurelia* on *P. caudatum*. If both counts for *P. aurelia* and *P. caudatum* are standardized to their respective carrying capacity values (as in Figure 2), then, the estimated competition factor of *P. caudatum* on *P. aurelia* varies from 0.7 to 0.9, while it ranges from 1.2 to 1.5 for the competition factor of *P. aurelia* on *P. caudatum,* suggesting that *P. aurelia* is a strong competitor while *P. caudatum* is a weak one, consistent with Gause's overall conclusions.

Taking into account the resource with the hybrid population dynamic model. The model inspired by Herbert introduced two major changes, compared to the original model (Table 2B, Figure 2). The first change was to take into account explicitly the dynamics of the trophic resource, an issue suggested by Gause, but never addressed. Secondly, we wished to account for a particularity of the protocol, that is the daily interruptions to the experiments: a.) to sample part of the population for counting (10% volume removed, Table 1) and b.)

renewal of medium and food resource with it. The system remained minimal since it did not add any parameters. Besides, doing this suppressed the parameters representing factors of competition, introducing instead parameters that represented the affinity of individuals for the substrate. Therefore, the competitive interactions between the two species become indirect in this formulation, since they are only represented in the equation for the dynamics of the resource.

The definitions of 'interactions' in our formulation is conditioned by the fact that the two populations are considered to use the resources in an independent manner (terms are additive), and hence competition can only be indirect. The main difficulty was that it was not possible to know the k-values representing the affinities of paramecia for the bacterial prey. They were therefore set to low values (k=0.1) for both paramecium species. They should be estimated from independent experiments controlling the concentration of bacteria and the density of protozoa. The net growth rates estimates (g-m) varied slightly compared to Gause's model (Table 2A) but maintained exactly the same trend among the different experiments. The initial amount of resources used by the paramecium species was first imposed at 100 for the 1-loop and Osterhout media, and 50 for the half-loop medium. In a second step, it was allowed to vary freely for the optimization. It then gave different estimates for the different species, suggesting that each species 'perceives' or 'detects' the resource availability differently. This result is a common issue in modelling predator-prey experiments; the description of how a predator detects and selects its prey is far from trivial and can be many fold. Here, this can be perceived as being only an artifact of the optimization procedure. After 5 days for the 1-loop and half-loop BM (Figure 2), and after 9 days for the Osterhout unbuffered medium, the resources are completly exhausted at the end of each 24h-cycle, suggesting that paramecium individuals of both species starved during a large part of the experimental period.

Using an unrelated approach: the individual-based model. The third model developed focused on individual properties and behaviours (their intra-cellular quota and their assimilation rate, respectively) and behaviors (nutrition and division), both controlled by their size (in terms of volume, since average individual volumes were estimated by Gause). Ecological populations are composed of individuals that act as independent functioning units (Figure 1). As such, it was assumed that at each time step, individuals get their food prey in a random manner. A probability, p, that a cell consumes a prey is associated with both the availability of food and the size of the microcosm population. Resources are then distributed at each time step according to a binomial distribution function $\mathscr{B}(n, p)$; p decreases as the food get restricted and the population abundance(s) increase(s).

For the buffered Osterhout medium (1-Loop and half-Loop conditions), the only set of parameters used was {θ_{nom}=0.640, *P. aurelia:* q_a=0.110, *P. caudatum:* q_c=0.010, θ_{min}=0.00}, and for the unbuffered Osterhout medium the set of parameters was {θ_{nom}=0.360, *P. aurelia:* q_a=0.036, *P. caudatum:* q_c=0.018, θ_{min}=0.00}. Cell dimensions are given in Table 1. Despite the

fact that no optimization is possible in this type of model, the model represented well the observed dynamics in all cases and with a much smaller number of parameters (Figure 2). Resources were exhausted quickly as was already observed in the hybrid population model (results not plotted here). Importantly, there is no competition *per se* in this model, since individuals are not taking resources at the expense of each other (attribution is purely random and changes from time to time). Instead, it is the state of starvation that is responsible for the decrease in population abundances. The values of the nominal quota and the assimilation rate suggested that the use of the unbuffered Osterhout medium is more efficient than the buffered medium, for which 1-Loop and half-Loop are strictly equivalent. The consumption rate is on the contrary higher in the unbuffered Osterhout medium than in either buffered media configuration.

Problems detected in Gause's approach. Two basic criticisms can be made: first he used a phenological model (the logistic growth model designed by Verhulst in 1838) to interpret the parameters, *a posteriori*. This model can of course represent coexisting species, as well as the exclusion of one, or more of them. Secondly, Gause inversed the logic behind the theory, starting with his intent to represent exclusion (for which the conditions are explicitly contained in the mathematical properties of the model) and then trying to find a rationale behind it. His experiments with mixed cultures consistently lead (at least for the conditions he tested) to *P. aurelia* tending to reach a non null equilibrium, while *P. caudatum* decreases asymptotically down to zero (Figure 2, "Mixed Populations" column). This is the pattern he interpreted as competitive exclusion, but this is far from a generalization.

In addition, several other fundamental problems can be identified:

1. His approach is not inductive and rests on concepts that were undefined, mainly his concepts of niche and competitive interactions. The hypothetico-deductive approach is not possible because the principle is purely phenological. The concept of niche has evolved since those developed by Joseph Grinnell (Grinnell, 1917) and Charles Elton (Elton, 1927) which Gause evidently referred to and partly accounts for his use of "biovolumes" in his presentation. Particularly, Leibold (1995) has revised the concept of the niche to integrate it into the population dynamics of the species, emphasizing individual processes without focusing on equilibrium at the population level.

2. The model formulation he used does not correspond to the conditions of his experiments. The Lotka-Volterra model is a continuous model while Gause interrupted daily the experiment in order to sample the population(s) and renew the medium. In our study, these two actions were considered, at the scale of the continous dynamics, as discrete events.

3. No information was collected on the dynamic of the prey resource. Specifically, it is not possible to quantify when this resource gets exhausted, although it appears likely

that this occurred every day after the point where the number of individuals becomes relatively high. It is unknown how long individuals could have been maintained in a starved state in these experiments.

4. Interactions are occuring at the individual level, therefore, the notion of interspecific competition in terms of populations is difficult to apprehend mainly when it is represented by a "factor of competition", which is a parameter that needs identification. Gause's argumentation gets laborious when he justified by attempting to provide an ecological meaning that β_1 and β_2 are "*coefficient*[s] *of the struggle for existence*", which "*indicate the degree of influence of every individual of the first species on the number of places suitable for the life of the second species*" (page 46).

Other ecologists have also criticized Gause's work, but mostly based on objections to the use of the logistic curve formulation or the extreme simplification of the ecological system (Kingsland 1995). Among the participants in these debates was F.J. Ayala (1969) who published experimental results that was claimed invalidated the principle of competitive exclusion, as Gause's conclusions had come to be known at the time. It started on the premise that the model represents exclusion if the parameters are chosen to do so. In Ayala's experiments, *Drosophilia* species coexist on the same resources and the model simulated this situation as well. The exchange between Ayala and Gause published in Nature in 1970 shows a clear drift of the argument toward the problem of the definition of the ecological niche. Ayala pointed out mainly that the term "competition" is ambiguous because it is characterized by phenological observations, but not described by actual mechanisms. This debate suggested strongly that the results of Gause on what he called "competitive exclusion" could not be characterized as either a "law" or "principle".

Re-considering Gause's 'Law' and competitive exclusion. Past decades have seen a number of articles published expressing concern about the epistemological progress within Ecology. Various reasons have been given for what is characterized as a lack of progress, such as: ecologists do not have a recursive practice (*e.g.* Graham and Dayton 2002), imprecisely defined concepts (*e.g.* Peters 1976) and a tendency to multiply very similar theories under different names (*e.g.* Palmer 1994), the absence of a law-based framework (*e.g.* Lawton 1999), not enough theory-testing (*e.g.* Scheiner 2013), little importance given to prediction (*e.g.* Houlahan *et al.* 2016), and a tendency to "jump on bandwagons" (Paine 2002), among others. While these debates concern Ecology in general, the concepts of co-existence and competition have attracted much of this attention within the perspective of community ecology and applications in conservation and management. While we recognize the importance of contributions by both Tilman (incorporation of resource competition, 1982) and Chesson (co-existence depends on relative fitness differences, niche overlap and outcomes of trophic interactions, 2000) to the general mathematical frameworks of modern co-existence theory, our goal here is to re-examine the original concepts underlying this theory.

As we have seen in the introduction, Gause was explicitly working to establish a fundamental law for the struggle for existence. He began controlled, laboratory experiments because he had become frustrated with his inability to observe the replacement of one species by another in his earlier field studies (Gause 1934). His primary assumption is that two species cannot coexist if they compete for the same resource, and thus "*the process of competition under our conditions has always resulted in one species being entirely displaced by another, in complete agreement with the predictions of the mathematical theory*" (Gause 1934: 103). Thus, mimicking the approach of an experimental physicist or chemist, he started from principles of inter-specific competition as he understood them, converting them into models using Lotka-Volterra formulations, and then tried to verify the theory with controlled experiments. Nonetheless, as noted above, his experiments were not well-controlled with respect to the prey (resource) added.

One of the major difficulties of phenological studies is that models which are able to represent phenomena (even very simple ones) are numerous and often cannot be differentiated in comparisons with experimental data. Here, indeed, all three models represent well the experimental data (Figure 2). This type of behavior is expected when the data themselves have strong stochastic components. In the present case, the stochasticity could be assumed to be mainly demographic if the environmental conditions were controlled enough, and generated by the fact that the objects of study (ecological populations) are made up of individuals, which are themselves independently functioning units. Demographic stochasticity is crucial for populations with low abundances (which is the case in Gause's experiments) because it can lead to rapid extinctions since the extinction probabilities are usually the inverse of the population size (Renshaw, 1991). It is crucial to recall that *all* underlying mechanisms evoked happen at the individual level and not at the population one, even if it is mainly the emergent properties (like stability, extinction, resilience ...) that are studied for groups of individuals.

Before to converge toward a law-based scientific practice, ecologists have to determine at which level of organisation of living organisms the properties are generated (and not at which level they emerge) and then start to build basic, testable concepts for this particular level of observation. Instead of describing actual mechanisms based on an observation, Gause started with a phenological description of the emergent property of what he called the "competition for common food". In combination with the previous citation, it is indeed very difficult to identify precisely what mathematical theory can support the conditions of the experiments.

We have shown that three different mechanistic models based on similar principles (two groups of individuals belonging to two different species are put together in an experimental culture in which they share the same resource) provide similar results. They were chosen because they are very different not only in terms of formulation, but also in terms of structure. Importantly, for two of the models (the Herbert hybrid dynamic and individual-based models), it is difficult to debate about competition as Gause defined it. In the first instance, the dynamics of the two populations are not directly dependent on each other and the rate at

which the resource is used is formulated as the sum of the rate of assimilation by each of the populations. In the second one, distribution of available food sources is a random process (*i.e.* the distribution can be perceived as inequal, but was set to change at each time step, in such a way that no individual can control what it receives regarding the others). What was actually represented then resembles a neutral interaction rather than competition.

CONCLUSIONS

Did we progress toward the establishment of a fundamental law to consolidate the competitive exclusion 'principle'? We believe that the most important innovation came from the individual based approach. First we have revised the concept of indirect competition, with the possibility of developing a concept of inequal opportunities if requirements of the individuals cannot be fulfilled and also taking into account their rate of energy assimilation and consumption. This is very close to the concept of niche developed by Leibold (1995), in which the "Zero Net Growth Isocline" of individuals (which was originally introduced in Tilman, 1982) is a boundary below which the Net Growth is negative, and the "population" goes extinct. Secondly, we have identified a certain permanency in the parameters, since the "nominal quota for division" and the "assimilation rate" of individuals are equivalent, regarding their volume ratio. Using these principles, the dynamics of individuals - whether they are from the same or different species - remain completely identical. Finally, nothing differs from Darwin's struggle for existence, since individuals need constant food resources to survive, and this resource becomes limiting when the quantity of individuals increases. As an emergent property at the population level, we did not find, in Gause's experimental context, conditions for coexistence of the two species, but this cannot be attributed to competition as he defined it. Another study using individual based modeling of predator-prey reactions has reached a similar conclusion about the problem of defining competition (Karsai et al. 2016).

To fully understand Gause's experiments, we obviously need more information about the dynamics of resource and allocation. In addition, the experiments should be repeated to prove the mechanisms suggested here at the individual level exist, which may lead to the revision of our preliminary minimal models. We suggest that we are still quite far from being able to formulate a fundamental law that will govern the conditions of (co-)existence of individuals and species in a given environment. Thus, in conclusion, eighty years after Gause, ecologists still struggle with very basic concepts and we feel that this constitutes one of the major obstacles to the development of the disciplinary field of ecology.

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TABLES

Table 1.

Experimental parameters for Gause's experiments on competition with two species of paramecia in microcosms. These are the conditions for the experimental results shown in Figures 21 - 26 of Gause's 1934 monograph, which constitute the primary evidence for competitive exclusion.

Tables 2A, B.

Results of the parameters optimization procedure performed on the model used by G.F. Gause in his monograph (Table 2A), and for the hybrid model that we have developed for this study (Table 2B). Gause's model, for the mixed culture, the second half of the table presents estimated sets of parameters for standardized Carrying Capacity (*i.e.* the asymptotic value was set to 1). Concerning the hybrid model, the affinity parameters k_1 and k_2 were set to $k_1=k_2=0.1$, and the resource was first fixed (to 100 for the Buffered 1-Loop and Osterhout medium, and to 50 for the Buffered half-Loop medium), before being submitted to optimization. The growth rate represented only if equal to (g-m) in this model. No uncertainty of the parameters was estimated because the hybrid nature of the model does not allow use of classical optimization procedures.

Table 1. Experimental parameters for Gause's experiments on competition with two species of paramecia in microcosms.
These are the conditions for the experimental results shown in Figures 21 - 26 of Gause's 1934 monograph.

Experimental conditions	Values given in text
Volume of a microcosm, mL	5
Volume removed to count, mL	0.5
Duration of experiments, days	16 - 25
Number of times Protozoans counted per day*	1
Number of times Bacteria counted per day	0
Number of times growth medium changed per day	1
Temperature, °C	26
"a" range, *P. caudatum,* ocular μm divisions**	17.1 - 18.3
"b" range, *P. caudatum*, ocular μm divisions	5.1 - 6.2
"a" range, *P. aurelia,* ocular μm divisions	12.6 - 13.8
"b" range, *P. aurelia*, ocular μm divisions	3.8 - 4.8
Gause's Volume ratio *P. aurelia : P. caudatum*	0.39
Length range, *P. caudatum,* μm	not reported
Width range, *P. caudatum,* μm	not reported
Length range, *P. aurelia,* μm	not reported
Width range, *P. aurelia,* μm	not reported

* Gause notes he stopped making separate counts for every culture at Day 20, after which he took "average samples from the similar cultures" (p. 99).
** Gause does not give the multiplication factor for his observations.

Table 2A. Gause recursive study results. Isolated and Mixed population experiments. GAUSE model.

BM = Buffered medium, "loops" refer to the amount of prey added to the microcosms. Underlined values are not refit as per Gause's protocol.

Species	Experiment	Parameters / Estimators	b / Net growth	K / Carrying capacity	Beta / Competition factor	correlation coefficients between b & K	between Beta i & Beta j
		ISOLATED					
P. aurelia	BM 1-loop	Nominal	1.145	188	-	-	-
		Mean	1.140	189	-	-	-
		Std Error	0.038	4	-	*-0.146*	-
		(Original)	*?*	*195*	-	-	-
	BM 1/2-loop	Nominal	1.401	104	1.811	-	-
		Mean	1.396	104	1.813	-	-
		Std Error	0.044	2	0.209	*-0.267*	-
		(Original)	*1.124*	*105*	-	-	-
	Osterhout	Nominal	0.781	207	-	-	-
		Mean	0.782	207	-	-	-
		Std Error	0.016	4	-	*-0.430*	-
		(Original)	*?*	*?*	-	-	-
P. caudatum	BM 1-loop	Nominal	1.177	130	-	-	-
		Mean	1.178	131	-	-	-
		Std Error	0.055	3	-	*-0.439*	-
		(Original)	*?*	*137*	-	-	-
	BM 1/2-loop	Nominal	0.968	59	2.194	-	-
		Mean	1.004	60	2.185	-	-
		Std Error	0.115	3	0.459	*-0.456*	-
		(Original)	*0.794*	*64*	-	-	-
	Osterhout	Nominal	0.686	202	-	-	-
		Mean	0.690	201	-	-	-
		Std Error	0.023	6	-	*-0.416*	-
		(Original)			-	-	-
		MIXED					
P. aurelia	BM 1-loop	Nominal	-	-	0.829	-	-
		Mean	<u>1.140</u>	<u>189</u>	0.840	-	-
		Std Error	-	-	0.075	-	*0.7775*
		(Original)	*?*	*?*			
P. caudatum		Nominal	-	-	0.940	-	-
		Mean	<u>1.178</u>	<u>131</u>	0.952	-	-
		Std Error	-	-	0.112	-	*0.7775*
		(Original)	*?*	*?*		-	
P. aurelia	BM 1/2-loop	Nominal	-	-	0.750	-	-
		Mean	<u>1.396</u>	<u>104</u>	0.774	-	-
		Std Error	-	-	0.132	-	*0.9261*
		(Original)	*?*	*?*			
P. caudatum		Nominal	-	-	1.454	-	-
		Mean	<u>1.004</u>	<u>60</u>	1.495	-	-
		Std Error	-	-	0.378	-	*0.9261*

Species	Experiment	Estimators	b Net growth	K Carrying capacity	Beta Competition factor	correlation coefficients	
						between b & K	between Beta i & Beta j
		(Original)	-	-		-	
P. aurelia	Osterhout	Nominal	-	-	1.206	-	-
		Mean	<u>0.782</u>	<u>207</u>	1.207	-	-
		Std Error	-	-	0.078	-	*0.9493*
		(Original)					
P. caudatum		Nominal	-	-	0.924	-	-
		Mean	<u>0.690</u>	<u>201</u>	0.923	-	-
		Std Error	-	-	0.069	-	*0.9493*
		(Original)	-	-		-	-
P. aurelia	BM 1-loop	Nominal	-	-	1.5457	-	-
		Mean	<u>1.140</u>	<u>1</u>	1.5212	-	-
		Std Error	-	-	0.2886	-	*0.9179*
		(Original)					
P. caudatum		Nominal	-	-	0.7253	-	-
		Mean	<u>1.178</u>	<u>1</u>	0.7013	-	-
		Std Error	-	-	0.1381	-	*0.9179*
		(Original)	-	-		-	
P. aurelia	BM 1/2-loop	Nominal	-	-	1.1888	-	-
		Mean	<u>1.396</u>	<u>1</u>	1.2064	-	-
		Std Error	-	-	0.0994	-	*0.9133*
		(Original)					
P. caudatum		Nominal	-	-	0.7259	-	-
		Mean	<u>1.004</u>	<u>1</u>	0.7375	-	-
		Std Error	-	-	0.1503	-	*0.9133*
		(Original)	-	-		-	
P. aurelia	Osterhout	Nominal	-	-	1.2482	-	-
		Mean	<u>0.782</u>	<u>1</u>	1.2496	-	-
		Std Error	-	-	0.0756	-	*0.9299*
		(Original)					
P. caudatum		Nominal	-	-	0.9133	-	-
		Mean	<u>0.690</u>	<u>1</u>	0.9125	-	-
		Std Error	-	-	0.0641	-	*0.9299*
		(Original)	-	-		-	-

Table 2B. Gause recursive study results. HYBRID DYNAMIC (Herbert-inspired) model only.

BM = Buffered medium, "loops" refer to the amount of prey added to the microcosms. The same column headings are used as in Table 2A (except for "Resource") to emphasize the difference in model parameters compared with Table 2A.

Species	Experiment	Parameters / Estimators	b / Net growth	K / Carrying capacity	Beta / Competition factor	correlation coefficients / between b & K	between Beta i & Beta j	Resources
		RESOURCE FIXED AS SPECIFIED BY GAUSE						
P. aurelia	BM 1-loop	Nominal	1.142	-	-	-	-	100
		Mean	-	-	-	-	-	
		Std Error	-	-	-	-	-	
P. caudatum		Nominal	1.085	-	-	-	-	100
		Mean	-	-	-	-	-	
		Std Error	-	-	-	-	-	
P. aurelia	BM 1/2-loop	Nominal	1.383	-	-	-	-	50
		Mean	-	-	-	-	-	
		Std Error	-			-	-	
P. caudatum		Nominal	0.774	-	-	-	-	50
		Mean	-	-	-	-	-	
		Std Error	-	-	-	-	-	
P. aurelia	Osterhout	Nominal	0.721	-	-	-	-	100
		Mean	-	-	-	-	-	
		Std Error	-	-	-	-	-	
P. caudatum		Nominal	0.599	-	-	-	-	100
		Mean	-	-	-	-	-	
		Std Error	-	-	-	-	-	
		RESOURCE ALLOWED TO FLUCTUATE						
P. aurelia	BM 1-loop	Nominal	1.153	-	-	-	-	89
		Mean	-	-	-	-	-	
		Std Error	-	-	-	-	-	
P. caudatum		Nominal	1.087	-	-	-	-	96
		Mean	-	-	-	-	-	
		Std Error	-	-	-	-	-	
P. aurelia	BM 1/2-loop	Nominal	1.322	-	-	-	-	77
		Mean	-	-	-	-	-	
		Std Error	-			-	-	
P. caudatum		Nominal	0.807	-	-	-	-	38
		Mean	-	-	-	-	-	
		Std Error	-	-	-	-	-	
P. aurelia	Osterhout	Nominal	0.758	-	-	-	-	89
		Mean	-	-	-	-	-	
		Std Error	-	-	-	-	-	
P. caudatum		Nominal	0.585	-	-	-	-	152
		Mean	-	-	-	-	-	
		Std Error	-	-	-	-	-	

FIGURES

Figure 1.

Conception of the individual-based model used for the Gause recursive study. The model is a hybrid dynamic model which calculates the population survival over the course of the experiments, and accounting for the periodic renewal of food (energy) resource in the microcosms as Gause (1934) described. Each step is indicated in the diagram as well as where cell renewal (through division) may occur. The individual cells survive, reproduce, or die depending on the amount of energy ("q") available to them at the time step. Under the conditions of Gause's experiments as described in his work, we estimate that the microcosms were near starvation when he renewed the food resource.

Figure 2.

Comparing all three models fit to Gause's 1934 experimental results on competition. for experimental conditions see text and Table 1. The column on then left is for microcosm experiments done with separate (isolated) populations of each paramecia species, the column on the right shows the results of the growth experiments where the populations were mixed. Only the best fit of the IBM model runs are shown here. No measure of competition can be derived from this dataset.

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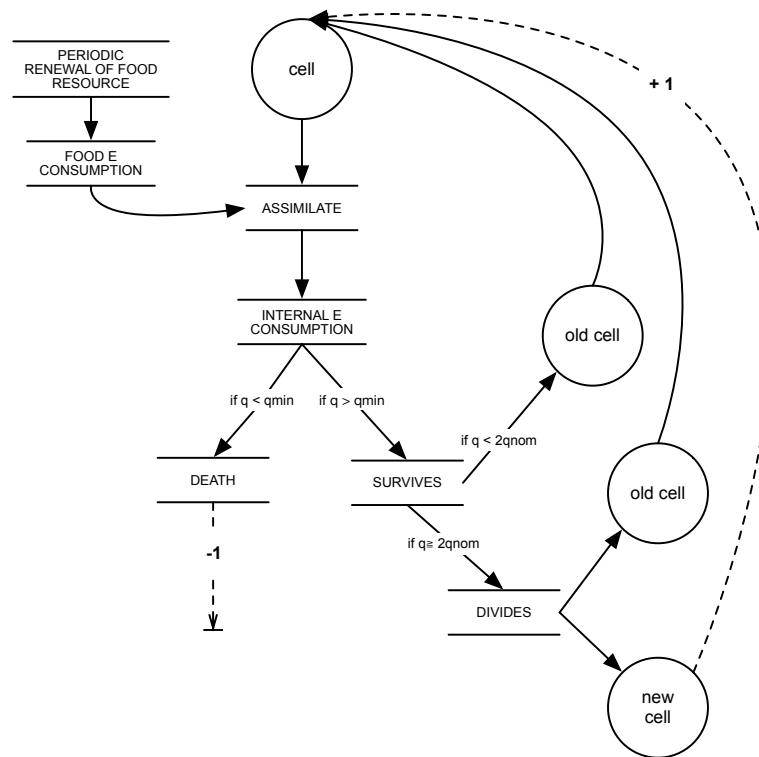
CHAPTER 7

QUANTIFYING ENVIRONMENTAL IMPACT

"We must have a system of ecological concepts which will allow of the inclusion of all forms of vegetational expression and activity. We cannot confine ourselves to the so-called " natural " entities and ignore the processes and expressions of vegetation now so abundantly provided us by the activities of man. Such a course is not scientifically sound, because scientific analysis must penetrate beneath the forms of the " natural" entities, and it is not practically useful because ecology must be applied to conditions brought about by human activity. The " natural " entities and the anthropogenic derivates alike must be analysed in terms of the most appropriate concepts we can find.""

-- Tansley (1935): 304

TITLE

A roadmap for a quantitative ecosystem-based environmental impact assessment

SUBMITTED TO:

ICES Journal of Marine Science "Special MSEAS-2016 issue"

as an ORIGINAL ARTICLE

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VERSION

1 Sept 2016

ABSTRACT

A new roadmap for quantitative methodologies of Environmental Impact Assessment (EIA) is proposed, using an ecosystem-based approach. EIA recommendations are currently based on case-by-case rankings, distant from statistical methodologies, and based on ecological ideas that lack proof of generality or predictive capacities. These qualitative approaches ignore process dynamics, scales of variations and interdependencies and are unable to address societal demands to link socio-economic and ecological processes (*e.g.* population dynamics). We propose to re-focus EIA around the systemic formulation of interactions between organisms (organized in populations and communities) and their environments but inserted within a strict statistical framework. A systemic formulation allows scenarios to be built that simulate impacts on chosen receptors. To illustrate the approach, we design a minimum ecosystem model that demonstrates non-trivial effects and complex responses to environmental changes. We suggest further that an Ecosystem-Based EIA - in which the socio-economic system is an evolving driver of the ecological one - is more promising than a socio-economic-ecological system where all variables are treated as equal. This refocuses the debate on cause-and-effect, processes, identification of essential portable variables, and a potential for quantitative comparisons between projects, which is important in cumulative effects determinations.

KEYWORDS

INTRODUCTION

When the USGS hydrologist and geomorphologist Luna Leopold (1915-2006) and his two co-authors published a system for environmental assessment in 1971 (Leopold *et al.*, 1971), they could not have foreseen that 50 years later, their report would be at the origin of a global industry (Morgan, 2012; Pope *et al.*, 2013). Leopold *et al.* produced their brief document at the request of the US Department of the Interior after the National Environmental Policy Act (NEPA) created a legal obligation for federally funded projects to assess impact. In the year following the passage into law, the scientific community was quick to point out the absence of any accepted protocol for either the content of the document or its evaluation (see characterisation in Gillette, 1971). In response, Leopold *et al.* describes a preliminary approach, with a simple decision-tree like diagram (Figure 1A) relying on structured information tables. These tables of variables and qualities, or 'interaction matrices', are intended to enforce production of uniform, comparable descriptions, while requiring only a minimum of technical knowledge from the user.

Impact inference rests on a statistical comparison of variables between impacted and non-impacted sites, but assessing an impact is understood to include value-based judgements about quality and importance (Leopold *et al.*, 1971) linked with attitudes held about the environment (Buttel and Flinn, 1976; Lawrence, 1997; Toro *et al.*, 2013). These judgements, often made *a priori* (Toro *et al.*, 2013), can conflict with the necessity to reach a legal standard of proof (Goodstein, 2011) when projects are contested. EIAs therefore embody a compromise between technical descriptions of the expected magnitude of an impact on a receptor and managerial recommendations about how to avoid that receptors exceed acceptable values, or mitigate, identified impacts (Lawrence, 1997; Cashmore *et al.*, 2010; Barker and Jones, 2013). By 1971, under pressure to move development projects forward (Gillette, 1971), the EIA process became institutionalised as a qualitative exercise focussed on collecting documentation about a project site supported by individuals' professional expertise, without requiring quantitative evaluations to back up statements (Lawrence, 1997; Cashmore *et al.*, 2010; Morgan, 2012; Toro *et al.*, 2013). Hence EIAs today still strongly resemble the preliminary instructions given by Leopold *et al.* (Figure 1B). Consequently, review articles, such as that of Barker and Jones (2013) on offshore EIAs in the UK, often report strong criticisms of the quality of environmental impact documents as being "driven by compliance rather than best practice".

Over the past decade, technologically sophisticated monitoring tools and baseline surveys have been integrated (*e.g.* Figure 1B, "Modelling"; Payraudeau and van der Werf, 2005; Nouri *et al.*, 2009) on a discretionary basis because they contribute to risk management of sensitive receptors as well as to new dynamic features like the "Life Cycle Assessment" of a project (Židonienė and Kruopienė, 2015). These changes suggest that EIA is poised to incorporate quantitative frameworks.

Inspired by the application of ecosystem-based management frameworks in fisheries (Smith *et al.*, 2007; Jacobsen *et al.*, 2016), and by the generalisation of modelling and statistical tools in ecological and environmental sciences, we describe in this article how the objective of a quantitative, ecosystem-based EIA could be achieved. We first examine briefly the awareness of impact and analytical approaches that exist to quantify this within ecological sciences. We then propose a quantitative reference framework linking statistical impact assessment to ecosystem functioning and discuss how the modelling approach may be used to provide reasonable predictions of different categories of impact. Finally, we explore how our ecological system will behave when socio-economic "drivers of change" (UNEP, 2005) are implemented. By imposing socio-economic factors as drivers (instead of as variables of a large integrated system), we show that different types of consequences can occur, which are not represented by classical feedbacks. For example, this permits the life cycle of the project to be described as a driver of the dynamic of the impacted system, or the explicit implementation of cumulative effects scenarios.

Awareness of environmental impact in the past. There is a long written record of the awareness that human activities affect the environment. Texts of 19th century naturalists commonly contain remarks about the disappearance of animals and plants attributed to human activities; some are quite detailed, like George P. Marsh's quasi-catalogue of the ways "physical geography" (natural environments) has been altered by development (Marsh, 1865). Most are ancillary comments to make rhetorical points, rather than scientific observations, like this quote from the marine zoologist Henri de Lacaze-Duthiers (1821-1901) (de Lacaze-Duthiers, 1881: 576-577):

"Ainsi, lorsque sera crée la nouvelle darse, qui n'a d'autre but que d'augmenter le mouvement du port, que deviendront les localités tranquilles où la faune était si riche ? Resteront-elles les mêmes ? l'eau ne se renouvelant pas, n'aura-t-elle pas le triste sort de celle des ports de Marseille, si le commerce et les arrivages prennent de grandes proportions ?

"Le mouvement du port augmente tous les jours. Les constructions des darses projetées ne modifieront-elles pas les conditions favorables actuelles ? On doit se demander encore si l'eau conservera son admirable pureté quand le nombre des bâtiments aura augmenté dans les proportions considérables que tout fait prévoir.

"Port-Vendres ne peut évidemment que se modifier profondément dans l'avenir, et cela tout à l'avantage du commerce, c'est-à-dire au détriment de la pureté, de la tranquillité de l'eau et du développement des animaux.

A Banyuls, il n'y a aucune crainte à avoir de ce côté."

When he wrote this, Lacaze-Duthiers had been lobbying for more than a decade for the creation of a network of marine stations in France. His text justifies why he chose a village without a port, instead of one with a thriving port. His reasoning is that economic development causes increases in buildings, docks, boat traffic, that damages the "tranquillity", "water purity", and the "favourable conditions for development of fauna". While he

acknowledges this is a gain for local commercial interests, it is also at the expense of faunal richness, and he predicts this will lead to the "sad situation of the port of Marseille". Lacaze-Duthiers feels this degradation should be a legal issue or a civil responsibility (as "*au détriment de*" indicates a legal context). The attitude and awareness of Lacaze-Duthiers are symptomatic of ambiguities about the environment (Nature) and the place of humans in it, that are also at the core of EIA (Cashmore, 2004; Wood, 2008; Morgan, 2012; Toro *et al.*, 2012). These political conflicts between a desire to preserve the natural world and its own functioning, and the desire to use, exploit, order and control parts of it are the main issues of impact assessment (Cashmore *et al.*, 2010).

Path to reconciliation. What changed in the latter half of the 20th century is that managers, regulators and stakeholders need to document and quantify impacts as well as their associated costs. However, important, historical contingencies complicated the development of quantitative tools for environmental impact. Ecosystem science, which pre-dates EIA by several decades, describes ecosystem functioning in terms of energy and mass flows (*e.g.* Odum, 1957) and the distribution of species is understood with respect to how well the 'conditions of existence' of a population are met and maintained (*e.g.* Gause, 1934; Ryabov and Blasius, 2011; Adler *et al.*, 2013). These approaches use paradigms from biology, physics and chemistry to describe functions and quantify fluxes. Consequently, ecosystem science was not concerned with characterising environmental quality, but determining when conditions of existence were met within dynamic, interacting systems. By the 1970s when EIA practice emerged, ecological research was busy with adaptation and community succession (Odum, 1969; McIntosh, 1985), while the concepts of environmental quality and impact were being defined under a "political imperative, not a scientific background" (Cashmore, 2004: 404) using static components like receptors and indices.

Today, several very different, co-existing strategies exist with regards to environmental management and conservation: ecosystem functioning (*e.g.* Moreno-Mateos *et al.*, 2012; Peterson *et al.*, 2009), ecosystem services and markets analysis (*e.g.* Beaumont *et al.*, 2008; Gómez-Baggethun *et al.*, 2010), and environmental impact. In this context, knitting together sociological and ecological frameworks has emerged as a very active area of interdisciplinary research (Binder *et al.*, 2013). An important theme has been to re-conceptualise environmental dynamics from an anthropogenic perspective to counter a perception that human activities have been excluded from ecological studies (Berkes and Folke, 1998; Tzanopoulos *et al.*, 2013). While this is clearly an unfair characterization (the classic introductory American text on ecology is entitled "Ecology: The link between the natural the social sciences"; Odum, 1975), we do recognize that, historically, ecological sciences have often ignored human behaviours and attitudes in ecosystem studies, despite numerous appeals (Odum, 1977; McIntosh, 1985; Berkes and Folke, 1998). Inspired by the criticisms of Lawrence (1997) about EIA and the challenge of working between both sociological and ecological systems (Rissman and Gillon, 2016), we propose a quantitative basis for systems-based impact assessment. Our

goal is to renew the understanding of impact in terms of the interactions and functions attributable to ecosystem processes, integrating the full dynamics of physical and biological processes, while allowing for effective evaluation of socio-economic dynamic alternatives within the modelling framework.

METHODOLOGY

Receptors. Assuming that the screening process has already demonstrated the requirement to perform an EIA for a given project, scoping identifies the receptors and the spatio-temporal scale of the study. Receptors are represented by variables being impacted by the project implementation. Receptors are determined by the experts in charge of the EIA. Their qualifications as receptors imply that they will be impacted and this cannot be questionable. In other words, what is called "testing" impact is statistically limited to a process of deciding if the observation data corresponding to samples of the receptor variables permits an impact to be detected. In no case should the selection of a receptor be made with the objective to decide *if there is* an impact or not. By definition, receptors are selected because they are sensitive to the impact. However, all declared receptor variables also represent objects of ecology and can be inserted into an ecosystem framework. These two points will now be reviewed in more detail, establishing an explicit link between them.

Statistical rationale for impact assessment detection. Impact assessment relies on statistical comparisons of receptor variables in impacted and non-impacted situations. Assuming that the expertise determined the nature of the impact (*i.e.* decreasing or increasing the variable), the impact assessment consists of testing if the absolute difference, Δ, between the non-impacted (μ_0) and the impacted variable means (μ_I) is greater than zero (H_I: $\Delta = |\mu_0 - \mu_I| > 0$). Classical testing procedure leads not to accepting H_I, but to rejecting H_0 (H_0: $\Delta = |\mu_0 - \mu_I| = 0$). However, the power of the test increases when Δ increases, which means that the more the variable is sensitive, the greater the impact has a chance to be detected.

Ideally, as EIAs start before the project implementation, samples of receptor variables are collected before and, then after the project. We focused on this case even if sampling may also be carried out concurrently for comparing non-impacted and impacted zones. For a receptor variable x, considering two samples of sizes n_0 (before implementation) and n_I (after implementation), the empirical averages are $\bar{x}_0$ and $\bar{x}_I$, respectively, and their standard deviations are s_0 and s_I. The statistics of the test is then:

$$y = \frac{|\bar{x}_0 - \bar{x}_I|}{s_0 \sqrt{n_0^{-1} + n_I^{-1}}} \qquad \text{[Eq. 1]}$$

emphasizing the importance of the sample (before implementation), which is used to estimate the 'baseline'. The dispersion around the average s_0 has a crucial role in the calculation of y (y decreases when s_0 increases). Besides the size n_0 will be fixed when the project is implemented (*i.e.* it is impossible to come back to the non-impacted situation when the project is implemented), while n_I can be determined and even modified *a posteriori*.

Under H_1 (hence when H_0 is rejected), y is normally distributed, $y \sim N(\Delta,1)$, and then it can be centred using:

$$\psi = \frac{\left| \bar{x}_0 - \bar{x}_I \right| - \Delta}{s_0 \sqrt{n_0^{-1} + n_I^{-1}}} \qquad \text{[Eq. 2]}$$

This allows us to state that ψ follows a Student law. Therefore the test leads to rejection of H_0 if ψ is greater than a threshold $t_{\upsilon,\alpha}$, where υ is the number of degrees of freedom ($\upsilon = n_0-1$) and α, the type 1 error (rejecting H_0 when H_0 is true), is $\alpha = \text{proba}\{\psi > t_{\upsilon,\alpha} \mid \Delta=0\}$). The type 2 error (failing to reject H_0 when H_0 is false) is then $\beta = \text{proba}\{\psi > t_{\upsilon,\alpha} \mid \Delta>0\}$ and the power of the text is $\pi=1-\beta$.

As ψ follows a Student law:

$$t_{\upsilon,1-\beta} = \frac{t_{\upsilon,\alpha} - \Delta}{s_0 \sqrt{n_0^{-1} + n_I^{-1}}} = -t_{\upsilon,\beta} \qquad \text{[Eq. 3]}$$

Considering that the baseline is estimated by a sampling performed before implementation, with n_0 becoming a fixed parameter, the question of detecting significantly the impact then consists of determining two unknown variables Δ and n_I by solving two functions:

$$\begin{cases} \Delta = f(n_I, \alpha, \beta) \\ n_I = g(\Delta, \alpha, \beta) \end{cases} \qquad \text{[Eq. 4]}$$

By introducing $\delta=\Delta/\mu_0$, the variation Δ relative to the baseline, and $C_0=s_0/\bar{x}_0$, the variation coefficient of the baseline sample, the system to solve is then:

$$\begin{cases} \delta = \left(t_{\upsilon,\alpha} + t_{\upsilon,\beta} \right) C_0 \sqrt{n_0^{-1} + n_I^{-1}} \\ n_I = \frac{n_0 C_0^2 \left(t_{\upsilon,\alpha} + t_{\upsilon,\beta} \right)^2}{n_0 \delta^2 - C_0^2 \left(t_{\upsilon,\alpha} + t_{\upsilon,\beta} \right)^2} \end{cases} \qquad \text{[Eq. 5]}$$

At this point in our development, we can make several remarks about how EIA practices shape the calculation of the impact:

1. The change relative to the baseline (δ) is positive if $\delta > C_0\left(t_{\upsilon,\alpha} + t_{\upsilon,\beta}\right)\big/\sqrt{n_0}$, and hence $\delta^* = C_0\left(t_{\upsilon,\alpha} + t_{\upsilon,\beta}\right)\big/\sqrt{n_0}$ is the detection limit of the receptor variable which can be calculated *a priori* (before impact). δ^* is the smallest absolute relative difference that can be characterized, and it depends only on s_0 and n_0 and the choice of Type 1 and 2 errors. Therefore, the quality of the expertise, which determines the receptors and the baseline, is a fundamental component of impact assessment.

2. The parametric framework has many constraints (*i.e.* homogeneity and stability of the variance, stability of the baseline ...), which have to be ensured, but is very useful for establishing a link with modelling. In particular, μ_0 and μ_I, hence Δ and δ, are descriptors of the states of the impacted ecosystem which can be simulated by calculation from a deterministic model.

3. *A fortiori*, the change relative to the baseline, δ, which depends on the nature of the impact and the temporal scale of the observations, can be determined *a priori* (or plausibly predicted) by the deterministic model. However it implies assuming that the variations which create the dispersion around the trend of the variable are white noises, e_t (defined by {$E(e_t) = 0$, $E(e_t^2) = s_0$, $E(e_{ti},e_{tj}) = 0$}. In this case, the design of the ecosystem becomes particularly important, not only for diagnosing the amplitude of the impact, but also the exact condition of the survey (*i.e.* calculation of n_I).

Building an ecosystem model with receptors. Our means to reconcile impact assessment with the theory of ecology is to replace the notion of receptors into a dynamic ecological model (Figure 2A). Receptors are placed in a network of interactions which represent an ecosystem. The "ecosystem" is a system in which the living components will find all conditions for their co-existence in the biotope (abiotic components and interactions that living organisms develop between themselves and with their environment). This classical definition (Tansley, 1935) encounters problems when translated into systemic frameworks. In particular, if the notion of co-existence is often linked to stable equilibrium, there is not one single definition of the notion of stability (Justus, 2008) and the precise nature of the complexity-stability relationship in ecosystems remains unsettled (Jacquet *et al.*, 2016).

Even with these caveats, the formulation is useful to explore a system-based EIA. First, stable equilibrium, for a given time scale (from the scale of the project implementation to the of the project life cycle scale) ensures that the baseline would not be subject to drift. Thus, variations will be due to the impact of the project and not by other sources. Secondly, spatial boundaries have to be determined such that the ecosystem has its own dynamics, even if it exchanges matter and energy with other systems. The stable equilibrium is then conditioned by the ecosystem states and not by external forcing factors. This last criterion ensures that the impact can be observable, and not masked by external conditions to the project. At the same time,

boundaries are defined by the actual system under investigation and not by the presumed extended area influenced by the project.

For sake of simplicity, we proposed to consider a minimum ecosystem model (Figure 2B). A minimum ecosystem has to ensure the co-existence of two populations: one population accomplishes primary production from inorganic nutrients, and a second degrades detrital matter generated by the first population to recycle nutrients. Hence, there must be four different compartments (pool of nutrients (R), population of primary producers (P), population of decomposers (D) and a pool of detrital organic matter (M)), plus the corresponding four processes linking them, namely, primary production, mortality of primary producers, degradation of detrital organic matter, and remineralization (Figure 2B). Remineralization is linked to the negative regulation of the population of decomposers. Our ecosystem is considered as contained within a well-defined geographic zone (*e.g.* it has a fixed volume), receiving and dissipating energy, but not exchanging matter with the 'exterior'. The energy source is considered unlimited and not limiting for any of the four biological processes. Finally, a generic process of distribution of matter and energy ensures homogeneity within the ecosystem. The formalism of signed digraphs (Levins, 1974) is employed in Figure 2B, emphasizing classical feedbacks as positive (the arrow) or negative (the solid dot) between compartments.

The minimum ecosystem defined as such, requires four variables: R, which represents the state of the nutrient pool, P, the state of the primary production population, M, the state of the pool of detrital organic matter, and D, the state of the decomposer population, and assumes that the units are all the same. The model is formulated by a system of four ordinary differential equations as:

$$
\begin{cases}
\dfrac{dR}{dt} = -p\,\dfrac{R}{k_R + R}P + rD \\[2mm]
\dfrac{dP}{dt} = +p\,\dfrac{R}{k_R + R}P - mP \\[2mm]
\dfrac{dM}{dt} = +mP - dMD \\[2mm]
\dfrac{dD}{dt} = +dMD - rD
\end{cases}
\qquad \text{[Eq. 6]}
$$

where p is a production rate (time^{-1}), r, a remineralization rate (time^{-1}), m, a primary producers mortality rate (time^{-1}), and d, a decomposition rate (unit of state^{-1}.time^{-1}). The constant, k_R (units of R) is a half-saturation constant of the Holling type II function (Holling, 1959) that regulates intake of nutrients by primary producers. The ecosystem is conservative in terms of matter; the sum or derivatives are equal to zero, hence R+P+M+D = I_0.

We then fix a set of initial conditions $\{R_0, P_0, M_0, D_0\} \in R^+$ which are the supposedly known conditions at time t_0. Equilibriums were calculated when time derivatives are all equal to zero [Eq. 7], and their stability properties are determined by studying the sign of the derivative around the calculated solutions:

$$E_1 : \left\{ R^* = R_0, P^* = 0, M^* = M_0, D^* = 0 \right\}$$

$$E_2 : \left\{ R^* = R_0 + M_0 + D_0, P^* = 0, M^* = 0, D^* = 0 \right\}$$

$$E_3 : \left\{ R^* = 0, P^* = 0, M^* = R_0 + P_0 + M_0, D^* = 0 \right\} \qquad \text{[Eq. 7]}$$

$$E_{4a} : \left\{ \begin{array}{l} R^* = \dfrac{km}{p-m}, P^* = \left(I_0 - \dfrac{dkm + r(m-p)}{d(p-m)} \right) \left(\dfrac{r}{r+m} \right), \\[3mm] M^* = \dfrac{r}{d}, D^* = \left(I_0 - \dfrac{dkm + r(m-p)}{d(p-m)} \right) \left(\dfrac{m}{r+m} \right) \end{array} \right\}$$

$$E_{4b} : \left\{ R^* = I - \dfrac{r}{d}, P^* = 0, M^* = \dfrac{r}{d}, D^* = 0 \right\}$$

where $R_0 > 0$, $P_0 > 0$, $M_0 \geq 0$ and $D_0 > 0$, and *a fortiori* $I_0 = R_0 + P_0 + M_0 + D_0 > 0$. All five equilibriums listed above are stable and coexisting with the unstable trivial equilibrium $\{R^* = 0, P^* = 0, M^* = 0, D^* = 0\}$. E_{4a} is reached if $p > m$ and E_{4b} is reached otherwise (assuming that the decomposers are acting fast with respect to the dynamics of the entire system). E_1, E_2 and E_3 equilibriums do not respect our definition of an ecosystem:

- E_1 is the case of no living organisms at the beginning (spontaneous generation is not allowed), and

- E_2 and E_3 are equilibriums with the initial absence of the primary producer or decomposer populations respectively, leading to the extinction of the other population (hence the condition of the co-existence of P and D is not fulfilled).

Calculating changes in receptors and modelling the influence of drivers of change. In the model presented above, many receptor variables X can be identified. They can be the state variables (mainly representing the living populations, *i.e.* P or D) or the processes (like the ecosystem functions: primary production, decomposition and nutrient recycling). For all these variables, we calculated an impact as $\delta = \Delta / X^*$, the relative variation from the baseline X^*, consecutive to a virtual project implementation. Δ is the difference between two equilibrium values X^* to X^{**}, after a change in states (such as nutrient or detrital organic matter inputs) or parameters (mostly decreases in primary production rate, increases in primary producers' mortality rate, decrease in decomposition and recycling rates) consecutive to project implementation.

For the Environmental Impact Assessment, it is only required to know the amplitude of the changes consecutive to modifications of states or parameters to predict an impact on

receptors. However, since we wish to include socio-economic aspects, we linked in a second step the change in ecosystem state and function to the possible influence of stakeholders on the project development (or the project 'Life Cycle'). The project development is controlled by groups of stakeholders, and the related "activity" depends on many factors that do not depend directly on ecosystem feedbacks (Binder *et al.*, 2013).

Treating a 'socio-economic-ecological system' using systemic principles generates outcomes with little interest due to possible socio-economic feedbacks that are not connected as reactions to a physical system (*i.e.* "A" has an action on "B", and in return, "B" modifies "A", as in Figure 2B). We thus revise the notion of feedbacks by "A" has an action on "B" until "A" *realizes that* the action on "B" can be unfavourable to its own development. This formulation partly overlaps with the notion of "vulnerability" presented in Toro *et al.*, 2012 and "risk" (Gray and Wiedemann, 1999). The socio-economic system is introduced as a driver of change for the minimum ecosystem, instead of as a state variable like in other SES frameworks (Binder *et al.*, 2013). Consequences for the impacts on receptors are described in terms of the relative "activity" A ($A \in [0\ 1]$) of the project, related to the change in states or parameters by minimal linear functions (*i.e.* if x represents any potential change rates - in parameters or states - the effective change rates, y, are expressed by $y = Ax$). The project activity is calculated as the complement of the relative socio-economic cost, C, of project development, expressed as:

$$\begin{cases} \dfrac{dC}{dt} = (\rho C + \sigma)(1 - C) \\ A = 1 - C \end{cases} \qquad \text{[Eq. 8]}$$

where σ is a relative social awareness rate (increase, in time^{-1}, of the number of stakeholders aware of the negative consequences of the project within the total number of stakeholders), and ρ is the reactivity rate (the standardized speed, in time^{-1}, at which the socio-economic cost corresponding to mitigation or remediation measures increases).

All simulations and related calculations were performed using open source software (Scilab Enterprises, 2012).

RESULTS

Examples of the impact predictions estimated by the model. Three different scenarios were set-up for specific receptors (Table 1). Examining the steady-states of the system and their stability stresses the position of the set of parameters $\theta = \{p, m, d, r, k_R\}$ and their relative importance in the definition of the system equilibrium. For building scenarios, it is assumed that the parameters' orders of magnitude are:

$$p \gg m \gg r \text{, and } r \approx d$$

Nonetheless, d is controlled by the quantity of substrate available. k is considered as small and the primary producers being assumed to have a good affinity for the available nutrients. When changes of parameters were simulated (as in Scenarios 2 and 3) they were varied in the same proportions. Inputs were simulated separately and then cumulated (CE), and their impacts on the 4 state variables at equilibrium (R^*, P^*, M^* and D^*) were examined.

The first scenario simulated direct inputs of nutrients and detrital organic matter. Results show that in all cases, R^* and M^* did not vary (despite their initial increase). On the contrary, the variables representing living compartments, P^* and D^*, increased. Results also show that the relative variation to the baseline, δ, is identical for P^* and D^* (both positive deviations, Table 1). Concerning processes at equilibrium, the primary production and the primary producer mortality both increased, as well as the processes of decomposition and recycling, since none of these parameters were affected by the project implementation.

The second scenario simulates an impact which consists of the decrease in primary producer performance. This could be due to the physiological capacities of the organisms being affected by the project or because the environmental conditions limit their expression (*e.g.* a strong increase in water column turbidity). In this situation, the parameters affected are k and m (which increased), and p (which decreased). It should be recalled that p was kept greater than m (p - m > 0), as per our parameter hierarchy. A decrease of p and an increase of k (global decrease of primary productivity) always has a negative effect on P^* (hence on primary production), a positive effect on R^*, and a negative effect on D^*. In both cases, the relative variations to the baseline, δ, are identical for P^* and D^*. An increase of m has a similar effect on P^* and R^*, but has a negative effect on D^*. The cumulative effect (p + m + k) is almost equal in magnitude to the effect of a decrease in m, which is much higher (by several orders of magnitude) than the effects of p and k. Effects of p and k are quite negligible, each having a typical order of magnitude of the parameters in θ.

The third and final scenario simulated a change in the decomposer activity. This could be triggered by a change in taxonomic composition, and also by the action of chemical substances released during the project. Decreases and increases in d and r were simulated, first separately and then together. Changes in d and r have no effect on R^*. A decrease of d as a negative effect on P^* (hence decreasing primary production) and D^*, and logically, an increase of d has a positive effect on P^* (thus the increasing primary production) as well as D^*. In both cases, the relative variations to the baseline, δ, are identical for P^* and D^*. Effects of a decrease or an increase in r on P^* and D^* are opposed. P^* increases and D^* decreases when r increases, and P^* decreases and D^* increases when r decreases. Cumulative effects reinforce slightly the effect of a change in r which is largely predominant in the dynamics of P and D. The changes of d and r affect the primary production *via* a change in the availability of R. When the

recycling is enhanced (mainly by the increase of r but also by an increase of d), R production increases but an excess of R is used to increase the state of the primary producer P. It is because the production rate p is high compared to r, that R* is not affected by changes in r or d. Changes in r and d have opposite effects on M^*. A decrease (respectively, increase) of d has a positive (respectively, negative) effect on M^*, and a single decrease (respectively, increase) of r has a negative (respectively, positive) effect on M^*. When changes are cumulated (in equal proportions), the effect of changes in r and d on M^* is null, showing that they have the same amplitude on M^*.

Behaviour of system when drivers of change were included. In the impact assessment *per se*, the effects of changes in ecosystems components (states and functions) were considered as a deviation of stable equilibrium values regardless of the time scales of the transitory phase. The consequences of introducing socio-economic drivers were considered by numerical simulations. To take into account the potential influence of socio-economic drivers, simulations were performed introducing explicitly a changing rate that depends on the relative project activity within Equation 6, affecting either states or parameters. Figure 3 shows results of simulations for just two different examples of impact taken from Table 1. The first scenario illustrated (Figure 3b, c) is for a project development that induces a change in state (a nutrient input triggering an initial increase of R, scenario 1), and the second illustration (Figure 3d, e) suggests what can occur when a project induces a change in parameters (in this case an increase in the mortality rate of primary producers and hence a decrease of their survival, scenario 2). The reactivity rate ρ was set to 0.02 (time^{-1}) and the awareness rate σ was set to 10^{-4} (time^{-1}). For both scenarios, the project activity starts at t = 200 (time), the dynamics being considered at steady state before. Figure 3a shows the activity of the project reaches instantaneously 1 at 'time' 200 when the project is implemented and then decreases smoothly as global awareness of negative impacts among stakeholders' increases [Eq. 8]. The project activity thus decreases to 0 by 'time' 800. This is a consequence of the relative socio-economic cost of the project reaching 1, which in our model, defines the limit of the exploitability of the project (*i.e.* when all possible time and resources are being invested in side issues).

In the first scenario, when R increased sharply, both P and D increased as well, but more slowly (Figure 3b). When the project activity stopped (outside the grey area, after 'time' 800), all states have reached an equilibrium, which is, for M, the equilibrium prior to the implementation of the project, but for P and D, a different higher equilibrium. In that sense, the outcome is similar to the outcome of the previous scenario 1. Figure 3c shows that the δ for P and D varies differently showing the modulation by the project activity tends to alter the final amplitude of the impacts on each of the receptors.

In the second scenario, the configurations for the relative socio-economic cost and activity of the project are identical, but the outcomes were very different from those in scenario 2. In this case, when project activity stopped, causes for changes in the mortality rates disappeared and

equilibrium states came back to the values prior to the project implementation (Figures 3 d, e). Therefore, around 'time' 400, the impact of the project on all receptors reaches a maximum, but all impacts relative to the baseline, δ, decreased and returned to zero afterward (Figure 3e).

DISCUSSION

The practice of EIA arose from a societal imperative to have documented expertise about potential impacts on the environment from development projects. This was the result of a legal framework created to defend environmental quality of communities and regions in the US (Cashmore, 2004; Morgan, 2012), and coinciding with a rise in visibility of ecological sciences (Supplementary Information, Figure A). Subsequently, similar requirements for environmental impact assessment were adopted by a majority of countries (Morgan, 2012). This has engendered repeated calls to develop a theory of impact assessment (Lawrence, 1997) as the practice dispersed. The need for an EIA process created a profession with a vital role in the safeguard of environmental quality, but that relies heavily on disputable methods and has an uneven record (*e.g.* Wood, 2008; Wärnbäck and Hilding-Rydevik, 2009; Barker and Jones, 2013). Public pressure from stakeholders may provide some measure of accountability, however, *post hoc* analyses are rare (Lawrence, 1997) and systems can differ significantly between countries (Lyhne *et al.*, 2015). Critical review may only happen in the aftermath of a dramatic accident, such as the Macondo well blow-out in 2010 (US Chemical Safety and Hazard Investigation Board, 2016) or after management failures (Rotherham *et al.*, 2011).

The value of quantification. Our study reflects on the two main scientific components of EIAs: expertise and prediction. The first is the role of the expertise. We have stressed the needs for the experts to identify receptors and to provide proper estimates of baselines. The second one is the ability of ecological theory to prediction ecosystem dynamics. We have emphasized the critical importance of the formulation of the ecosystem model to calculate correctly baselines and predict impacts. The intention of Leopold *et al.* (1971) was however far from this approach. Their approach consisted in providing a sort of template for EIA and EIS documents and to ensure a common logic for how the "magnitude and importance" of the impacts identified would be presented to federal evaluators. They did not provide any details about how exactly impacts would be assessed beyond a comparison between conditions before and after the project. We therefore replaced this generic matrix approach by a quantification of system dynamics, which allows scenarios to be designed and tested.

Receptor selection. Scenarios are selection of the possible combinations that could be examined, and which are usually specific to the type of project that would be implemented. The ecosystem model is then used as a tool to helps experts identifying specific receptors. Receptors can only be identified if their δ is different from zero (either strictly positive or strictly negative). It can be identified easily in Table 1, but this is not the only condition: to be

a receptor the δ must indeed be greater (in absolute value) than the δ^* corresponding to the limit of detection of the impact [Eq 5]; this is a statistical concept required to estimate the dispersion of the values of the receptor variables around their average. These two conditions then define what receptors are. Receptors are indeed subject to change and must be sensitive enough to be detectable with the statistical tests applied. Hence, an EIA, in contrast with a risk assessment, implies automatically a change in the receptors and aims to quantify them with a defined level of certainty and accuracy. A consequence of this is that if two receptor variables were identified as having the same dispersion, the impact will be better assessed if the averages have higher values. For example, in a marine system, the biomass of decomposers D, can be much greater than the biomass of the primary producers, P (Simon *et al.*, 1992), which means that it could be better to assess impact on D, than on P. This can be completely different for terrestrial ecosystems (Cebrian and Lartigue, 2004).

Baselines and reference conditions. In our model, the description of changes is based on the calculation of equilibrium (the baseline) and their stability, and then follows the displacement of the equilibrium values under changes in state variables, forcing variables, or parameters (Figure 3b-e). This description is a basis for clarifying our understanding of the problem. A dynamic model constrains our investigation to plausible causal relationships between the variables (receptors) and permits us to explore their contribution to the entire system. The dynamic behaviour provides a point of reference for comparisons between scenarios (as shown in Table 1 and Figure 3), or as they correspond to a specific project development. Formulating a minimum ecosystem as an example, has shown that complex behaviours can emerge with only four state variables. These results illustrate for the first time the dynamics of impact responses by receptors, revealing how complicated the evaluation of recommendations to mitigate impact may be. Furthermore, this underscores the importance of monitoring to ensure accountability over the project life cycle, including cumulative effects.

Minimum ecosystems and complexity. Models are simulation tools which aid exploration of possible outcomes and the evaluation of the simulated baseline, as well as the relevance to simulated scenarios (Tett *et al.*, 2011). Our minimum ecosystem model is essentially a representation of a perfect and autonomous bioreactor, which does not exist, nor can one be created as presented. Nutrients and detrital organic matter are 100% recyclable by one functional group of decomposers. Populations are stable indefinitely if conditions on the parameters (essentially p > m) are respected. These conditions are not realistic, but serve the development and presentation of our approach. The proposed procedures can be applied to more complex systems, encompassing large quantity of variables (or compartments) as well as non-linear processes and hybrid dynamics, like what would be expected in more realistic representations of ecosystems. However, the condition that a certain form of stability can exist in the system must be respected. It should be noted that the question of stability in ecology is part of an on-going scientific discussion recently summarized by Jacquet *et al.* (2016). This is critical to environmental impact theory because it is the presumption of

stability which ensures the baseline is maintained (does not drift) during the project life cycle (Thorne and Thomas, 2008; Pearson *et al.*, 2012). In other words, an EIA is supposed to certify that what is measured as change only corresponds to an impact from the project, not external variations. Hence, monitoring takes on a new importance. For example, monitoring a non-impacted site as a reference to detect possible ecosystem drift, may be one way to assure that this condition of baseline stability is valid. This solution is conditioned itself by the necessity to have a reference site which can be characterized by exactly the same ecosystem.

The second basic assumption of our minimum ecosystem implies that the distribution of elements is homogeneous inside the project area. This is not always (and even rarely) the case and in aquatic systems, hydrodynamics leads to partial mixing that cannot be assimilated to complete homogeneity. Therefore, accounting for the spatial distribution structure of the elements would require the model structure be modified. For example, we can use partial differential equations or any other formulation that can treat spatial covariance. When spatial covariance is proven to exist for relevant receptors, the corresponding statistics for the test of impact must account for the spatial covariance using geostatistical methods (*e.g.* Agbayani *et al.*, 2015; Wanderer and Herle, 2015).

Socio-ecological systems. The idea that all components (*i.e.* Environmental, Social, Health … impacts) can be inserted into a single system framework remains quite challenging. While a considerable number of propositions for conceptual frameworks and planning charts exist (Haberl *et al.*, 2009; Binder *et al.*, 2013; Bowd *et al.*, 2015; Ford *et al.*, 2015) offering some insights into the complex social interactions and policy constraints involved, there is little in the way of theoretical development for impact theory. We only studied here the project activity controlled by its socio-economic cost (side costs being related to remediation and mitigation measures) as a driver of ecosystem changes. We have not, for example, considered that changes in some receptors can trigger an increase in cost and a decrease in activity. In other words, we have not considered feedbacks between the receptors and cost, because it did not appear clearly how awareness of stakeholders and reactivity of managers could be directly linked to changes in receptors (Binder *et al.*, 2013; Bowd *et al.*, 2015) for which "acceptable" remediation or mitigation measures should have already been considered during the process (Figure 2B; Drayson and Thompson, 2013). Indeed, stakeholders' awareness depends on many factors, like information or education (Zobrist *et al.*, 2009), and reactivity of managers can be constraints by many other economic and political factors (Ford *et al.*, 2015). However, the minimal model that we proposed for expressing the dynamics of the drivers of change [Equation 6] can (and should) become more rich to take into account more complete descriptions of the mechanisms that modulate awareness, activity and reactivity rates within sociological networks. We suggest that our approach could be particularly useful in the scoping step as a means to explore possible scenarios outcomes.

CONCLUSIONS

This study has linked statistical tests and mathematical modelling to assess an impact and consider some of the socio-economic drivers that mitigate it. This constitutes a first step toward an ecosystem-based approach for EIA, which needs to be proven and improved. If technically, there are possibilities for EIA to rest on objective quantitative approaches, these can only be valid if the predictive capacity of the model is assured. This was, and still is, a major limitation. Furthermore, all forms of environmental impact assessment are complicated by the absence of fundamental laws in ecology (Lange, 2002) which has limited the understanding of complex objects in ecosystems. Most of the time, ecosystem models simulate dynamics with properties that are not found in realistic systems (May, 1977). We believe that to progress toward quantitative EIA it is necessary to build much closer, interdisciplinary collaborations between applied and fundamental research on ecosystems, to overcome the historical divergences. This exchange could be encouraged through concrete measures such as including funding for fundamental development within EIA as well as requiring that data collected for IA be made available in open source repositories, accessible for fundamental research.

SUPPLMENTARY MATERIAL

The following supplementary material is available at ICESJMS online:

Figure A. N-gram frequencies compared for three different corpora, US, UK, and FR.

ACKNOWLEDGEMENTS

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TABLE

Table 1. Summary of model outcomes for three scenarios. Relative changes in impact are calculated in terms of mass or energy content and compared for the scenarios described in the results.

Table 1. Model Outcomes.

Relative changes in impact calculated in terms of mass or energy content for each scenario

	Nutrients	Primary Producers	Detritic Organic Matter	Decomposers
	R^*	P^*	M^*	D^*
Scenario 1: project leads to R and/or M inputs to system				
R_{inp}[1]	0	+	0	+
M_{inp}	0	+	0	+
R_{inp} + M_{inp} (CE)	0	+	0	+
Scenario 2: project leads to decrease of primary producer performance				
p (decrease)	+	-	0	-
m (increase)[2]	+	-	0	+
k (increase)	+	-	0	-
p+m+k (CE)	+	-	0	+
Scenario 3: project leads to change in decomposers performance				
d (decrease)	0	-	+	-
r (decrease)	0	-	-	+
d+r (CE)	0	-	0	+
d (increase)	0	+	-	+
r (increase)	0	+	+	-
d+r (CE)	0	+	0	-

[1] Simulation results shown in Figure 3b,c

[2] Simulation results shown in Figure 3d,e

FIGURES

Figure 1. Environmental impact assessment, then and now.

(a) The original flow chart as it appeared in Leopold *et al.* 1971. This chart responds to a specific request by the US Department of the Interior to propose a system that would structure information in EI documents. The original figure is captioned: "Evaluating the environmental impact of an action program or proposal is a late step in a series of events which can be outlined in the following manner."

(b) Example of a flow chart used by consultants today in offshore projects. Important changes include: the addition monitoring and the possibility of using modeling. Steps external to the core EIA steps are in grey. Redrawn after Edmunds *et al.* 2016.

**Figure 2.** The minimum ecosystem model.

(a) The simplest representation of a model in ecology requires two state variables at least one parameter and a 'forcing' variable to describe the external forcing by dynamic environmental conditions such as light, temperature, tides. State variables (compartments) are written as a function of the parameters, forcing variables, or other state variables, for a given time interval. Because these vary dynamically they are written as differential equations. Forcing variables are fixed externally, and are not affected by the model calculation of the interaction represented between the two state variables (dashed line).

(b) The minimum ecosystem model used in this article is closed in matter but not energy, the energy source is unlimited (forcing variable) and the environment is well-mixed. Feedback interactions between the receptors (state variables) are shown using Levin's notation, where positive feedback is indicated by arrows and the negative feedback direction is shown by filled circles. Parameter values may be taken from the literature, experiments or field observations.

Figure 3. Impact as influenced by stakeholder awareness and project cost-effectiveness.

(a) Inverse relationship between the Project Activity and Project social cost (awareness of a negative impact among stakeholders) for the simulated scenarios. The grey shaded area is the project activity duration (between time step 200 and 800 here).

Behaviour of the four state variables (b, d) and the relative changes in impact (c, e) during scenario 1 and 2, respectively. These scenarios are also listed in Table 1. Filled triangles indicate in which direction the relative impacts are changing for each of the four compartments as the state variables evolve (b, d), and the unfilled triangles are placed at or near the end of the curves. All curves start at "0" in these simulations.
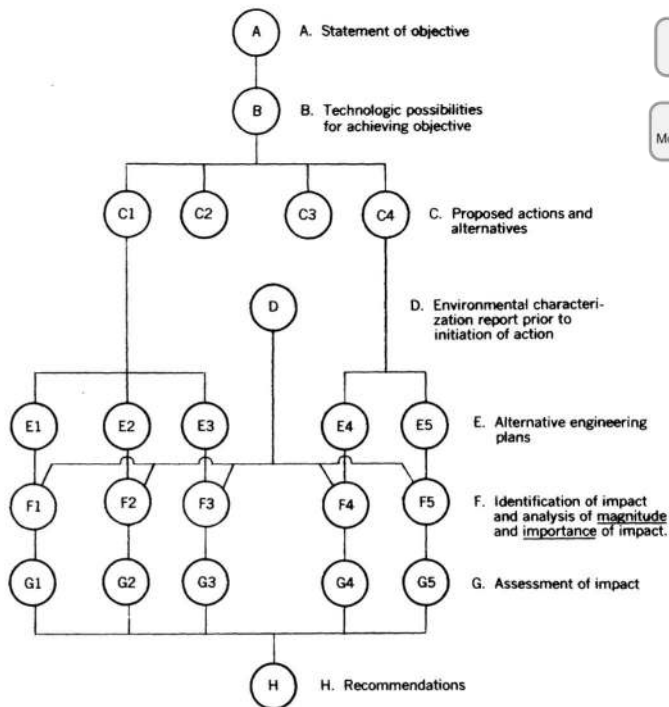
(a) 1971
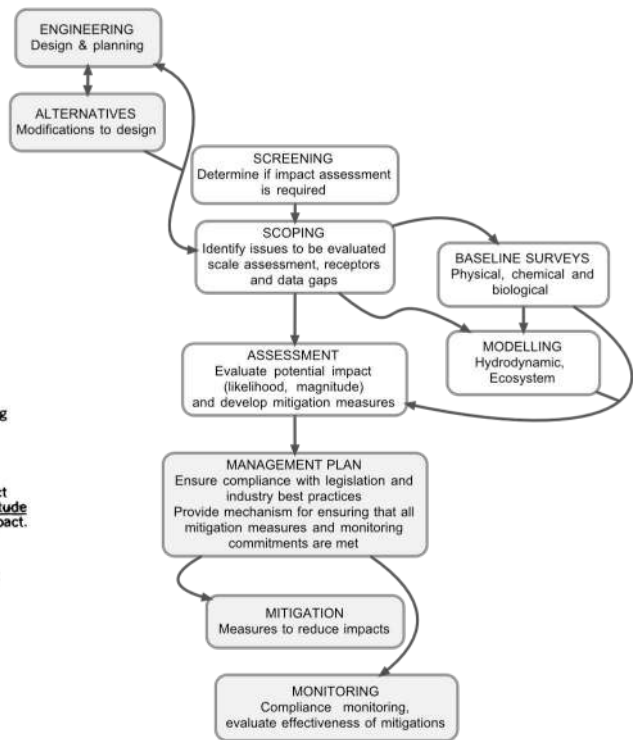
(b) 2016

FIGURE 1.

Coston-Guarini, J. et al. "A Roadmap for a quantitative ecosystem-based environmental impact assessment"

submitted ICES Journal of Marine Sciences, 2016

(a)

(b)

FIGURE 2.

Coston-Guarini, J. et al. "A Roadmap for a quantitative ecosystem-based environmental impact assessment"

submitted ICES Journal of Marine Sciences, 2016

FIGURE 3.

Coston-Guarini, J. et al. "A Roadmap for a quantitative ecosystem-based
environmental impact assessment"

submitted ICES Journal of Marine Sciences, 2016

SUPPLEMENTARY INFORMATION (*not included here*)

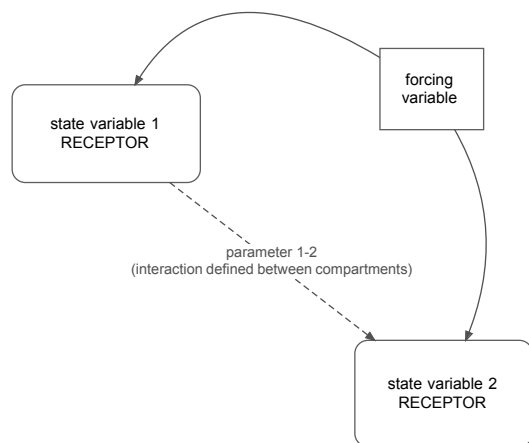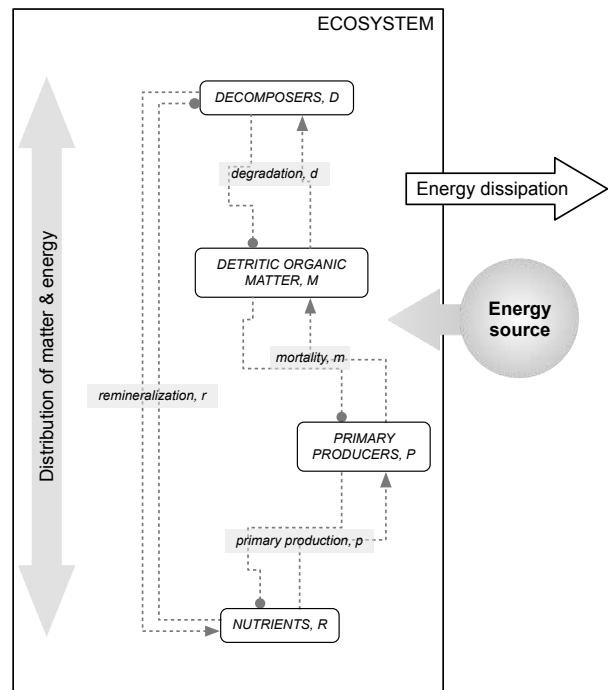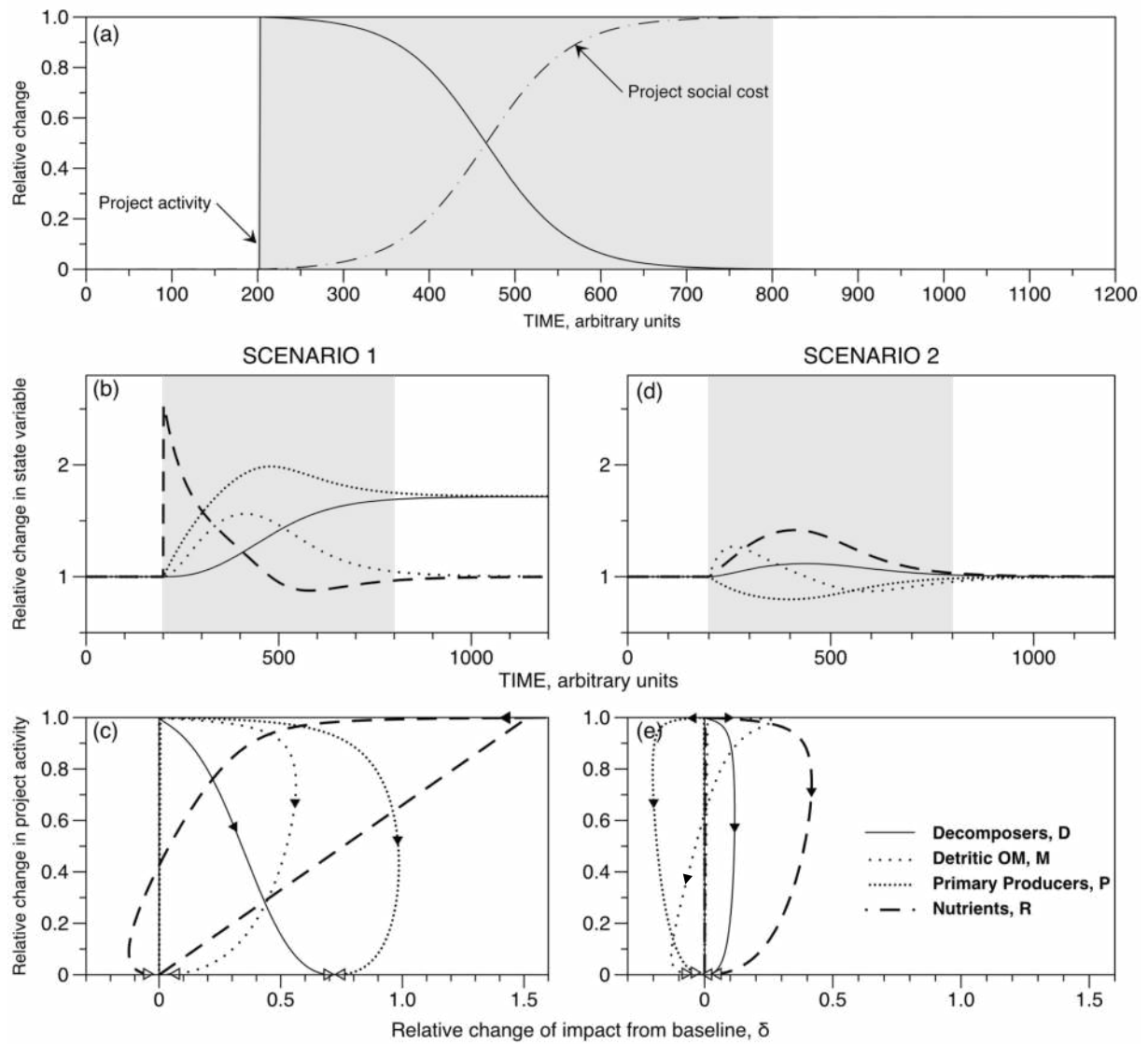The appearance of concepts in different cultures can be examined qualitatively by exploring the breakthrough of iconic phrases in corpora constructed of digitised publications. Frequency plots of n-grams representing these iconic phrases can then be examined by the publication language. These patterns then are qualitative signposts of the evolution in the usage.

Method

Each plot shows the relative change in n-gram frequencies per year in American (US), British (UK) and French (FR) corpora created by the Google Books project (http://books.google.com/ngrams, viewed on 26 Aug 2016). Searches were completed in May 2016 using the Google Ngram viewer interface with 2012 versions of all corpora. Complete details for the construction of these datasets are available on the website cited above.

Figure A.

N-gram frequencies for concepts associated with ecological sciences and the regulation of environmental impact compared for the corpora: US, UK, and FR.

(top) The rise in visibility of ecological sciences (1-gram for neologism "ecosystem") slightly precedes the sharp rise in 2-grams such as "environmental impact" and "environmental protection" in search results from the US English (2012 version) corpus. Tansley's 1935 neologism - ecosystem - marks the break from 19th century natural history style of ecological research and the current systems-based approaches. The term "environmental impact" enters widespread usage following the passage of the US NEPA legislation in December 1969 that required the evaluation of environmental impact and ushered in an era of environmental protection (thus the third 2-gram, "environmental protection"), in large part due to the creation of the US Environmental Protection Agency (US EPA).

(bottom) Examining these concepts in corpora from other cultures suggests how rapidly these terms spread into other cultures. Here, the relative changes in 2-gram frequencies per year of the phrase "environmental impact" in US and UK corpora are compared with the phrase '*impact environnemental*' in the FR corpus. The time lag (or retardation) is shortest between US and the UK delayed by about two decades in the FR corpus. Penetration of the English term in French is retarded, because it's use is tied to the translation of EU directives into French law during the 1980s (as for other EU member states). Prior to this, a similar concept would have been represented by other terminology such as: '*étude environnementale*'.

PART III. Conclusions and perspectives

SUMMARY

This doctoral project is a constructive criticism of ecology motivated by the fundamental theoretical challenges that data re-use and a historical perspective raise. It constitutes the first historical epistemology of ecology and could have been entitled, "Ungovernable by nature? A re-examination of ecological theory and the study of co-existence".

Drawing on history of science philosophy and theoretical ecology the text suggests reasons why scientific knowledge in ecology is so often sidelined and ineffective in the policy arena. It also discusses why ecology has had no stable conceptual development resting on laws, in contrast with physics and chemistry. Ecology is defined as a science that focuses on interactions between organisms and with their environment. Yet, at a time when there is a critical need for globalized, shared information about the state of the biosphere, ecological sciences are still not able to furnish adequate diagnostics or prognostics. And, beyond the window-dressing of endangered species lists biodiversity hotspots, and protected areas, there has been little concrete conceptual progress in recent decades. I explore how this situation arose and then using examples from marine ecology in environmental impact assessment, conservation of species and the uses of historical data, propose some new perspectives.

CHAPTER 8

"HISTORY" AND ECOLOGY

"It is, of course, in itself completely
unimportant whether or not one
calls a certain type of work by a
special name, as long as one agrees
that it has a place in the progress of
science, but the issue has important
implications."

-- Tinbergen (1963): 416

OVERVIEW

Calls by ecologists to integrate the study of historical material into ecological questions have circulated for several decades.[1] But these efforts remained episodic and isolated until advances in other disciplines (*e.g.* the digital humanities, archeology, climatology, and environmental history) for the treatment of historical texts and imagery, as well as accompanying technological changes (such as global biodiversity databases, ancient DNA analysis, and GIS) built the rich and deep set of data resources about the historical past from which ecologists can draw on today. In this environment, the sub-discipline of historical ecology whose initial goal has been to address questions that require estimate of past ecological trends,[2] will surely expand to include the re-evaluation of past concepts and results developed and used within ecology, as I have done here.

My research explores the body of ecological theory used to reconstruct population trends. Theories about population dynamics should be applied extensively when managing resources and ecosystems, for example, for making decisions about fish stocks, for understanding why species go extinct, or why others may spread beyond their normal range, but this has not often been the case. Instead statistical methods to estimate trends have replaced mechanistic approaches, and explanations based on processes have been replaced with a phenological description of what can be observed.

Ecology, like biology, has developed a scientific practice without fundamental and general scientific laws. For the better part of a century, ecological theories have emerged from observations accumulated by individual ecologists working on problems in thousands of local environments.[3] Meanwhile, preservationist, conservation and protection movements wrote a myriad of regulations and legal descriptions to govern the quality and access to those environments which pre-date much of ecological theory. Concurrently, management of agricultural production and harvesting practices demonstrated how biological production

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[1] For example, the re-analysis of biological materials in museum collections (Ricklefs, 1980; Drew, 2011), ancillary data collected from historical documents (Malin, 1953), as well as the quantification of observer bias (Al-Abdulrazzak et al., 2012).

[2] Lotze and McClenachan (2014), McClenachan et al., (2012)

[3] The global distribution of field stations (Tydecks et al., 2016) give a very rough idea of the number of different local environments investigated.

could be manipulated and augmented. In a sense, both nature protection and agriculture can be characterized as vast experiments in ecology, begun long before a science of ecology existed.

Today, under an operating principle that 'complexity cannot be the object of reductionism', ecology and biology advance based on integrated systems and phenological principles to describe their dynamics. This practice renders results vulnerable to both misinterpretation and misrepresentation (whether intentional or not) since conclusions are reached under strict *ceteris paribus* conditions. In other words, it is accepted scientific practice in ecology that results may not be either transposable or comparable. This situation has had adverse implications for society's demands on ecology to provide information about everything from effects of climate change and the conservation of species, to how we assess the impacts of human activities on the environment. It also concerns how researchers in new fields like synthetic biology and synthetic ecology, or the uncontrolled genetic manipulation of living organisms in their environment (*e.g.* the CRISPR/Cas9[4] debates) can apprehend the consequences of their experiments.

Ecological theory has drawn on and continues to draw on a set of deeply interconnected ideas in science, philosophy and economics for its epistemological development. To understand how earlier historical context affects the ecology as a science that is practiced today, the central object of ecology (populations of individuals from the same species) and theories describing population variations are re-examined. This leads to discussions about how ecological theory treats the conditions of existence and co-existence, and how it was used to make predictions about the dynamics of populations.

Historical ecology is thus not restricted to the act of collecting and re-typing data from old logbooks. Historical ecology offers a means to reconsider past decisions and to delve deeper into the foundational concepts of ecology and the conditions in which they arose. Physics has evolved by proposing fundamental (*i.e.* universal) laws. These often appear to be inexact or inaccurate, and then are revised or abandoned to be replaced by others. The continual re-evaluation of physics' concepts and theories, without which no real progress could have been made, is deeply embedded in its practice. Historical quantitative ecology aims at performing this task for ecology, but from a retrospective point of view.

By using both reconstruction and recursive analyses to examine the concept of species' populations, it is primarily suggested that current reliance on theories describing interactions at the level of the population should evolve toward individual-based approaches. Individual-based approaches provide better representation of actual ecological processes and can accommodate a wide range of possible behaviors. On the one hand, all ecological interactions occur between individuals (whether they are from the same species or not), both with and

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[4] CRISPR/Cas9 = Clustered Regularly Interspaced Short Palindromic Repeats / Cas9 nuclease genome engineering technique

within the environment they perceive. There is no complete possible transposition of these processes to the level of populations (which then appear as a computational shortcut to group individuals of the same species). On the other hand, properties can emerge from individual interactive dynamics, at the level of groups of individuals that need to be redefined not using the concept of species (as population or communities) but from an organizational point of view.

I therefore propose that the fundamental objects of ecology should be reappraised, as well as all the concepts of interaction-based processes derived from population-based reasoning (competition, invasion ...). Numerous technological advances have made it possible to experiment with and measure directly individual interactions, both in the laboratory and in field environments. These should permit the development of a more functional body of theory (converging toward laws) concerning ecological interactions at the individual level and the development of ensemble forecasting model approaches. It will also certainly affect applications of ecological theory, as for example how we assess and monitor impact in environmental management.

ECOLOGY'S BACKGROUND

It is always a delicate exercise to fix an exact date for the creation of a scientific discipline. Typically, we can state that ecology begins with the invention of the word and definition in 1866 by Ernst Haeckel (1834 - 1919). However, scientific disciplines are built from brick and mortar programs that involve training students, building departments, and creating research programs and scientific forums for exchange. Thus ecology could not be labeled a separate discipline until the first textbooks and university courses appear in the 1890s. From the viewpoint of the historian of science, ecology is indeed a very young discipline.

A discipline born of controversy

I have explained that ecology's origins are found in the writings of well-known natural historians, like the Comte de Buffon, and in works by authors concerned by agriculture, forestry and fisheries. Vast national administrations, often associated with colonial ambitions, located and controlled access to natural resources across the globe, ensuring their production, extraction and transport. By the early 19th century, natural historians were re-inventing themselves as biologists, physiologists and zoologists, and were also promoting themselves as public lecturers, book authors and tour guides. Simultaneously the products and effects of the Industrial Revolution were being widely documented by the newly invented technique of photography. Progress was associated in the public mind with amazing technological inventions and new scientific discoveries, as well as with pollution, exploitation and destruction of wilderness areas, rivers and streams, and the disappearance of the pre-industrial era.

A sharp rise in public interest for the marine world swept across Europe when the British aquarium craze (1840 - 1855) brought marine organisms directly into middle class homes.[5] Marine sciences as a discipline arose as scientists gained access to marine environments through technological progress in diving and navigation.[6] Zoologists freely adopted and adapted tools of fishing and aquaculture to projects in biogeography, biological development and physiological reactions.

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[5] Rehbock (1980)
[6] Deacon (1971)

Theory caught up with the accumulating practical knowledge when Alfred Russel Wallace (1823-1913) and Charles Darwin (1809-1882) provided a coherent theoretical framework to investigate the role of the environment on organisms. Within their framework, known as the "struggle for existence", the conditions of existence were transformed from a means to control the production of natural resources for agriculture (with a need to eradicate 'competitors' of cultivated organisms), into a search to understand the fundamental nature of interactions between living organisms and their environment.

The objects of study in ecology

I've recalled that, in the twenty years after Haeckel created his neologism, the objects of study in ecology emerged along quite different lines than those of biology. While biologists were examining internal physiological and cellular functions, ecologists focused their studies primarily on individual organisms, then organized as populations and communities of organisms in particular environments. These objects of study fit well with the interest in spatial distribution patterns present in earlier biogeographical works. Thus we have three corresponding scales: local, regional and global, which accompany these objects. Regardless of whether ecologists perform observations in marine or terrestrial environments, or study models and perform experiments, these objects and scales began to organize ecological theory.

The processes invoked within ecological theory are described as interactions within a particular (*ad hoc*) type of system: the ecosystem. Most theory concerns ways to explain the outcomes of interactions between the objects of study and the environment in which they occur. A large body of theory aims to predict how the presence of a particular species may affect (through their function and place) other species in a community (e.g. predator-prey interactions). Outcomes are analyzed in terms of equilibrium, stability, drift and thresholds. In turn, these theories inform management challenges, such as protection against destruction (before extinction of the species occur) or invasive species, the prediction of stock renewal (*e.g.* fish stocks or agricultural production), or the evaluation of environmental impact on communities and ecosystems.

However straightforward this may appear, each of these terms comes wrapped in a particular set of assumptions. Particularly, because if ecology has a central object of study, it would be populations of organisms of the same species. A population cannot be compared to a 'thing' since it is also a statistical concept, resting on the conceptual notion of species. The concept of species is itself a flexible concept without a universal definition encompassing all life forms. This absence of consistent and coherent applicable results after a century of work is feeding a rising concern among some ecologists about the absence of ecological scientific laws.

Troubles caused by the absence of laws

If scientists consider the description of a scientific law to be a desirable goal, is there a consensus about what a scientific law is? Physics and chemistry both have law-based scientific

practice. From this has emerged incontestably significant and fundamental progress, and this knowledge has played a crucial role in increasing the understanding of topics like climate and global change.

However, the definition of exactly what a scientific law is, is under considerable discussion. The primary question in philosophy is: how does a scientific law govern? This is not precisely the same as the working scientist's point of view, which is: does this statement (of a law) describe how measurable variables can be predicted? The two sides do agree that most of the laws should be based on mathematical statements. The debate also considers if (all) sciences need scientific laws at all and would this change the scientific practice in a discipline like ecology?

The origins of the use of the term 'law' in science, as part of modern scientific method, can be attributed to the work of Francis Bacon (1561-1626). The use of law by other writers was readily adopted especially in regards to the results of Isaac Newton (1643-1727). By comparing the use of the n-gram 'law' (or '*loi*') in several works, spanning the end of the Enlightenment (Buffon's *Histoire Naturelle*) to today's Wikipedia it becomes clear that this word is used to lend weight to statements proposed by scientists rather than to characterize an absolute statement of natural governance. In other word, few laws in ecology are based on canonical equations, hence contain properties that can be applied to all particular cases, and, canonical equations are sometimes purely mathematical constructions with no particular ecological meaning. This suggests that a law-based scientific practice (described as an ideal by Karl Popper (1902-1994)) is not as clear-cut as it might appear. The absence of laws in ecology and biology is indicative of intrinsic underlying difficulties.

The phenology-based practice that emerged in ecology has important repercussions for the way this disciplinary field is practiced today. For example, the rarity of long time series of ecological observations and long term ecological experiments can be attributed to this situation. Instead of developing laws, baselines and reference states, ecology is built around the phenomenological description of populations. This opens the door to the transmission of unexamined assumptions and misconceptions arising in particular historical contexts.

Putting theory and objects back in context

Ecology and biology have both arisen from concepts far in advance of the technological capacities to investigate nature, hence attempting to explain what cannot be observed. The molecular basis of natural selection and evolution were described decades after principles were pronounced. Ecology has had an even slower development, such that today, there is a gap between ecological observations, theory, and societal demands for tools and explanations to determine and regulate ecological problems. Environmental protection legislation has been a boon to ecological sciences, permitting the generalization of monitoring programs over

different spatial and temporal scales. But regulation of the environment also had the unfortunate effect of fixing into legislation imperfectly tested ecological concepts.

There are means to enforce regulation about environmental quality and ecosystem functions. But if scientific laws do not exist to provide objective predictive frameworks, then decisions are taken from scenarios and empirical models submitted to constant revision. In conservation ecology, it is necessary to be able to reconstruct changes (by assembling appropriate data series) in the distribution and state of populations over long time periods because they can be used to constraint statistical model projections. Species presence data are the main information that can be recovered in ecological literature because of the way ecology was practiced. However, simply knowing the species present in an area is usually insufficient to analyze areas of concern in conservation and environmental impact using ecological interactions. In addition, this type of assimilation procedure is never tested generally because of the scarcity of long series of ecological observations in any environment. As a first consequence, past results and their progression, for both concepts and observations, need to be re-examined. Studying the epistemic progress of ecology offers a means to reconsider potential candidates for a framework of scientific law in ecology that were overlooked in earlier contexts. It also permits identifying when and why concepts and theories led to dead ends.

TREATING HISTORICAL CONTEXT

From the previous chapters, it was concluded that to test ecological laws, undertaking a detailed study of how the dynamics of populations are described and modeled should be a reasonable direction of investigation. Ecologists who made important contributions to theory post 1900, simply set aside the possibility of historical contingency in their work. For example, when the ecosystem concept was invented in the 1930s the original discussions were highly critical regarding ecological succession. At this point, changes in species distributions observed over time were considered either as evidence of community succession or as consequences of evolutionary adaptations (and thus within the domain of biology). The new ideas of population dynamics presented in Lotka and Volterra's models (between 1920 and 1926) associated with Raymond Pearl's (1879-1940) relentless promotion of the logistic curve,[7] and other concepts taken from chemistry (i.e. saturation), moved away from dealing with contingencies and replaced time as a continuous variable in their equations. Yet no sense of standardization or reference conditions emerged, instead new statistical treatments were applied. This epistemological development means errors can be propagated easily if historical bias in sources are not addressed. Different approaches to integrating this contextual and observational information into ecological studies are presented.

Epistemic progress or cycles of accumulation?

In the 1980s when the first historiographies of ecology appeared, the lack of an historical facet in ecology was commented on. But even if the term 'historical ecology' was coined in the 1980s by an ecologist in a research program title, historical ecology was developed and promoted by anthropologists and archeologists. Instead, another phrase, "museum ecology",[8] was elaborated on. The idea was to promote museum collections as resources for documenting the timing and prevalence of contaminants. Calls to exploit information about the past state of sites for environmental problems arose over a brief period, between 1980 and 2000, in anthropology, archeology, climatology and ecology quasi simultaneously. It coincides with increasing ease of access to historical documentation through digitization programs, the generalization of geographic information systems and the new research paradigms of global climate change and biodiversity conservation.

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[7] Kingsland (1995)
[8] Ricklefs (1980): 207; Winker et al. (1991); Alberch (1993); Allmon (1994)

This intellectual promiscuity brought Historians, concerned with discerning motivations and intentions, in direct contact with Scientists who strive for objectivity. 'Historical time' is primarily concerned with determining when someone acquires knowledge or could have acquired it: time is often imprecisely known and events are treated within particular cultural settings. There is an explicit assumption that extracting facts and dates without historical context permits the transmission of misunderstandings about both the past and the facts that were extracted. The scientific concept of time stands in stark contrast to this approach. 'Scientific time' is a continuous or discrete variable, in other words a set of numeric values, within a dynamical equation. Simultaneously treating these different concepts of time in the same system raises many technical issues, and has implications for descriptions of the behavior of living organisms, including humans.

Curiously though, it was overlooked among most ecologists that integrating a historical perspective provides an opportunity to examine the epistemic progress of ecology.[9] The scientific method relies on repetition and re-analysis of previously published results, but phenological-type reasoning has rendered re-analysis uncommon in ecological studies. Any study in ecology may always be criticized by saying that 'conditions are not exactly the same between studies, which explains why results differ'. On the one hand this sounds true, if it is assumed that ecology does deal with complex dynamic systems that do not have a clear starting point and exact replication is not possible. But this style of reasoning obscures more fundamental questions about what the actual objectives of ecology are about. Furthermore, as pointed out by ecologists in different specialties, this state of affairs undermines conceptual progress by encouraging the accumulation of hundreds of different theories that address a few commonly held principles under different names.[10]

Difficulties of introducing a recursive method into ecology

At this juncture a recursive approach is needed in ecology. The consequences of the lack of re-analysis and comparative practice have stalled progress when societal demands are very high for more information about how ecosystems will react to predicted global changes. Moreover, there are important holes in the actual body of ecological theory. For example, no ecological theory predicts if a species is missing from a particular time or place. This situation is an obvious, critical weakness for conservation science and environmental impact assessment. In another example, there are no reference measurement systems in ecology which permit comparison across ecosystems. Thus biodiversity, as a set of information about the diversity of life, measured in one site has no relevance to the biodiversity in another site. The number of species has no fundamental ecological meaning and even more seriously there are no means to describe the state of an ecological system based on the information given in earlier studies. Ecology, unlike physics or chemistry, has no such tool like a thermometer that

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[9] "… history would suggest that scientists tend to underestimate the future." Koshland (1995): 1575
[10] Palmer (1994)

can be calibrated across epochs and environments. This means there are currently no existing means to compare the functioning of an ecosystem in 1960 with one studied in 1990, and one studied in 2015.

The difficulties are not only technical though. As noted by other observers, typically scientists abandon old literature which is perceived as impossibly out-of-date, and students of science lack any training in dealing with context and contingencies. The perceived imprecision of historical documents is considered as trivial detail. Problems of anachronistic interpretations, appreciation for cultural cues and the fluidity of measurement and description systems between different cultures and time periods contribute to this stereotype. Yet, recursion and retrospection offer fertile grounds to suggest answers to questions such as "what might ecological progress look like?" and "where should we invest our efforts, based on past failures, their causes and consequences?"

Another expected hurdle is that developing new sources from historical information requires collaboration with other disciplines (*e.g.* anthropologists, archeologists, economists, geographers, sociologists and historians) that do not share a common vocabulary with ecological theory (Figure 8-1). Using local knowledge can require knowing about theories in sociology describing social power structures and belief frameworks to develop an operational understanding of how this information can be re-used. In addition, this type of interdisciplinary work requires close collaboration from institutional computing platforms as well as input from specialists in database and algorithm development. Despite the potential, few institutional structures exist at the present time designed to support these types of studies. This is unfortunate as these programs touch numerous areas of research and their associated teaching programs, as well as justifying investment in existing institutional infrastructure concerned with collections, archives, and data management.

Integrating history into ecological sciences

Integrating social, historical and ecological systems is not a trivial matter of getting dates right. There is very little concordance between sciences and the humanities; in this sense, CP Snow's insights in his 1959 essay about two academic cultures remains quite actual.[11] Digitization programs accomplish the miracle of turning documents and any other material object into analyzable data (Figure 8-2). However, despite continuous improvements in database accessibility and access, considerable effort must be invested to locate and use these resources. Multiple, complementary tools have to be applied to assess the robustness of the information available. This includes detecting and treating systematic bias and realizing the limits of scientific value of specific data types, in addition to identifying data quality issues and equivalencies.
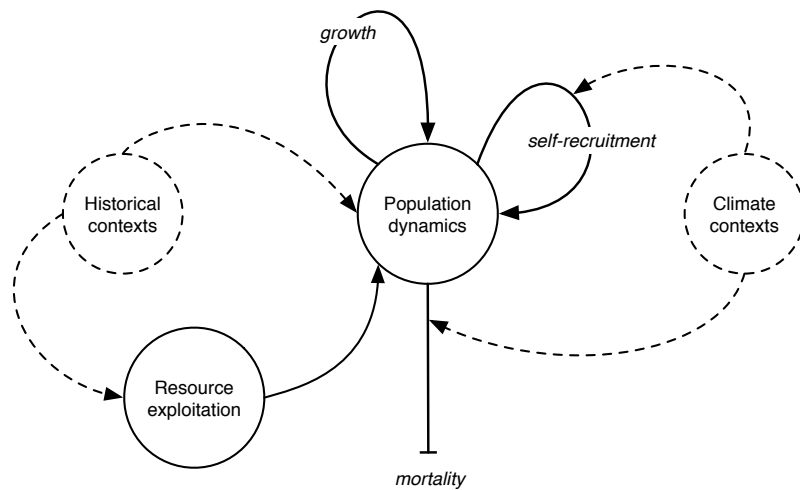
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[11] Snow (1959)

FIGURE 8-1. Simplified presentation showing where historical context contributes information about both ecological variability (population dynamics) and resource exploitation conditions when reconstructing ecological trends in the presence of human societies. Climate contexts (*e.g.* NAO patterns) influence processes of population dynamics, while historical contexts influence populations through resource exploitation, or directly witness changes through scientific works.

The rarity of long time series of ecological observations has made reconstruction an important step. Thus ecologists have turned to historical documents as alternative sources of additional observations. Besides the technical challenges of validating these data, reconciling scaling problems, and identifying the limits of applicability, re-using historical information demands explicit knowledge of the epistemological state of the original observations in context. Unlike in historical climatology, which is engaged in similar data recovery activities, ecology does not have any common instrument or tool which can be cross-calibrated with modern techniques, like the meterologist's thermometer. Further complicating the situation is the absence of a body of scientific laws specific to ecology. Reconstructions of ecological trends using historical documentation must account for the expertise and original intention of the observer. Unfortunately, many ecological studies relying on historical information have overlooked this point.

INSCRIPTIONS

DATE,
TIME PERIOD

GEOREFERENCE
Point, or region

PROVENANCE

IDENTIFICATION
Species, Persons, Places, Objects

PRACTICE, USE
Resource exploitation
Recreational uses
Economic uses (Trade,
manufacture, agriculture)
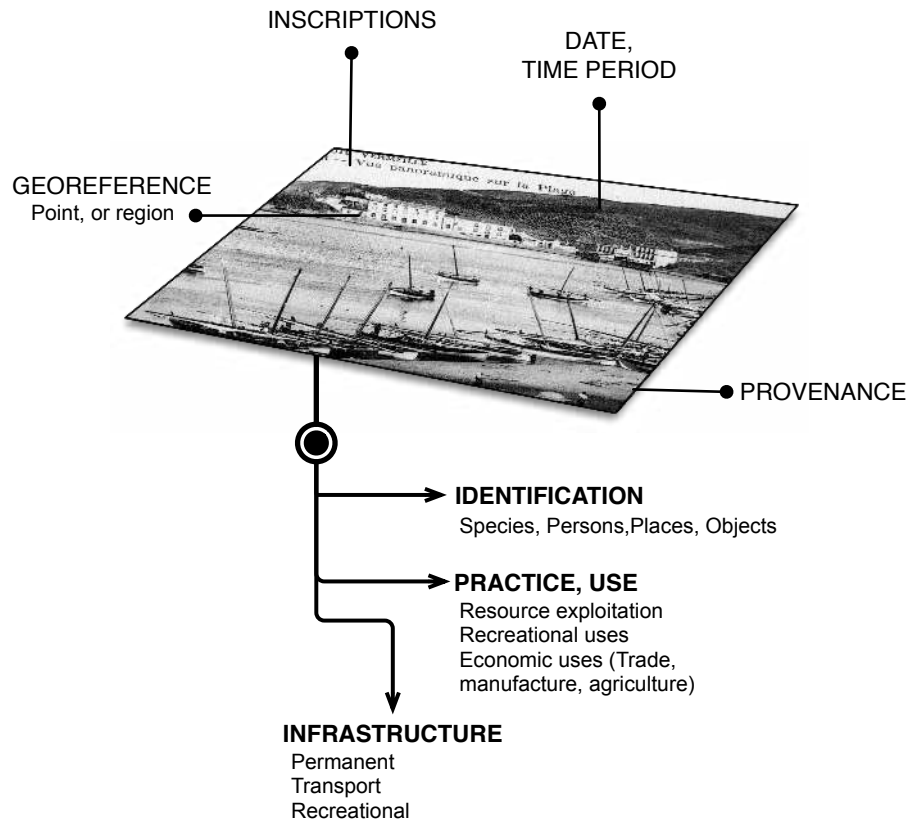
INFRASTRUCTURE
Permanent
Transport
Recreational

FIGURE 8-2. The transformation of documentary information
into data has elevated once throwaway items into valuable tools
for historical studies. Digital surrogates can be analyzed to
recover environmental information present in the image, as well
as from materials analysis of the document itself. Every object
has a different representation and potential as a data source.
This postcard, for example, contains information about at least
seven different categories of environmental and sociological
observations, in addition to the information pertaining to the
creation and history of the object itself (provenance).

Historical ecology studies draw heavily from the principles of
archeological and museological analyses of objects. Every
object embodies multiple facets of information about its origins
as well as providing evidence of ecological and cultural
knowledge. Materials analysis identifies the origin and
provenance of the materials from which the object is made.
Images, such as this postcard, provide documentation about
the state of the environment and infrastructure, as well as local
economic uses. Any object that can be assigned a date and a
place of origin, even imprecise ones, becomes another potential
observation for chronological studies and trend reconstruction.

One means of performing this integrated task is to develop historical profiles of problems. A historical profile is an information gathering technique from decision-making and diagnostic medicine that complements other "soft" modeling approaches, like qualitative mathematical modeling frameworks.[12] It has been used for laying the groundwork of causal analysis in complex situations like those that arise in natural resources management and sustainable agriculture programs. It can be extended further to predict what records may potentially exist (or be expected to exist) and to address provenance issues related to bias. Since these techniques provide structured data they can be used to constrain models, including capturing expertise in Bayesian network analysis. Secondly, it can help resolve a major problem with historical information which is simply locating relevant sources. Collections are not "natural" accumulations analogous to the fossil record, they are associated and defined by the intentions (whether known or not) of persons and institutions (Figure 8-3). The content of any collection depends on who created it as well as any existing organizational culture; backlogs of uncatalogued material can be significant. They are highly idiosyncratic and many, if not most, collections are not described in ways that permit interrogating catalogues based on scientific questions. Providing a structured, systematic means to think about what "should be available" can be the key to building targeted inquiries to locate sources for long ecological series, instead of relying on chance encounters.

Contextual treatment of scientific practice at marine stations

We have already seen that natural history and ecology have shared origins and that the historical contingencies affect not only the terminology used in ecological theories, but also the way the discipline of ecology has developed. Recent work by the historian Lorraine Daston on the history of scientific objectivity and expertise[13] show simple transcription to be insufficient. The retrospective construction of data series starts at one particular point of knowledge (which is a consequence of past accumulation of information), and a calculation could be made of the probability to have accurate information at each previous time interval. This is one perspective that could be developed to formalize the processes of knowledge accumulation within scientific disciplines and their associated sociological communities. To appreciate more fully the implications, the development of a small part of the infrastructure of ecology, the field station, is examined. In particular, I look at briefly how the functioning of these structures favored the emergence of certain aspects of ecology over others, and the continuing impact of these facilities today. The discussion focuses on the network of marine stations developed along European coastlines[14] from the mid-19th century onwards.

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[12] Norton and Mumford (1993); Dambacher et al. (2003); Austen et al. (2015)
[13] Daston and Galison (2010)
[14] da Bont (2015)

Figure 8-3. Examples of stratigraphies of materials accumulated in the working spaces of marine scientists with full academic tenure (images taken between 2011-2015 in offices on French university campuses). These notes, specimens, samples, tools, data, publications, images *etc.* are technically hidden collections, organized according to the preferences of the individual scientists and may or may not constitute a research tool for the scientist and their collaborators. When the researcher retires, or leaves, this material is often discarded without any professional curatorial evaluation by the institution, creating gaps in archival records. These gaps are just one of many loss processes that erode collection integrity.

In general, field stations were primarily justified as a means to facilitate regular and controlled access to organisms in their "natural" conditions.[15] They are by definition present in isolated regions, frequently quite distant from academic centers. Some provided simply a shelter for field biologists while they were making observations in a particular area; others, especially those run by agricultural groups, also managed experimental plots and had active laboratories. All had some role in training students and thus shaped attitudes about field *vs.* experimental studies.

Marine stations in particular engender tremendous additional costs not associated with terrestrial stations. We can find numerous examples of these additional needs in the early histories of marine stations which are recounted in some detail by their respective founders in popular scientific literature. For instance, the richly documented history of the founding of the Laboratoire Arago located in Banyuls-sur-Mer (France). Created in 1881 by the Sorbonne professor, Henri de Lacaze-Duthiers (1821-1901), it was a purpose-built structure, unlike his first marine station in Roscoff. The marine station required boats, aquariums, water supply systems, complicated sampling equipment and specialized personnel to access the marine environment (Figure 8-4, 8-5). Thus, many marine stations promoted a pseudo-commercial activity to supply organisms and even seawater to other scientists and inland laboratories. Others used applied aquaculture studies as a means of support. Most organized regular activities aimed at attracting support from the general public and potential financial partners (demonstrations, lectures, field trips, summer schools; Figures 8-4, 8-6).

By the late 1880s European marine stations were well-placed to provide a research infrastructure for ecology. French institutions were at the center of this activity, but their eternal financial fragility encouraged short-term research. In general though, there are three main types of research: developmental biology of organisms, descriptive biogeographical studies, and finally fisheries-related investigations.[16] Despite the fact that individual scientists noted negative environmental changes along coastlines where they worked,[17] marine stations, especially the French ones, only intermittently monitored environmental conditions in their vicinity. The reasons for this lie with the individual personalities of the marine station founders and their personal research expertise, as well as the way these institutions were managed. If enough institutional documentation exists on the functioning of a particular laboratory or marine station, this can be graphed and treated as a social network suitable for Bayesian analysis. Linking sociological processes of collection creation and conservation with knowledge production in this way provides a means to estimate the probability that information about local conditions within a marine station could exist. Figure 8-7 shows a preliminary treatment of one of these networks.
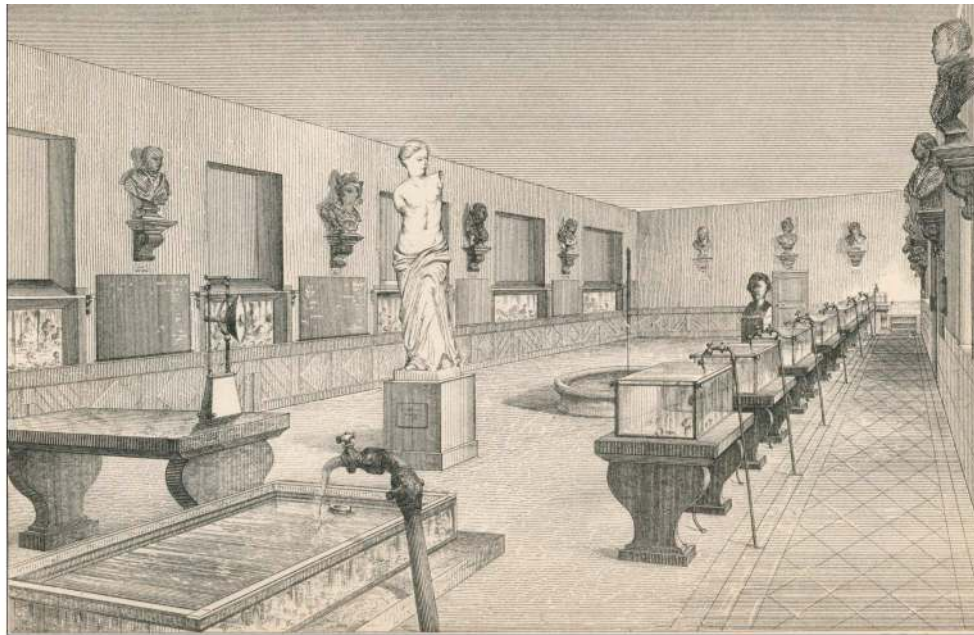
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[15] Kohler (2002)
[16] Kofoid (1910)
[17] Coston-Guarini *et al.* 2017. This is the manuscript of Chapter 7.

(a). Idealized view of the public Aquarium on the first floor of the marine station. This engraving published in 1891, is based on a photograph supplied by H. Prouho below. From: Lacaze-Duthiers, F.J. Henri. (1891) "Les Laboratoires Maritimes de Roscoff et de Banyuls en 1891." Archives de Zoologie Expérimentale et Générale 2éme serie, Tome IX : 256–363. Plate XIII.

(b). The Aquarium as photographed by Henri Prouho in about 1890. Notice the changes from the engraving above. The Aquarium remained more or less in this configuration, until it suffered heavy damage during the German occupation in WWII. It was then completely redesigned between 1947 and 1949. Only the plaster cast of the Venus de Milo (foreground) and the air pump for the *scaphandrier* (partly visible at the back left), still exist at the station.

Figure 8-4. The aquarium of the *Laboratoire Arago* (Banyuls-sur-Mer, France) was originally conceived as a mixed-use space, shared by the public and researchers alike. With his inflated public declarations about the benefits of 'Science', Prof. de Lacaze-Duthiers had agreed to include a public aquarium for the benefit of the village and the local economy. In reality, the scientists found this type of mixed-use very impractical and they retreated to the laboratories on the upper floors. By the mid-1890s, the cost of upkeep had already become a point of contention when the annual subsidy from the village to the station was cut.

Modified from the 2012 exposition, "*Les scaphandriers de la Côte Vermeille*" created by J. Coston-Guarini in collaboration with the *Conseil Général 66* detailing the importance of the Laboratoire Arago infrastructure for Louis Boutan's projects in underwater photography conducted at the marine station between 1893 and 1899.

Le Professeur Lacaze-Duthiers, barque catalane, 1882-1900.

NOT PICTURED, Le Roland, steam-driven, custom design, 1893-1900.

Le Roland II, steam-driven, custom design, 1901-1914.

L' Orvet, diesel-driven, military reconversion, 1919-1932.

Le Saint Vincent, motorized, fishing boat, 1932-1940.

L' Amphioxus, motorized?, barque catalane, 1947-1965.

Le Professeur Lacaze-Duthiers, custom-design trawler, 1951-1982.

Le Rufi, motorized, fishing boat, 1965-1980s.
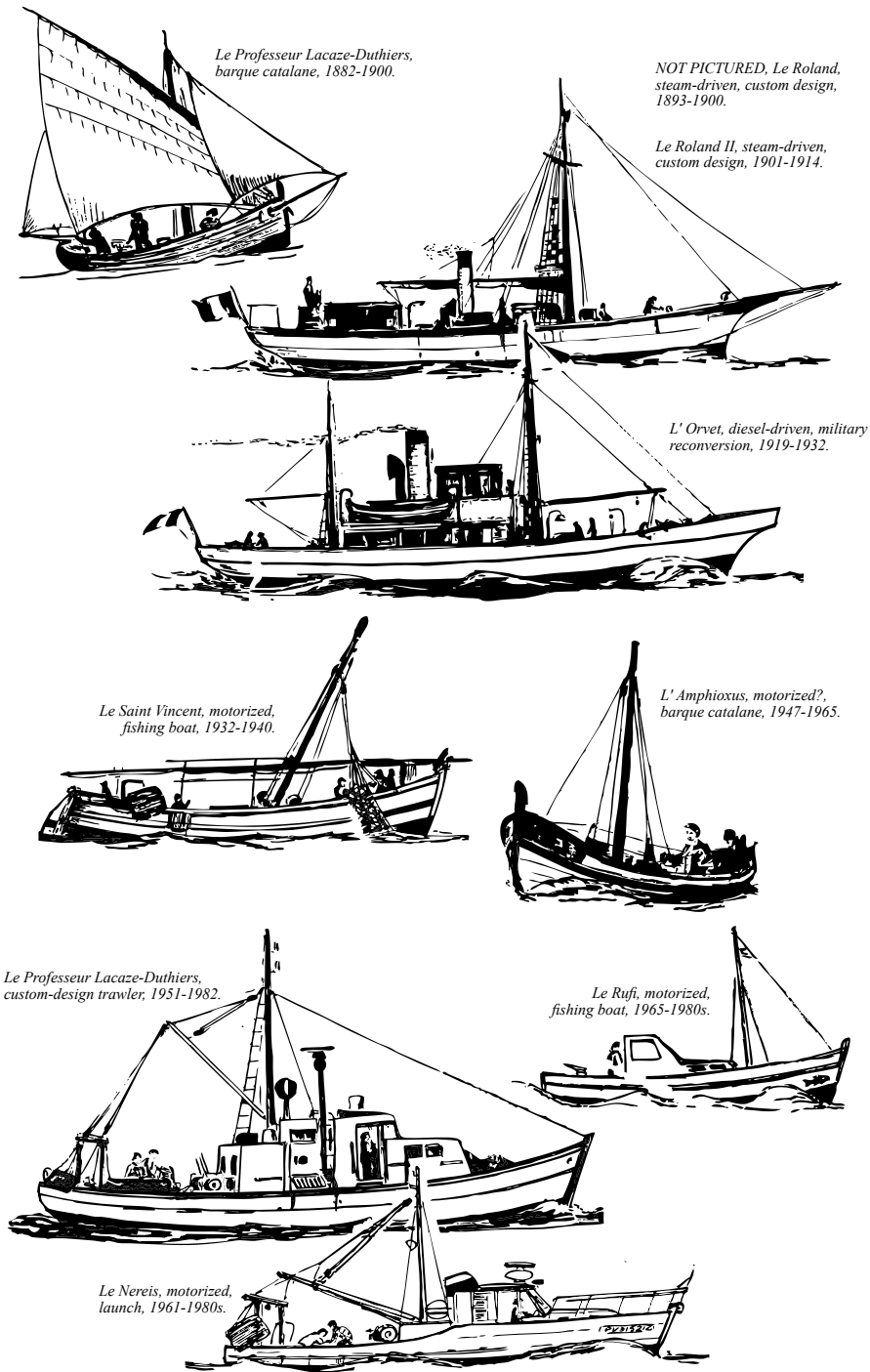
Le Nereis, motorized, launch, 1961-1980s.

Figure 8-5. Example of how access to the marine environment can change at one institution over a century. This series of boats was operated by the marine station, the Laboratoire Arago, in Banyuls-sur-Mer (France) between 1882 and 1982. The marine station used primarily sail-powered traditional fishing boats (*barque catalan*, or lateen-sail boats) until the the mid-1960s. The first engine-driven boat was the unfortunate iron-hulled "Roland" donated by the wealthy geographer-explorer, Prince Roland Bonaparte in 1893 (not pictured). This boat permitted the first systematic exploration of the region around the station; it was boat replaced by the "Roland II" in 1901. Between 1914 and 1947 the station scientists adapted to boats that happened to become available. After WWII, research investment programs permitted custom-built boats again.

Illustration modified after Figure 1 drawn by H. Boutière, on page 240 of Alain Guille's article, "*L'Océanographie biologique au laboratoire Arago : les temps modernes*" in the centennial issue of Vie et Milieu published by the marine station in 1982.

ÉCOLE PRATIQUE DES HAUTES ÉTUDES

ZOOLOGIE EXPÉRIMENTALE

LABORATOIRE ARAGO

VACANCES DE PAQUES DE 1891

M. H. DE LACAZE-DUTHIERS, membre de l'Institut, fondateur et directeur du Laboratoire, accompagné de **M. le Dr PRUVOT**, maître de conférences, à la Sorbonne, et de **MM. les Dr H. PROUHO et GUITEL**, assistants, fera et dirigera des Conférences et des Excursions dans l'Aquarium et sur les Côtes de Banyuls-sur-Mer (Pyrénées-Orientales).

EXCURSIONS : A PORT-VENDRES, COLLIOURE, PAULILLE, CERBÈRE; EN ESPAGNE : A PORT-BOU, LLIANZA, LA SELVA ET ROSAS

PÊCHES PÉLAGIQUES, AU CHALUT, AU SCAPHANDRE, DRAGAGES DES BRACHIOPODES DU CORAIL ET DE L'AMPHIOXUS, ETC.

Le Président de la Section des Sciences naturelles de l'École des Hautes Études,

H. DE LACAZE-DUTHIERS
Directeur du Laboratoire.

Paris. — Typographie de DELALAIN FRÈRES, Imprimeurs de l'Université, rue de la Sorbonne, 1 et 3.
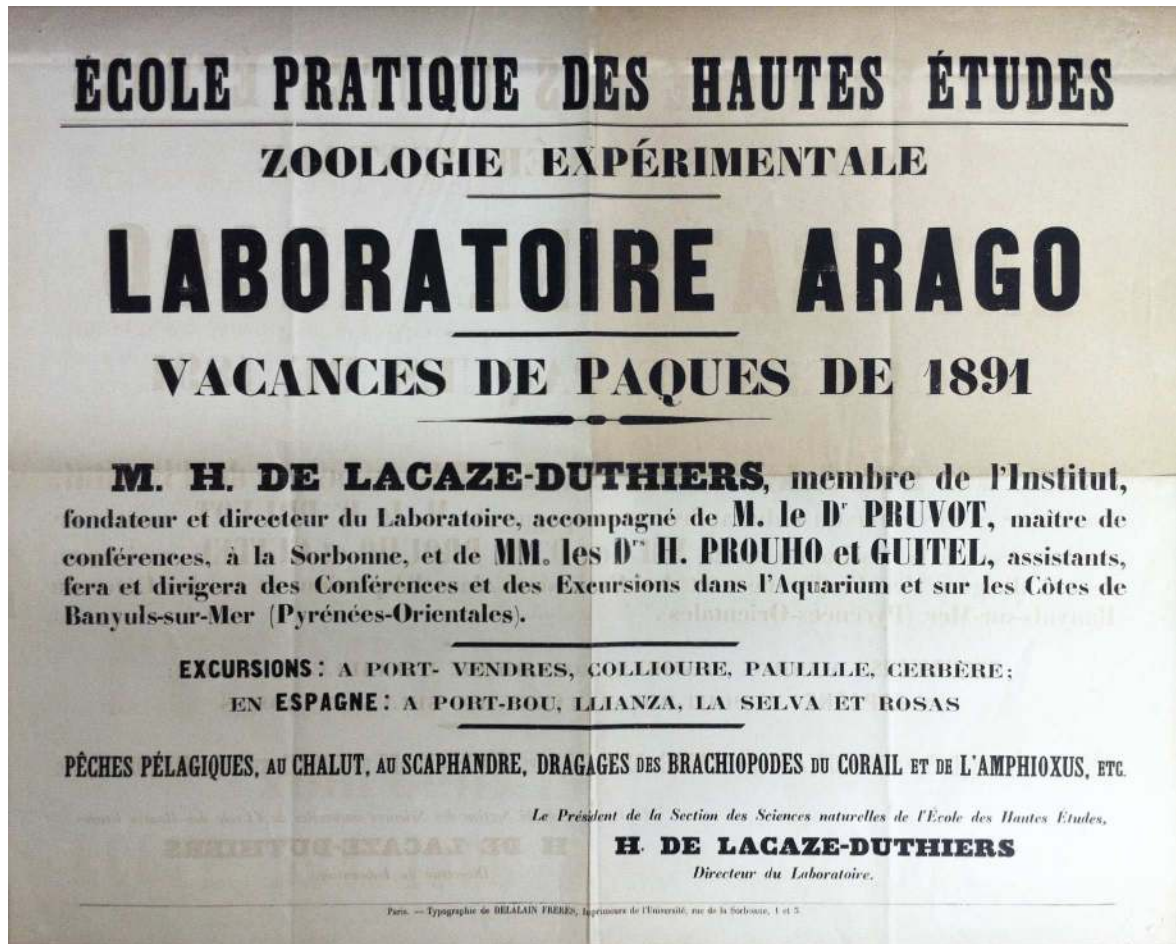
Figure 8-6. Example publicity for an annual field school held at the marine station, the *Laboratoire Arago*, in 1891. One of Professor de Lacaze-Duthiers' most prominent arguments for operating marine stations was not research, but teaching. To that end, he organized regular field schools at both his marine stations in Roscoff and Banyuls during breaks in the university calendar. This poster is for the first field school organized in Banyuls-sur-Mer (France), after the first building phase was completed. Later, these would be known as "*Les Excursions zoologiques*". Interestingly, the activities listed for the Laboratoire Arago (pelagic fishing by trawls and diving) and the organisms specified by de Lacaze-Duthiers (*i.e.* red coral, Amphioxus) remained emblematic of the marine station teaching programs well into the 1970s, despite the amount of research done on other groups and topics.

From his correspondence we know that de Lacaze-Duthiers used these courses as a means to entice well-established Francophone naturalists to undertake the voyage to Banyuls. By the mid-1890s, the field schools took on an international character when Prof. Oden de Buen (University of Barcelona) began participating. These co-organized field schools constituted the longest international teaching program at the station, until the European Masters in marine biodiversity and conservation (EMBC) was organized in 2007. All other international teaching was simply hosted at the station (treated as an income source, not a collaboration).

Modified from the 2012 exposition, "Les scaphandriers de la Côte Vermeille" created by J. Coston-Guarini in collaboration with the Conseil Général 66 detailing the importance of the Laboratoire Arago infrastructure for Louis Boutan's projects in underwater photography conducted at the marine station between 1893 and 1899.
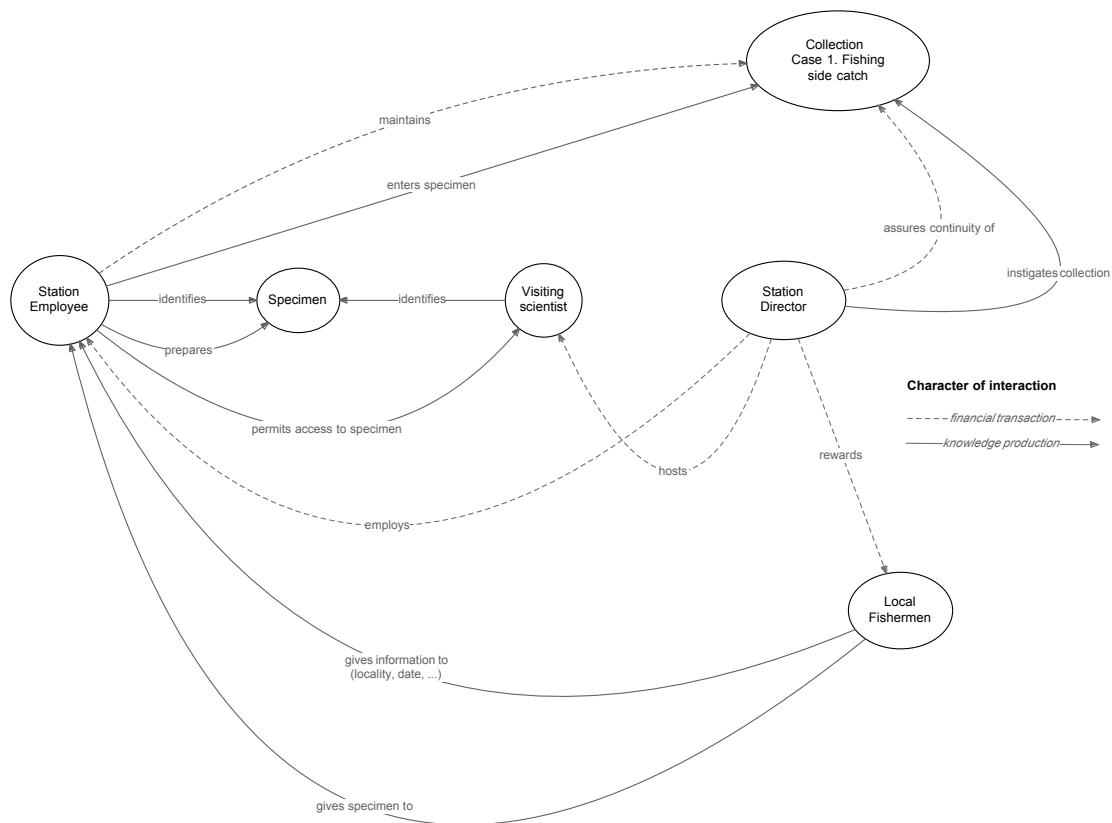
Figure 8-7. Example of the sociological processes within a small marine station involved in the creation and maintenance of a scientific collection. This example comes from the description of how a collection of fish by-catch species came to be created at the NIOZ station between 1930 and 1993 (de Vooys and van der Meer, 1998).

There are two basic categories of interactions, those involving financial transactions and those involved in knowledge production. Two persons have key roles: the director and the station employee who maintains the collection. In this example, local fishermen were rewarded for providing information about by-catch to the station. These data eventually constituted a valuable record for species other than targeted ones in the region.

The historical context of the scientific work accomplished in the marine stations as well as the state of their historical records, deserves further investigation, in order to fully characterize the type of historical records that they could furnish for analysis of past trends as well as their potential bias with respect to current research questions.

REVISION AND RECONSTRUCTION

Ecology, as a science, is characterized by the absence of a law-based practice and an absence of reproducible measuring techniques like a thermometer to take the "temperature" (i.e. to measure the state) of ecological systems. Reconstruction and recursive analyses are therefore the only methods available to build time series of ecological observations necessary to evaluate trends.

I present four concrete examples showing how historical information can be used to inform current ecological theory. Combining historical frameworks with the rationale of ecology these examples consider how historical context may influence different facets of the reconstruction of ecological trends. This could be viewed as an extension of the museological concept of provenance to data analysis. Three topics in ecological theory related to population dynamics are: the population abundance estimates, the spatio-temporal variations, and co-existence of two species in competition for the same resource. These concepts are relevant to the conservation of marine populations and the re-use of historical data and theories to respond to protection issues. The examples concern two groups of invertebrates (muricid gastropods, a serpulid polychaete) and the experimental framework of the theory of competitive exclusion proposed by G.F. Gause (1910-1986), who was possibly the first ecologist to have attempted to develop a law from combining experiments and models. Each example evokes both analytical and epistemological concerns. The final study develops a statistical basis for environmental impact assessment and a minimum ecosystem model linking two populations (a primary producer and a decomposer), in a purely theoretical exercise exploring the possibility of applying an ecosystem-based approach to the evaluation of impact as was originally intended.

1. Reconstruction of population dynamics

The way that population abundances change over time and space was the subject of many developments. It is nonetheless a sensitive topic because inferred trends are used to declare if a species is invasive or endangered (or not) in conservation. Different methods to assess population abundances were proposed, often without any transmission of knowledge, overlaps or attempts at cross-calibration. Ideally, there are observations of the organism of interest that can be used to validate hindcasts and therefore, analyses of past results have been proposed as a logical solution to recreate series from the scientific literature and other sources.

Returning to the historical profile of the marine stations, a potential issue is raised that few scientists were doing systematic sampling of the coastal habitats. This type of sampling was attached to the career of single researchers, or was used as a teaching exercise. Organisms

caught in teaching programs were not generally recorded[18], although records of organisms collected for re-distribution to other laboratories may exist in the form of shipping records held in archives. However, these are not substantiated observations of easily distinguished groups, rare catches or special requests. At best partial information can be recovered, but no reliable baseline information about communities even in the vicinity of the marine station is expected prior to the 1950s and 1960s. Ancillary archives therefore become very important for researching earlier observations. The existence of this documentation depends on the organizational culture at the individual marine station (such as the presence of a library at the marine station, for example).

So what happens when I question the possibility to reconstruct the population dynamics of a small benthic polychaete, *Ditrupa arietina*, with no particular economic interest attached to it? Reconstruction in this case proceeds based on fluctuations in suitable habitat conditions estimated by other factors. The population dynamics of *D. arietina* were rebuilt for two centuries using the North Atlantic Oscillation (NAO) index as a proxy for recruitment success or failure. The results suggested that despite very large fluctuations locally, the population is maintained.

The population dynamics are calculated based on the known life history traits of the species, independently of the observed presence. In this approach any available traces of the presence of the species - at the regional and local scales - can be used to check, or "ground-truth" the population dynamics model. Despite of the scarcity of information, the re-analysis underscores the weakness of earlier studies that have characterized the population as both "extinct" and "invasive" based on anachronistic interpretations by local observers.

Nonetheless, even if this method provides a means to explore the conditions of existence for the species population, it is not robust enough to confirm without additional analyses of habitat and recruitment conditions at particular times in the past. The absence of presence information in earlier literature is confounded by sparse, "accidental" observations (in this case, the shells were remarked on as present in a bottom sample because the researcher found them aesthetically pleasing) and some taxonomic confusion may have occurred between similar looking species from distant taxonomic groups.

These results suggested that the population dynamics approach, as sophisticated as it could be, quickly reaches limits concerning forecasting or hindcasting. Knowledge about the species traits, necessary to simulation variations in abundances (growth, mortality, recruitment ...), seem well established but uncertainties generated a large variability in scenarios that cannot be explained ecologically. From this study case, I began to challenge the notion of population size estimates, which is the key concept of population dynamics.

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[18] Exceptions exist though, see Dybern, (1964). This work was recently re-analyzed and is the object of a new collaboration.

2. Reconstruction of population size estimates

The prerequisite for any population dynamics studies, and the sine qua non condition for their exploitation, is the estimate of population size and their uncertainty. Archeological evidence provides in some cases quite detailed documentation about specific marine populations that were exploited and regulated since the Bronze Age, at least. However, the techniques of harvest and collection used have little or no equivalence today. Because these exploited species have long, even if heterogeneous, documentation histories, they provide grounds for testing different approaches to reconstruct population abundances.

There are several emblematic invertebrate species known to have long exploitation histories. Among these species, perhaps the most interesting example are the muricid species collected to produce a purple pigment that is among one of the most permanent, stable dyestuffs known to date. Species from this group are known to have been exploited on every continent (except Antarctica). Several species were harvested and processed on an industrial scale for centuries, especially in the eastern basin of the Mediterranean.

The history of work at the marine stations suggested that only presence information could be expected within the scientific literature if biogeographical studies were done. These species were viewed as both common and ubiquitous and without any particular interest, apart from as a demonstration species. In addition, because the artificial dye industry arose at the same time as the natural pigment processes were rediscovered by marine biologists in the 1830 - 1850s,[19] the need to determine abundances no longer existed in the heyday of marine stations. Today, although, these same species (*Hexaplex trunculus, Bolinus brandaris*) are targeted in several Mediterranean artisanal fisheries, little information is available about their distribution and abundance. In addition, they are also used for monitoring tributyltin contamination in ports because it causes imposex disorders in female gastropods; but monitoring protocols do not require determining population abundances, only their presence in a particular region.

Therefore, to study the exploitation of these species from the period of the dye industry to their current use in local fisheries, methods of reconstruction based on archeological descriptions that can also be applied to study modern populations should be determined. To do this, I developed a stochastic modelling approach, describing how traditional trapping techniques for muricid species work. The stochastic model was formulated and tested in the field. Integrating behavioral information, this approach has led to the development of a probabilistic method for estimating the expected amount of individuals that could be caught in a specific area (the area of attraction) based on the trap configuration. It provides not only a means to survey cheaply and quickly modern populations, but also a method to estimate the impact of the purple dye industry on Mediterranean and Red Sea gastropod populations during Antiquity.

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[19] de Lacaze-Duthiers (1859), Ghiretti (1994). The aniline dye industry arose, post 1856.

The study has shown how individual behaviors can be taken into account in a method to estimate abundances. It emphasizes the importance of individual variability within groups that have a common specific objective, performing a similar set of 'tasks' (reaching a baited trap). The weakness of the study is the lack of knowledge we have on individual behaviors. The correlated random walk used to simulate the spatial movement of individuals in the vicinity of the bait is likely to be only a crude approximation of the actual individual range of behaviors. Nonetheless, it shows that there is a wide range of possible behaviors for which emergent properties cannot be described by a single population dynamics model. This is probably one of the most important limitations of ecology: when it tries to represent the dynamics of a group of individuals from a common integrated property, while each individual has their own dynamics and interacts with their local environment. Individual-based approaches are not new in behavioral and quantitative ecology,[20] however, they have not been studied from the point of view of the fundamental ecological knowledge they may carry.

3. Recursive analysis to examine laws of co-existence

Having examined different issues regarding the problems encountered in reconstructing populations, the final step in my approach was to look at how sets of fundamental rules allowing prediction of ecological dynamics can be defined. Many insurmountable problems arise with the numerous limitations encountered in the earlier model developments. They addressed particular species for which characteristics - or traits - are more or less known and they are usually not supported by historical sources that may help to assess presence or absence at a particular time or place. This led to re-thinking the theoretical foundation of these approaches. Linking observations to specific interactions outcomes is very challenging because it is difficult to assess the absence and past-presence of species and because interactions do not happen at the population level, but only between individual organisms and within their perceived environment. Therefore, one possible solution was to try to conduct experiments in controlled conditions, generating interactions between individuals of several species, and observe the outcomes.

In the 1930s, G.F. Gause, carried out a series of experiments with the express goal of establishing a law for predicting the outcome of competition between species. Measurement of what he conceived of as "competition" (a process during which individuals of a population try to appropriate resources at the expense of other species) is not directly possible. Therefore, Gause conceived an indirect measure the intensity of the competition based on recording changes in abundance or biomass under different conditions. For this, he fitted a model (inspired by Lotka and Volterra's works) to experimental observations, to estimate inter-specific competition factors that are explicit parameters in the mathematical formulation. Competition among individuals of different populations is interpreted as a potential factor of species exclusion in ecosystems. He intended from the beginning to find a fundamental law

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[20] Interestingly, Haeckel was fascinated by the concept of the individual in his early works (Richards, 2008).

supporting the competitive exclusion within the framework of the struggle for existence proposed by Darwin. After his work became known, it triggered a still on-going debate on the topic of laws in ecology and how to discover, or rather uncover, them.

Since his original data and study have never been fully re-analyzed it seemed to be a good candidate for recursive analysis. To achieve this, it was necessary to rebuild the original model description proposed and published by Gause in a series of papers he compiled in his 1934 book, "The Struggle for Existence". A more modern optimization procedure was applied to fit the model to the observations. Two other models were then built and compared independently to the original microcosm data collected, as well as with each other. The particularity of Gause's model is that it assumes that competition exists and, at the same time, that all sorts of outcomes are possible (co-existence, exclusion, and dominance) for both species. The two models I proposed take into account the resource explicitly, but they do not parameterize competition. The first model represents the hybrid dynamics of the actual experimental protocol (the discrete events are represented by the resource renewals at each 24h cycles). In this model inspired by Herbert's approach, it is not possible to decide whether or not individuals of one species appropriates resources at the expense of the individuals of the second species. However, it shows clearly that the dynamics are controlled by the depletion of the resources suggesting that all individuals starved at each cycle during the experiment. The second model is an individual-based approach representing the assimilation and consumption of food, cell division and mortality of each of the individuals present in the microcosms, according to their traits and according to the food availability. In this model, competition can be explicitly represented when individuals take part of the food from another individual, or prevent other individuals to take 'their' part. It also fits well the data without invoking such mechanisms. In other words, it was possible to represent Gause's experiments without implementing mechanisms of competition at the individual level (from the same species as well as from different ones). Once again, outcomes are consequences of starvation, but it emphasized that individuals have unequal opportunities to feed according to their characteristics.

All models showed that they can simulate the same curves. However, population dynamic models need new parameter estimates for each of the different experimental conditions, while the individual-based model tends to represent all conditions with only one set of individual parameters, and indeed represents the eco-physiological explanations provided by Gause better than the other models.

The results indicate also that part of the frustration from these reconstruction studies arises because fundamental concepts like "competition" and "niche" have not been adequately defined. In other words, the interaction of competition is not being represented explicitly by the data collected and thus not by the model either, while assuming in all cases that the data represent the objective 'truth'. What ecological interactions actually are and how they can be

modeled will certainly need to be reconsidered as new technological solutions for observing the actions-reactions of individual organisms in populations become available.

4. A look at applications of ecological concepts for Environmental Impact Assessment

In this last example, I left the theoretical development aside to concentrate on one of the objectives of ecology regarding societal demands for the application of ecological expertise. Specifically, being able to provide a quantitative tool for impact assessment (that is the effects generated by an infrastructure project implementation or by any kind of regulated economic activity related to living resources). I recall that ecology and impact assessments (as well as conservation) have developed on parallel paths. While ecology promoted concepts based on ecosystems, impact assessment evolved under pressure of regulatory frameworks and tried to find a rationale in statistical inference (such as, setting legal thresholds for the acceptance of the amplitude of perturbations).

To reconcile both approaches, I re-examined the basic concepts in both fields and proposed some new concepts for an ecosystem-based impact assessment. To strengthen the role of ecological concepts, I based my reasoning on a minimum ecosystem model (two populations interacting in a well-mixed environment composed of inorganic nutrients and detrital organic matter) for which the mathematical properties can be characterized. I considered also that socio-economic factors can control this system, not through classical feedbacks, but rather as "drivers of change". The link with statistical impact assessment then becomes straightforward. I found that the response of the system is far from being trivial and the propagation of the disturbance within a network of receptors can provide many unexpected outcomes, which make the work of consulting experts quite difficult outside of a quantitative framework.

The minimum ecosystem formulation is interesting in many applied perspectives, and should be used in experimental studies to consider what impact assessment really characterizes. It can be enriched by individual-based concepts and variability (using stochastic models for example) to test how realistic it could be to represent the dynamics of a controlled bio-reactor. However, the approach deserves additional testing on realistic representations of actual impact assessment situations, in order to be accepted as legitimate.

PERSPECTIVES

Today the world is seen and analyzed in terms of systems. Ecology and ecological principles inform and influence many areas of activity that are extremely different from the intentions of its early contributors. Subjects as diverse as individual cells to global business are interpreted in terms of ecosystems. This concept of "ecosystem" has created an enticing picture of linked systems, working together in seductive and compelling, almost inevitable manner, when associated to other diverted adjectives like "organic". Nevertheless, the real work of transferring description and information from one system to another generates a lot of press but few concrete results.

The roles of fieldwork, experiments, and theory in the development and application of ecological concepts today has been examined from two different points of view. First the importance that reconstruction holds in ecology to rebuild long series of ecological data to study trends. The difficulties encountered with recovering observations and calibrating models led to a complete reconsideration of the theories of co-existence and basic concepts of population dynamics. Second, I argued that most of the difficulties arise because of the absence of a law-based scientific practice in ecology (as well as in biology). This is due to the difficulties of defining adequately concepts and it has a large impact on how we conceive tools to manage marine populations, as well as global issues related to climate change and ecosystem function.

Ecological sciences depend on direct observation to determine presence of species, and on statistical correlations to determine cause and effect in purely phenological approaches. There has been no general consensus about standards or states of reference, and comparative approaches remain atypical. By studying in detail how and when certain concepts in ecology arose, it becomes evident that a key concept - the population of species - was developed at a time when it was impossible to make corresponding calculations, measurements and analyses at the individual level. Thus an important part of theoretical ecology is based on manipulating conceptual objects quite distant from where the actual mechanisms and processes take place (*i.e.* what comes from the interactions between the individual organism and its perceived environment).

Are ecologists ready for such a challenge? The short answer should be: almost. Such a challenge requires developing more fundamental approaches specific to ecology. But we are a long way from developing regular, intensive surveys of ecological systems which can match

with data collected for the weather, hydrologic or oceanographic studies. The complex dynamics of ecosystems require ecological observations as dense and frequent as those collected in other monitoring systems, instead of the usual seasonal or annual sampling schemes. In addition, socio-economic challenges are crystallized by new areas in ecology that aim to develop predictive models of scenarios evaluating ecosystem responses under different societal imperatives (*i.e.* environmental impact, protected areas, pathogen control, among others). A case in point is the Environmental Impact Assessment (EIA). EIAs identify "receptors" for which potential changes are predicted, loosely based on ecological principles about the responses of populations and communities to new conditions. Recent disasters (in particular the 2010 Macondo blow-out and subsequent oil release in the Gulf of Mexico) have shown how ineffective these reports can be. In consequence there is a renewed desire to revise these tools among a new generation of EIA specialists, but an approach which links impact and risk assessment to ecological diagnostic and prognostic is far from being fully developed and accepted.

Finally, the study of the interactions between individuals and their environments has always included considerations about human behaviors and activities. For many decades, debates about impact of human behaviors and activities were limited to understanding plausible effects without possible feedbacks, at least partly because of the uncomfortable political situation in which ecology is often placed. Recent years have seen a rise in spectacular, sensationalistic type headlines about the state of the oceans and biological diversity. Even if we can applaud efforts by some groups to get a message out, this sensationalism may produce unfortunate setbacks when headlines don't connect well with people's actual experiences. I believe ecology has much to learn from the experiences and scientific practice developed by climatologists in this domain. As historical ecology and environmental history develop their own literature, old stereotypes about "natural", "pristine", and "untouched" environments are disappearing. Is the recent attempt to propose frameworks of portable (that is comparable) variables that can be measured both in time and in space to understand the complex dynamics of interacting biological, chemical and physical systems a solution?

Providing the same type of scientific data and forecasting about ecological trends, as climatology provides today, is an important goal for ecological sciences. All during my investigation, I progressively emphasized that ecology is not structured by scientific laws like the disciplines of physics, chemistry and mathematics. Laws in physics and chemistry govern general areas of knowledge about interactions between elements and forces and energy. It is undeniable that laws affect how these sciences are practiced. The repercussions of a scientific practice not structured by laws are starting to be visible now because of the emergence of major social challenges like predicting consequences of changes in biodiversity on the biosphere. All of these challenges require almost immediate responses that ecology cannot provide effectively. Suddenly, ecological scientific practice, which was based on phenological observations, was confronted with a need to understand ecological mechanisms in order to

predict responses. Even the "traditional way" to forecast trends is made very difficult, because of the challenges in recovering earlier data that can be standardized and validated.

The on-going, but often ignored, debate about the existence of ecological laws suggests that the right questions are not being asked. My results point to a problem in the fundamental definitions of the objects of ecology as well as all the concepts of interaction-based processes that were derived from population-based reasoning (competition, invasion ...). Ecological laws should concern the coexistence of different populations (i.e. different species), but coexistence is only an emergent property. Mechanisms should be studied and formalized at the individual level because they are expressed at this level. For instance, when we did a study on bivalve growth, finding a damped oscillator that was interpreted as a compensatory growth mechanism,[21] we have tried to infer a supposed emergent property (which is a common growth pattern) for a mean value, but not the actual mechanism (expressed only at the individual level). To find that the individual growth rate dynamic pattern has significant variability and is even a completely random signal can indicate that an adaptive strategy could modulate growth in a random way, in order to cope better with an unknown variability, that could be forecasted by the individual as many factors are implied (Figure 8-8). Technological advances over the past two decades are at last making possible experimentation and direct measurement of individuals' actions, reactions and interactions. This is probably the *sine qua non* condition for the development of a more functional body of theories (converging toward fundamental laws) in ecology, and would affect strongly how we evaluate and assess impact in environmental management or how we consider evolution at ecological scales.[22]

I have presented (and use extensively) mathematical models as a way to explore ecological systems. Once again, this way to examine natural phenomenon was inherited from physics. I have seen that even if calculation of mathematical properties should be possible for an individual-based model, it is blurred by the random characteristics of individual behaviors, and by the fact that many of these behaviors depart from quantitative functions to become rules-based statements of programming (*e.g.* if ... then ..., or while ... then). Therefore, in ecology, the mathematical efficiency, what Eugene Wigner called "The unreasonable effectiveness of mathematics in the natural sciences"[23] may reach quickly its limit. A second limitation is that ecological reasoning considers that some factors, seen as forces but quite undefined, act beyond individual perception; they condition the choices that are made by organisms, in such a way that it could drive common behavioral outcomes. Yet, individual behaviors could be seen as a very limited perception of their proximal environment. Individuals can have their own trajectory according to particular environmental stimuli. Can this make a law? If many

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[21] Guarini *et al.* (2011)

[22] Today, adaptive dynamics is largely based on a pseudo-mechanistic approach, which is a phenomenological as the rest of ecology.

[23] Wigner, E. 1960 Richard Courant lecture in mathematical sciences, Communications on Pure and Applied Mathematics. 13: 1–14.
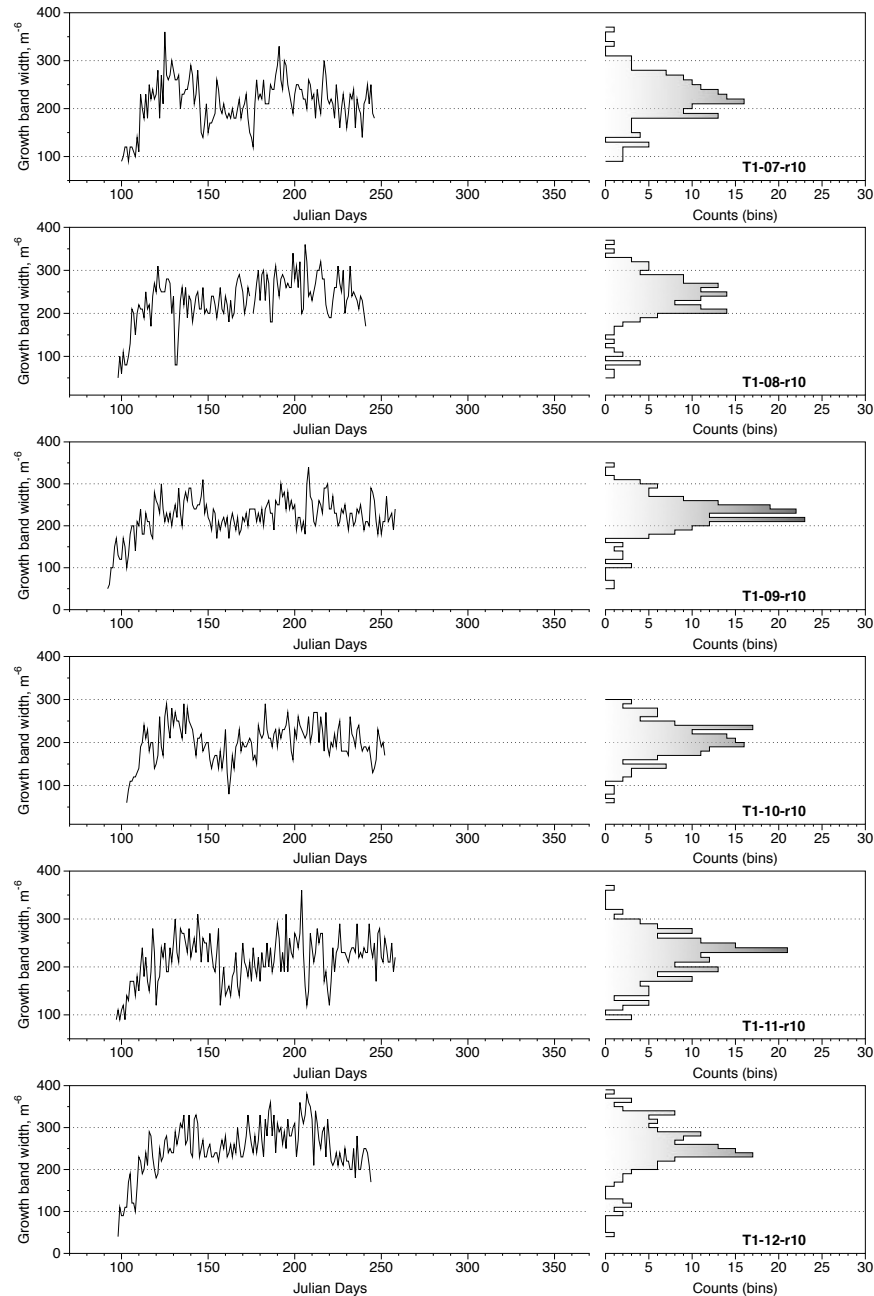
FIGURE 8-8. Example of how approaching ecological studies from a predictive perspective changes scientific practice. These are plots of the daily growth record from *Pecten maximus* individuals at one site sample in the Bay of Seine (France). The minimum detectable change in width is 10 micrometers (histograms on right show the distribution of values). This group of individuals is assumed to be representative of a reference state in the original study design.

Sclerochronological protocols rely on the relative change between measured daily growth bands of calcium carbonate mineral accumulated at the edge of the shell. Measurements are made across the shell surface without accounting for the shell spiral and then the means of data like these are reported as evidence of ecological trends. However, the use of means makes an explicit assumption that the changes between individuals are correlated: there is no basis for this. Indeed these curves exhibit random behavior. If comparisons will be made in space and time (as for an "observatory") an approach based on a theoretical representation of the growth morphodynamics will be required.

From Coston-Guarini, J. *et al.* in preparation.

stimuli are sent to each of the individuals with different intensities, will they organize themselves or start to have a random (dispersed) sets of trajectories? How can this govern dynamics?

These studies have generated many more questions than they have answered. But, in all cases, I believe that individual-based studies should be at the center of theoretical ecological preoccupations. I believe also that experimental work (together with modeling efforts) should the first step in these studies. I am not forgetting natural history and ecosystems, but seeking to understand of their complexity should be considered based on the proximal sensorial perception of individuals, that is where the interactions happen. This is the one framework that could help progress toward laws that ecology needs to consolidate and to finally win its autonomy from other disciplines, as Marc Lange suggested.

FIN

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PART IV. Supplementary data

SUMMARY

These four tables contain the supplementary data for Chapter 3. These were graphed in Figure 3-3 and also appear in Tables 3-3, 3-4.

Tables A, B contain the data from Buffon's Histoire Naturelle.

Table C contains the data from Darwin's 1859 edition of the Origin of Species.

Table D contains data downloaded from Wikipedia on scientific laws.

Data tables not included in this version

La valeur épistémologique de l'information historique en écologie et conservation marine

Coston-Guarini, J. (2016)

RESUME court

Ce projet explore la valeur épistémologique des collections historiques pour aborder des questions scientifiques actuelles sur les changements environnementaux dans les écosystèmes marins. Le challenge principal est de pouvoir caractériser le processus d'assimilation des connaissances dans un champ scientifique particulier, l'écologie. Les réseaux émergents de collections de données et d'objets permet l'exploration de questions sur comment le contexte historique a pu biaiser les observations qui sont utilisées maintenant pour analyser les tendances écologiques et environnementales du passé. Cette démarche devrait permettre in fine de contribuer à l'amélioration de nos connaissances sur la dynamique des réponses des systèmes écologiques. Plusieurs exemples différents sont traités en détail, couvrant le contexte historique de la recherche dans les stations marines et l'examen récursif des concepts de base en écologie tels que la dynamique des populations, la théorie de l'exclusion compétitive, et l'estimation de l'impact sur l'environnement.

Epistemic values of historical information in marine ecology and conservation

Coston-Guarini, J. (2016)

condensed ABSTRACT

This project explores the epistemic value of heritage collections for addressing modern scientific questions about environmental change in marine ecosystems. The main challenge is to investigate processes of knowledge assimilation within a specific scientific discipline, ecology. Emerging networks of data and object collections permit addressing questions about how historical context may bias observations used for analysis of ecological and environmental trends. The main goal is to synthesize historical concepts and data using meta-analysis and recursive techniques to reconstruct ecological trends. It is hoped that this will ultimately contribute to improving our understanding of the dynamics of ecological systems responses. Several different examples are treated in detail, covering the historical context of research work in marine stations as well as a critical re-examination of basic ecological concepts of population dynamics, competitive exclusion, and the estimation of environmental impact.