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LORENZO CAMERANO'S CONTRIBUTION TO EARLY FOOD WEB THEORY

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INTRODUCTION

> When you first learn science, you want to know the facts. You want to know Mendel's laws, though you don't really care who Mendel was. Later, if you go on to do research, it's quite important to know the history of your field. ... Research students who know the past have a decided advantage over those who don't.
>
> James D. Watson, in Campbell (1986, p. 730)

In 1880, Lorenzo Camerano, then a 24-year-old assistant in the laboratory of the Royal Zoological Museum of Torino, Italy, published a paper "On the equilibrium of living beings by means of reciprocal destruction" in the *Acts of the Royal Academy of Sciences of Torino.* This pioneering paper contains an early, perhaps the first, graphical representation of a food web as a network of groups of species linked by feeding relations. It also contains a vivid dynamic model of the consequences of trophic links for population dynamics. The model is based on the propagation of sound waves in an organ pipe. An English translation of Camerano's paper follows this introductory essay.

The purpose of this introduction is to summarize briefly Camerano's life and work, to place his 1880 article in the context of his other works, and to relate his paper to earlier and later works of others.

A BRIEF LIFE OF CAMERANO

The following summary of his life relies largely on the memoir of Rosa (1919). Camerano was born April 9, 1856, in Biella, at the foot of the Alps in northern Italy, and died in Torino November 22, 1917. His father was a functionary of the Piedmont prefectorial government. With his father's job, the family moved to Torino, where Camerano studied at Liceo Gioberti and enrolled in the School of Painting at Accademia Albertina. Among his school friends were Camillo and Mario, sons of Michele Lessona, a Member of the Royal Academy of Sciences of Torino since December 1, 1867.

On February 14, 1874, Camillo and Mario asked Camerano if he would make some drawings their father needed for zoological demonstrations. After school, Camerano went with them to meet their father at the Museum of Zoology, then located at the Academy of Sciences. The elder Lessona was an "ingenious proponent of the theory of evolution, at a time when this excited passionate conflict" (Rosa 1919, p. 688). Camerano fell under Lessona's spell and, in many ways, followed in his footsteps. Camerano eventually married Lessona's daughter Luigia.

On June 24, 1877, Camerano's first publication was approved for publication in the *Acts of the Royal Academy of Sciences of Torino*. Written when Camerano was a student in natural sciences at the University, it dealt with the polymorphism of females of the species *Hydrophylus piceus*. In 1878, Camerano received his "laurea" degree and was named an assistant in the Zoological Museum of the Royal University of Torino. Two years later, Camerano received the degree of "Dottore aggregato" in the Faculty of Sciences of the University. That same year, Lessona introduced Camerano's paper "On the equilibrium of living beings" for publication in the *Acts of the Royal Academy*.

Camerano's last publication, dated May 21, 1917, appeared in the *Bulletin of the Museum of Zoology and Comparative Anatomy of the Royal University of Torino* and dealt with researches on the subspecies of *Capra sibirica* Mayer. Camerano was then president of the Royal Academy of Sciences of Torino (following Lessona, who had been president from 1889 to 1895) and a Senator of the Kingdom. He died a few months later. His bibliography contains 341 items (Rosa 1919, pp. 714-736).

CAMERANO'S 1880 PAPER IN RELATION TO HIS OTHER WORK

Camerano's early papers were largely descriptive. They were often well-illustrated but showed little inclination towards abstraction or generalization. A year before his 1880 paper, Camerano (1879) published his first major book (344 pages) on entomology. Two years later, he (1882a) published another book (252 pages) on the anatomy of insects. Few of his later papers had titles as titillating as his 1884 essay on "Anomalous loves of the amphibia" (Camerano 1884), published in *Archives of Psychiatry*. Some descriptions are accompanied by attempts to construct phylogenetic trees. He published in Italian, Latin, French, German, and English in journals originated all over Europe.

Camerano's 1880 essay, which follows, appears to be unique in his oeuvre with regard to the abstraction and generality of its ideas and its illustrations. There are two central ideas. First, the abundance of each plant, phytophagous animal, carnivore and parasite has a natural equilibrium level, and this equilibrium is maintained through feeding relations or, in today's language, trophic links. Second, when the abundance of any component of a natural community is perturbed from its equilibrium level, the perturbation propagates along the food chains much as the perturbations from equilibrium of a sound wave propagate along the length of an organ pipe. These two ideas are

illustrated in differing degrees of detail, and with characteristic redundancy, in plates I and II, and in plates III and IV, respectively.

It appears that the 1880 paper was a one-time flight of fancy for Camerano. Though I have not examined every one of his publications, I saw figures like these nowhere else in his work. In two later papers on themes closely related to that of his 1880 paper (Camerano 1882b, 1885), he cites this 1880 paper and repeats the argument of an equilibrium in which perturbations from equilibrium are linked through feeding, but does not repeat any theoretical pictures. No similar pictures appear in a bound volume that contains a complete collection of his works published in the *Bulletin of the Museum of Zoology and Comparative Anatomy of the Royal University of Torino* (Camerano 1886-1917).

The central ideas of Camerano's 1880 paper appear to be closely related to contemporary ideas and graphic devices of Darwin and Helmholtz. Among Italian biologists, as among biologists everywhere, Darwinism was ascendant. Michele Lessona, Camerano's mentor, was a leading proponent of Darwinism in Italy and had translated *Origin of Species* into Italian. According to Camerano's (1902) review of biology in the nineteenth century, the Royal Academy of Sciences of Torino in its session of December 28, 1879, awarded Charles Darwin the first of the grand prizes of the Bressa Foundation. Though Darwin is not cited in the 1880 essay, Camerano refers to the "struggle for life", a phrase that suggests Darwin's "struggle for existence". The first edition of Darwin's *Origin of Species* (Darwin 1859) contains a single illustration, a plate inserted between pages 116 and 117, which illustrates the principle of divergence in phylogenetic trees. The visual image (Figure 1) of divergent treelike branching is remarkably similar to that of Camerano's first plate. There is one important difference. Darwin's phylogenetic tree is crossed by horizontal lines that suggest geological strata, time progressing from bottom to top. By contrast, Camerano's first plate is marked by concentric rings expanding outward from vegetation. The rings suggest the propagation of perturbations along a food web, by analogy to the propagation of sound waves.

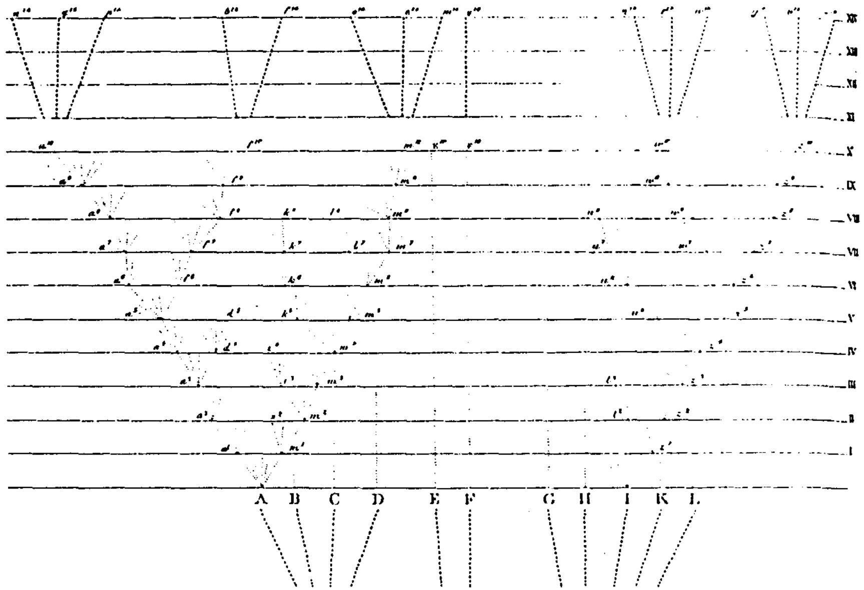

FIGURE 1.

Three years before Camerano published his essay, Helmholtz (1877) published the fourth and last German edition of his great book *On the Sensations of Tone as a Physiological Basis for the Theory of Music*. Helmholtz described the vibrations of sound by means of a graphical device (Figure 2), with a horizontal line indicating equilibrium, and small vertical lines above or below the horizontal indicating deviations from equilibrium, that is remarkably close to Camerano's plates III and IV. .

It is tempting to speculate that the graphics of Darwin and Helmholtz provided the inspiration for Camerano's graphic representations of the connections and mutual perturbations of groups of species in a natural community. But the graphics of Darwin and Helmholtz do not explain why Camerano adapted them to ecological purposes. I speculate that Camerano's childhood artistic inclinations and training led him to seek a visual representation of the population-dynamical

phenomena he observed in his entomological field work, and that he adapted the graphical ideas available to him at that time.

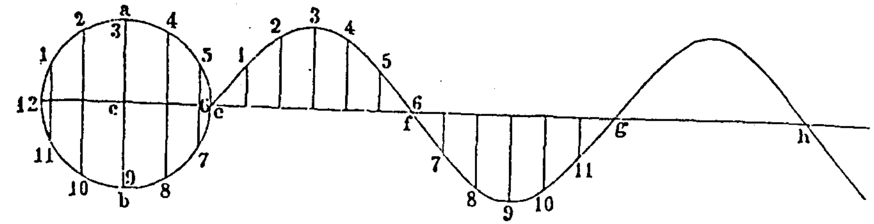

FIGURE 2.

Another recurrent motif of the 1880 essay is that the equilibrium among different kinds of organisms is maintained, and re-established following disturbance, by the organisms and the habitat "without any action of man". Camerano may have had practical or scientific motives in emphasizing this theme. Given the contemporary influence of agricultural entomology, he may have been trying to show that many interventions in nature by applied zoologists were not really necessary. Or, as a question of pure science, he may have sought to remove man's throne from ecology just as Darwin removed it from evolution.

THE HISTORICAL SETTING OF CAMERANO'S 1880 ESSAY

Camerano was not the first to try to describe the food of animals, either in a general way or exactly. He cites papers by agricultural entomologists, published in the 1870s, which described the feeding habits of insects and birds in agricultural areas. But nearly half a century earlier, in February, 1832, Darwin (1839, p. 10) described the food web of St. Paul's Rocks near the equator in the middle of the Atlantic Ocean, and remarked with surprise on the apparent absence of plants. The notion that the abundance of each species has a natural equilibrium level maintained through feeding relations apparently also did not originate with Camerano. According to D'Ancona (1954, p. 20), "Moebius, 1877 [unfortunately, the citation is missing from the bibliography]... recognized the importance of interspecific nutritive relationships while he was studying the organisms living on the oysterbeds of Schleswig-Holstein. To Moebius is due also the credit for noting that the effect of these interspecific relationships is to establish a state of equilibrium."

In America, detailed quantitative studies of the diet of birds, fishes, and insects were already well under way by 1880. Forbes ([1878-1883] 1977), in papers published from 1878 onwards, cites several works on animals of the Great Lakes region published in the decade or so prior to his own works, and gives numerous quantitative tables of food taken by different consumers, in a format now called a predation matrix or feeding matrix. Some ideas of Forbes and Camerano show remarkable convergence. Forbes (1880a, p. 3) states the theme of a theoretical essay thus: "The serious modification of any group [of organisms], either in numbers, habits, or distribution, must modify, considerably, various other groups; and each of these must transmit the change in turn, or initiate some other form of change, the disturbance thus propagating itself in a far extending circle." Introducing his empirical work on the food of birds, Forbes (1880b, p. 84) states:

> Now a species is stable because the rate of its reproduction is uniform, because the checks upon its increase are substantially unvarying, and because these two forces balance each other. To set up any vibration in any one of these checks, will necessarily cause a corresponding vibration in the numbers of the species limited by it. More explicitly, to set up an oscillation in a predaceous or parasitic species must produce a reverse oscillation in the species parasitized or preyed upon. As the former increases, the latter must diminish, and *vice versa*. But either a marked decrease or a marked increase of a species will cause it to oscillate, unless made with extreme slowness, a slowness so extreme as to allow progressive adjustments of all kinds to keep pace with it.

The 1880 papers of Forbes and Camerano clearly share the ideas of a natural equilibrium population level maintained through checks by food supplies and consumers, and the propagation of perturbations along food webs. The last sentence quoted shows Forbes's awareness of the importance of the rate of change of population abundance. Forbes (1880a, p. 11) also remarks on a relation between the connectivity of food webs and the stability of communities:

> It is a general truth, that those animals and plants are least likely to oscillate widely which are preyed upon by the greatest number of species, of the most varied habit. Then the occasional diminution of a single enemy will not greatly affect them, as any consequent excess of their own numbers will be largely cut down by their other enemies, and especially as, in most cases, the backward oscillations of one set of enemies will be neutralized by the forward oscillations of another set. But by the operations of natural selection, most animals are compelled to maintain a varied food habit,-- so that if one element fails, others may be available.

Nevertheless, none of the reprinted papers of Forbes ([1878-1883] 1977) contains a food web graph. Camerano's introduction of the food web graph appears to be a genuine innovation.
That innovation was evidently not noticed for some time. The earliest citation in the bibliography of D'Ancona (1954; first German edition 1939) is to Camerano (1880), but the reference in the text (D'Ancona 1954, p. 26) makes no mention of the food web graph. The development of food web data, concepts and representations that included Camerano, Forbes and D'Ancona seems to have

been generally ignored recently. For example, Worster's (1977) history of ecological ideas cites none of these three writers in its index and traces food webs and food chains no further back than Charles Elton (see Worster 1977, pp. 295-298). D'Ancona and Forbes, but not Camerano, are cited by Kingsland (1985). Elton (1927) refers to neither Camerano nor Forbes in what is hardly the only instance when an English writer has overlooked the work of continental and American scientists. It seems likely that food web graphs had to be invented several times before their general use became established. Food web graphs are not unique in this respect (Merton 1961, 1965).

CAMERANO'S IDEAS TODAY

Generalized food web graphs in which large numbers of functionally similar species are lumped together in broad categories such as plants, herbivores, and carnivores have become standard illustrations in introductory ecology texts. Though they are pedagogically useful, such pictures are no longer acceptable as data for analyses of food web structure (Pimm, Lawton and Cohen 1991).

Camerano's and Forbes' descriptions of the propagation of disturbances from equilibrium along food chains resemble remarkably the cascade model of population dynamics in lakes developed recently by Carpenter and colleagues (e.g., Carpenter, Kitchell and Hodgson 1985; Carpenter 1988). "[W]e consider a lake food web that includes limiting nutrients and four trophic levels: piscivores such as bass, pike, or salmon, zooplanktivores, herbivorous zooplankton, and phytoplankton... Simply put, a rise in piscivore biomass brings decreased planktivore biomass, increased herbivore biomass, and decreased phytoplankton biomass" (Carpenter et al. 1985, p. 634).

Camerano did not develop further his 1880 symbolic formalism for the propagation of disturbances from equilibrium along a food chain, and others seem to have overlooked his suggestion. The development of a coherent formalism for the interactions Camerano described had to await the work of Lotka (1880-1949) and Volterra (1860-1940).

Oksanen (1991) pointed out that some insights of another early ecologist, the Finn A. K. Cajander, have also recently been overlooked, then independently re-invented. As Oksanen suggested, an acquaintance with earlier work could add efficiency to progress in ecology today.

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Many of Camerano's papers were published both in journals and separately as booklets. This dual publication accounts for the discrepancy in the numbering of the plates of his 1880 paper and for the incompleteness of the journal references to some of his other papers. The numbers given in square brackets at the end of some references are the call numbers in the library of the Academy of Sciences of Torino.

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