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The early limnological tradition as an ecological resource: a historical account between Europe and the United States of America on the concept of the organism-environment relationship

Pier Luigi Pireddu

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ABSTRACT

This paper proposes that lake ecosystems have historically provided fertile ground for the advancement of ecological concepts. It argues that foundational ecological ideas, such as ecosystems and the organism-environment relationship, have their roots in limnology, the scientific study of lakes. In other words, these concepts were developed by approaching lake ecosystems as primitive ecological models. To illustrate this point, it examines the scientific endeavors of François Forel (1841-1912) in Geneva, Switzerland, and Stephen Forbes (1844-1930) in Illinois and Wisconsin, United States. Both were pioneering figures for the development of the limnological or, even more broadly, the ecological discipline. Curiously, they contemporaneously developed their respective scientific accounts in two different scientific traditions.

Keywords: history of ecology, limnology, ecosystem, François Forel, Stephen Forbes

ARTICLE

Introduction

The history of limnology has been widely addressed, especially concerning the Anglo-American context (McINTOSH 1985; EGERTON 2015). However, this paper aims to discuss the conceptual establishment of the organism-environment relationship within the nascent limnological tradition. It provides an account of the first limnologists active between Europe and the United States, analyzing their early ecological works. In particular, the efforts of Stephen Forbes and François Forel are given historical contextualization, as well as Edward Asahel Birge and Chancey Juday. While the American case has

Pier Luigi Pireddu is a doctoral candidate at the Interuniversity Centre for the History of Science and Technology (CIUHCT) in the Faculdade de Ciências of the Universidade de Lisboa (Portugal).

been widely studied, the same cannot be said of its European counterpart. To address the topic, I will first attempt a historical account of the limnological tradition to provide the general context of analysis. Then, I will discuss the work of Forel, the founder of limnology, focusing on his scientific production. The third part is dedicated to Forbes's limnological studies, some of the best-known works in limnology. Finally, I provide a discussion, highlighting ways that the concept of organism-environment relationship was approached in this early limnological tradition. I argue that the discourse emerging from this context can offer insights into the formulation of the ecosystem concept. Moreover, I contend that it clarifies essential aspects of the ecological discipline. Therefore, this article aims to shed light on these aspects, revealing lesser-known scientific writings and offering a comparative view between these two scientific contexts.

1. The early limnological tradition: historical notes

The first rigorous scientific work on the lacustrine system was provided by F. Forel, who also coined the term "limnology" in 1892 (EGERTON 1962). From his early works, carried out during the late 1860s, emerged the tendency, common in those years both to limnologists and oceanographers, to highlight how biological phenomena are closely related to physical and chemical factors. In particular, limnology began with Forel's publication of the paper *Introduction à l'étude de la faune profonde du Lac Léman* (1869), although his first study was three years earlier (FOREL 1866). Forel was a Swiss scientist, and his bibliography lists 126 titles for limnology. His main work is the three-volume *Le Léman*, published between 1892-1904. The work is structured as follows: the first part (1892) includes geography, hydrography, geology, climate, and hydrology; the second (1895) refers to other physical factors useful for the study of lakes, such as temperature, optics, acoustics, and chemistry; and the last volume (1904) is devoted mainly to fauna. From Forel's work emerges the importance and constant consideration of physical and biological factors for a complete understanding of lake phenomena. It is in this volume that it is possible to find both the first definition of limnology and the introduction of the term. Indeed, Forel observed:

> I have not been able to call my study limnography because the word limnograph is already appropriated for some instruments used in lake measurements; therefore, I have coined limnology. Limnology, then is the oceanography of lakes (FOREL 1892, vi, in EGERTON, 2015).

Forel carried out his research in Europe, primarily on Lake Geneva (or Lac Léman), laying the foundations for later limnological research (EGERTON 2014; CAMPANELLA 2016). Also in Europe, but this time in Germany, operated a second prominent scholar in the novel limnological field: August Friedrich Thienemann (JAX 1998; EGERTON 2015; BERG 2017). Thienemann started his research activity in 1909, delving into benthonic fauna and publishing his first works after traveling the continent (THIENEMANN 1913, 1920, 1922, 1939). Notable for his classification system of lakes, he made a significant contribution through a volume published in 1925, entitled *Die Binnengewdsser Mitteleuropas*, which was reviewed by C. Juday (1926). In this work, Thienemann (1925) analyzed the hydrobiological properties of the lacustrine environments in central European lakes, considering their physical, chemical, and biological features.

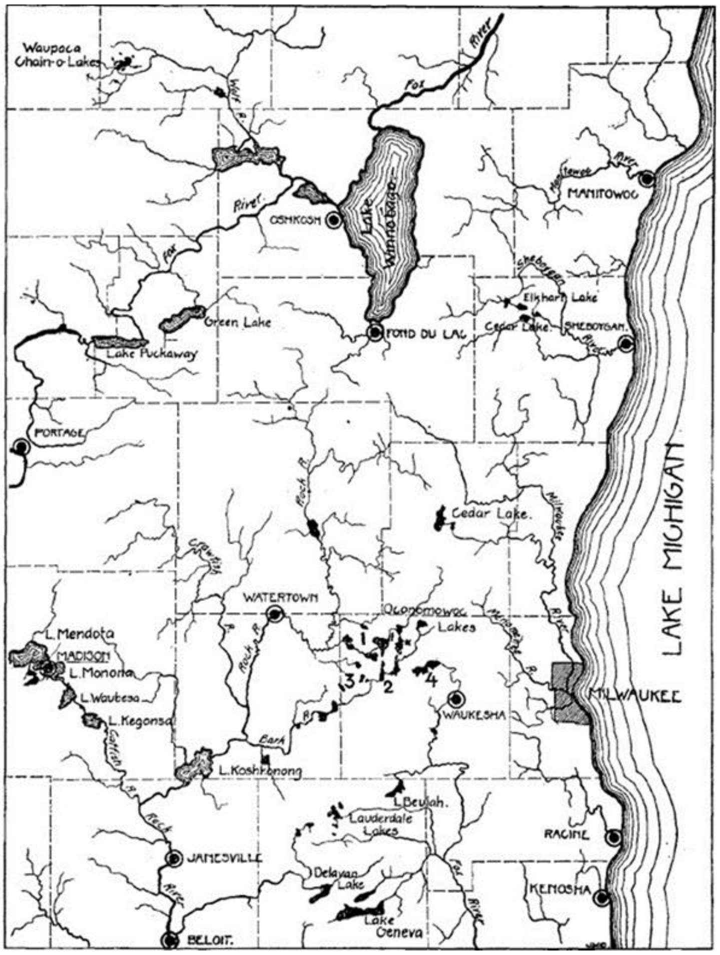

Figure 1: Map of Southeastern Wisconsin, with the principal lakes and lake districts. (BIRGE and JUDAY 1911: 24)

As concerns the United States of America, limnology began with the work of S. Forbes and his classic article *The lake as a microcosm* (1887). Here, he developed an account of a lake system as a complex unit of interactions, with all its components deeply interconnected in terms of biological and environmental factors (McINTOSH 1980; FROST et al. 1999). Forbes participated in the foundation of the Illinois Natural History Survey (today known as the Illinois State Laboratory of Natural History) and occupied its leading position from 1917 to 1930. Further development in the USA was made possible through the work of Birge and Juday, active during the late nineteenth and early twentieth centuries (McINTOSH 1985; LEHMAN 1986; FREY 1966). Conducting their research mainly in the Wisconsin area, they believed that a collaborative effort aimed at integrating several disciplines for the study of lake systems could provide a comprehensive understanding of the lacustrine environment (BIRGE & JUDAY 1908, 1911, 1929). As had Forel, Forbes, and Thienemann, they promoted a field-research approach. Around them coalesced a school of limnology with a scientific production counting more than 400 publications. Their first comprehensive work was *The inland lakes of Wisconsin: the dissolved gases of the water and their biological significance* (1911). Here, the authors organized and developed an account of these lakes considering biological, physical, and chemical components. It was the scientific output of a substantial collaborative effort, by different experts from different fields, and the result of a long period of research, started in 1904, carried out at more than 150 lakes (fig. 1).

According to McIntosh (1985), aquatic bodies are more evidently physical systems than terrestrial systems. Limnology, given the very nature of the lacustrine environment, forced a scientific conceptualization that confronts the fundamental interaction between biotic and abiotic factors. This tendency is explicit in the scientific writings of the early limnologists: Forel and Forbes. In contemporary literature, several publications consider and discuss the history of limnology (WORSTER 1977; HAGEN 1992; GOLLEY 1991, 1993; COOPER 2003).

2. François Forel: the beginning of limnology in Europe

In Forel's seminal article, *Introduction à l'étude de la faune profonde du Lac Léman* (1869), the organisms inhabiting the lake bottom were addressed, followed by a discussion of how there could be living beings in that zone. He considered such organisms ("deep fauna") to be a kind of "special fauna" and tried to provide insights on the matter, writing:

> The fact is that the lake's mud is inhabited by a special fauna, quite rich in species. I say special fauna, and I must justify these words. The environmental conditions these animals inhabit in the lake are strange enough to allow me to claim that they represent a special fauna, which I shall call the lake's deep fauna (FOREL 1869, 217, author's trans.).[1]

It was the odd environmental conditions that lead him to call such fauna "special"; indeed, high pressure, constant temperature, and the absence of motion and light make this environment very severe. This contribution marked the first attempt to understand the dynamics behind the organisms living in such environmental conditions (CAMPANELLA 2016). Forel's discovery of this "deep society", in 1869, came just three years after Haeckel's (1866) definition of ecology.

Such inquiry into deep fauna is thus characterized as Forel's first scientific approach to Lake Leman (fig. 2). In 1872, he deepened this research and provided a more complete picture in two further works: *La faune profonde des lacs suisses* (1885) and *Le leman* (1892-1904).

Forel arrived at treating the diversity of fauna within a lake system by distinguishing three areas with different characteristics and properties: namely, the coastal, pelagic, and deep regions. As Forel explained:

> Environmental conditions are sufficiently different in the various regions of the lake that animals and plants living in one zone are unlikely, except in accidental cases, to be found in

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[1] Original French:

> Le fait est que la vase du lac, à de grandes profondeurs, est habitée par une faune spéciale, assez riche en espèces et très nombreuse en individus. Je dis faune spéciale, et je dois justifier ces mots. L'on appelle faune l'ensemble des animaux qui vivent en commun dans des conditions de milieu identiques ou analogues; or les conditions de milieu dans lesquelles se trouvent ces animaux sont assez étranges et assez différentes de celles de toutes les autres faunes, pour que a priori je puisse prétendre qu'elles caractérisent une faune spéciale que j'appellerai faune profonde du lac.

another; we must therefore recognize distinct local faunas and flora (FOREL 1885, author's trans.).

On the other hand, it is to be stressed that Forel saw these three zones as deeply interconnected, and not as distinct blocks with discrete and isolated dynamics. He noted:

> From the point of view of this cycle of organic matter utilization, what is particularly interesting in our lake faunas is the necessary relationship between the pelagic and the deep region; while it is generally on the spot that organized matter is used for animal feed, in lakes, materials organized on the surface are used in the deep region. Pelagic fauna feed on material assimilated at the lake surface. When the pelagic entomostracans die, their bodies are deposited in the lake bottom, where they serve as food for the deep fauna. They carry the food assimilated at the lake surface by the small pelagic algae. Accordingly, the existence of pelagic fauna and flora are essential and indispensable conditions for the maintenance of deep fauna (FOREL 1885, 159, author's trans.).

Figure 2: *Le Leman* (FOREL 1892).

The basic assumption here, which echoes the fundamental concept of the organism-environment relationship, is that to certain environmental conditions correspond a certain flora and fauna. This discussion by Forel highlights two essential ecological ideas, which provide an important theoretical framework for defining how early limnological studies of pelagic and deep fauna contributed to the development of the scientific debate. The first issue concerns the organism-environment relationship. The second issue concerns trophic relationships among organisms.

In this context, a less-known article by Forel (1888) provides further insights. Focusing on the problem of deep fauna and trying to address the complexity of organisms living in an extreme environment (FOREL 1885, 1892), Forel called the attention of the scientific community to the pelagic fauna in a brief article – entitled *Les micro-organismes pélagiques des lacs de la région subalpine* (1888). Within this framework, Forel noted that the regions of the lake, each one with specific environmental conditions, were the components of a larger system.

Moreover, Forel (1888) specified that within the lake systems, there is an exchange of organic matter between organisms. He contextualized this point by highlighting the cycle of matter within the lacustrine system. In particular, Forel observed that the pelagic fauna is vital to understanding the cycles of living matter between organisms living in different areas of the lake. For Forel,

> These discoveries are precious, they give us the missing links that we lack to understand the cycle of the circulation of organic matter, between dead nature and living nature, in our lakes. These considerations on the circulation of organic matter between beings are not special to our lake; they are analogous to those that the study of any district of nature provokes. But they are new to us, who have only recently come to know the population of these transparent waters, which were supposed to be deserted or little inhabited until now. Perhaps also, with other titles, they will interest naturalists who deal with the problems of life in other regions and in other conditions of the environment (FOREL 1887, 172, author's trans.).

From a limnological point of view and, even more broadly, from an ecological point of view, this type of approach stands out in its concern with the interrelated dynamics of the various components of the lake system. Moreover, the account that Forel proposed is essentially characterized by the intimate correlation it draws between the organic and the inorganic components. Indeed, trophic relationships among the different layers of the system are pointed out repeatedly. These conceptualizations are possible only if the fundamental concept of the organism-environment relationship is undertaken from a scientific point of view.

This idea of the lake as a holistic system of interactions, and as a complex functional unit, arose almost contemporaneously in the American scientific milieu, to which I now turn.

3. The concept of microcosm: Stephen Forbes

Forbes (1887) emphasized the interdependence of lacustrine phenomena, not just the complex web of biotic interactions among the organisms living there but also the impact of the physical circumstances of the environment. The consequence of this interdependence is that a part of the aquatic system could not be addressed in isolation from the whole. Forbes stressed this concept at the beginning of his article, stating, "I now propose to give you in this paper a brief general account of the physical characters and the fauna of these lakes, and of the relations of the one to the other" (FORBES 1887, 540). Moreover, for the purpose of this work, it is worth noting a key point Forbes sought to transmit:

> The animals of such a body of water are, as a whole, remarkably isolated – closely related among themselves in all their interests, but so far independent of the land about them that if every terrestrial animal were suddenly annihilated it would doubtless be long before the general multitude of the inhabitants of the lake would feel the effects of this event in any important way. […] It forms a little world within itself – a microcosm within which all the elemental forces are at work and the play of life goes on in full, but on so small a scale as to bring it easily within the mental grasp. […] Perhaps no phenomenon of life in such a situation is more remarkable than the steady balance of organic nature, which holds each species within the limit of a uniform average number, year after year, although each one is always doing its best to break across boundaries on every side. (FORBES 1887, 537).[2]

Two essential concepts emerged from Forbes's account. First, ecological systems are complex systems of interactions, where influences occur not only between organisms themselves, but also through abiotic elements. Second, there is an organic unity or equilibrium that emerges at the level of the microcosm (COOPER 2003). Such a complex system of interrelationships, involving not only the organic domain, but also environmental factors, implies the impossibility of isolating one component from the broader network of relationships within which it is embedded. The several parts of an aquatic system, in this case, should be analyzed according to the whole system (LEFKADITOU & STAMOU 2006; LEFKADITOU 2010). From here emerges the necessity of treating the functioning of the whole lake system as a whole, and not just as singular components (GOLLEY 1993). Forbes pointed out that it is imperative to consider the entire mechanism of aquatic life, addressing both the physical characteristics and the fauna, as well as their mutual relationships. This complexity comes through in his influential paper of 1887, where he remarked:

> Nowhere can one see more clearly illustrated what may be called the sensibility of such an organic complex, expressed by the fact that whatever affects any species belonging to it, must have its influence of some sort upon the whole assemblage. He will thus be made to see the impossibility of studying completely any form out of relation to the other forms; the necessity

[2] This concept appears in Forbes's scientific writings, in a previous article; according to him: "one finds in a single body of water a far more complete and independent equilibrium of organic life and activity than in any equal body of land. It forms a little world within itself – a microcosm within which all the elemental forces are at work and the play of life goes on in full" (FORBES 1880, 19). Moreover, this concept of the lake as a microcosm has been reconsidered by G. E. Hutchinson (1964).

for taking a comprehensive survey of the whole as a condition to a satisfactory understanding of any part (FORBES 1887, 537).

The view of the lake as a microcosm, embracing the whole complexity of physical and chemical factors of the environment as well as the properties of the biota, became a principal characteristic of the ecosystem concept. In a sense, it anticipated the notion that Tansley (1935) systematized almost 50 years later, outlining the concept of ecosystem (for further insights, see Tansley (1935), Clements (1905, 1916), and J Phillips (1934, 1935a, 1935b)). Indeed, Forbes's microcosm recalls the essential holistic aspects of the idea of a complex system, where biological and physical-chemical components of the environment are integrated into a single ecological unit. Forbes's scientific account of the lake as a microcosm defined the lacustrine ecosystem as a discrete unit whose constituent parts, although distinctive, were inextricably interrelated.

Final discussion

This paper has provided examples from early limnological accounts for two main purposes: to illustrate how the concept of the organism-environment relationship took shape in the tradition, and to show how it was at the core of limnological investigation during the second half of the 19th century, when the discipline was starting to systematize. It has stressed the fact that the assumption of a fundamental organism-environment relationship was central to the research of early limnologists, because understanding these dynamics allows us to trace, historically, the conceptual roots of modern scientific notions such as the ecosystem concept. The cases offered here demonstrate that the limnological tradition was an important channel to the ecological framework of inquiry.

This paper aims to point out that two pioneers of the limnological tradition during the 19th century worked within a specific framework that looked at the relationship between organisms and the environment as a scientific/conceptual entity. In other words, it was possible to study those relationships through scientific practice and individualize the terms that can consider this mechanism. In one case, Forbes (1880, 1887) described the lake system as a microcosm, where organisms and the environment, being part of the same ecological unit, are interconnected with each other. On the other hand, Forel understood that the several areas of the lake are not isolated realities, but there is a deep relationship. Moreover, since organisms inhabiting the different areas are under different environmental conditions, he individualized the cycles of organic matter between them (FOREL 1885, 1888, 1892-1904).

It is worth briefly outlining the characteristics of some of the models adopted in the limnological tradition, focusing on the proposals of Forbes, Forel, and other American and European limnologists. These ideas can be juxtaposed against the analogous assumption Tansley emphasized 1935, who remarked, "When we are trying to think fundamentally we cannot separate them [the organisms] from their special environment, with which they form one physical system", allowing us to retrace the roots of his influential conceptualization (TANSLEY 1935, 299).

Forbes's model, like those of Forel, Thienemann, Birge, and Juday, tends to emphasize the role of abiotic factors, thus stressing both the physical and biological conditions of the lake. Curiously, Forel used the concept of the microcosm to describe Lake Leman, although it is not certain that he read Forbes, who coined this expression some years before him. This suggests the power of such a conceptualization. The throughline is clear: using the microcosm concept, it is possible to point out the idea of wholeness, of joint parts forming a whole single entity where all the components are related to each other. In this sense, the organism-environment relationship emerges as a holistic structure. This lay the theoretical ground for Tansley (1935) and, in a more consistent manner, for Hutchinson (HUTCHINSON & WOLLACK, 1940; HUTCHINSON, 1941, 1948) and Lindeman (1942).

It was first with Birge and Juday in the USA and Thienemann in Europe, and finally with Hutchinson, that an essential integration of biological and physical-chemical components of the environment found a complete ecological picture (PIREDDU 2023). The so-called biogeochemical approach offered a consistent scientific framework for the study of lacustrine ecosystems (HUTCHINSON & WOLLACK, 1940). Biogeochemistry became a central feature of the ecological field, first with Hutchinson (1938, 1941, 1944) and then with Eugene (1953) and Howard Thomas Odum (1950).

Ecology is the scientific study of natural systems, focusing on the intricate relationships between biotic and abiotic components. This essay presented evidence suggesting that early ecologists studying lake ecosystems had a rudimentary understanding of the organism-environment relationship.

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