History of Ecological Sciences, Part 49: Formalizing Animal Ecology, 1870s to 1920s

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W. C. Allee (1949) and T. Park (1949) have surveyed the history of animal ecology before 1900, and 1900–1940, respectively. R. T. McIntosh (1985:61–68) also did so, more briefly. W. R. Thompson (1939) wrote a history of "Biological control and the theories of the interactions of populations" (1939: see 301–318). The scientific contributions of Charles Darwin, Henry W. Bates, Alfred R. Wallace, and Ernst Haeckel, discussed previously (Egerton 2010, 2011, 2012*a*, *b*, *c*, 2013*c*), contributed significantly to the ultimate emergence of animal ecology. Aspects of the history of animal ecology in the later 1800s were discussed in parts 45–46 (Egerton 2013*a*, *b*), on entomology and parasitology; those developments were absorbed into a separate science of animal ecology after it emerged. In this part 49, developments in Europe and North America are discussed separately; then, a formal synthesis in textbooks is discussed.

Europe

Belgian zoologist Pierre-Joseph van Beneden (1809–1894) was most known for his parasitology studies (Florkin 1970). One of his books was *Les commensaux et les parasites dans le règne animal* (1875, English 1876). As a Catholic, he found Darwin's emphasis on the struggle for existence distasteful (Sapp 1994:7–8, 18–20). His book classified relations between species of animals as parasitism, commensalism, and mutualism. Commensals he defined as sharing the food of a neighbor without doing it harm, and mutualists as both benefiting (1876:1).

Alfred Victor Espinas (1844–1922) published *Des Sociétés Animales* (1878), which tends toward what we call synecology, and drew upon van Beneden's book. Espinas was a controversial French philosopher, who nevertheless was liked by his students and colleagues (Brooks 1998:97–133). His introduction to evolution was from Herbert Spencer, whose *Principles of Psychology* Espinas and a colleague translated into French. He wrote Darwin two extant letters (March 1872, 1 July 1877), and Darwin responded (before 1 July 1877) that corals should not be considered social animals. In retrospect one might say that Espinas was a sort of precursor of ethology and sociobiology: he thought that human societies had evolved out of animal societies, and that humans could gain insights into cooperation from studying animal societies. Some controversy arose because *Des Sociétés Animales* seemed like a scientific treatise, yet was submitted successfully in Paris for a Ph.D. degree in philosophy. Since it was a philosophical treatise, French zoologists felt justified in ignoring it. In reality, it was a scientific work with philosophical implications. However, it was based on library research, not first-hand observations. His survey included: I: Accidental Societies among Animals of Different Species, Parasites, Commensals, Mutualists; II. Normal Societies among Animals of the Same Species; III. Function of Reproduction, chapter 1: Of the Family, Conjugal Society; chapter 2: Maternal Societies, Families of Insects; chapter 3: Paternal Societies, Families among Fish, Reptiles, Birds, and Mammals. Edward O. Wilson (1975:16) noted that William M. Wheeler's five basic kinds of societies (1930) were influenced by Espinas' book, and Allee (1949:32) acknowledged that although "Espinas' (1877) great work" had little contemporary influence, "more recently many have come to recognize the value of his work."

Carl Gottfried Semper (1832–1893), whom we met in part 47 as a hostile rival of Haeckel (Egerton 2013*b*:229), published *Animal Life as Affected by the Natural Conditions of Existence* in both German and English editions, which devotes 290 pages to what we call "autecology," while 75 pages can be called "synecology" (two terms coined in 1896: Allee 1949:42). He attended the University of Würzburg and later was its Professor of Zoology and Director of its Zoological Institute (Beard 1893, Mayr 1975). His doctoral dissertation (1856) was on the anatomy and physiology of snails, and he continued studying invertebrates during his travels to Pacific islands, December 1858–May 1865. He spent 1862 on the Palau Islands and the rest of the time in the Philippines, and his five volumes of the 10-volume *Reisen im Archipel der Philippinen* (1868–1905) were on Holothuria (sea cucumbers), terrestrial mollusks, and Lepidoptera (Johnson 1969). As Semper's attacks on Haeckel in *Animal Life* (Semper 1881:v–vi, 461–463) make clear, he was quite familiar with Haeckel's works, but being averse to them (or him), he did not use Haeckel's term "oekologie" for the science on which he wrote his book. His alternative was "the natural conditions of existence" (in title of his book). Semper's occasion for writing *Animal Life* was an invitation to lecture at the Lowell Institute in Boston in 1877. That invitation enabled him to take a broad perspective on his life's work, but with the advantage that he had a wealth of illustrative Pacific research and discovery on which to draw. His "autecology" encompassed the influence of light, temperature, stagnant water, atmosphere, water currents, gravity, electricity, and water pressure. In less detail, he discussed the influence of living organisms on animals: reciprocal influences, parasitism, competition, mimicry, and more. In a discussion of the food of herbivores and carnivores, he pointed out that when herbivores transform vegetation into flesh, there is a loss of mass due to oxidation of organic material, and that the same is true when carnivores transform flesh of prey into their own flesh (Semper 1881:51–52). To illustrate this, he arbitrarily assumed a 10:1 ratio of food to flesh, a ratio that is in accord with a more recent estimate (Pequegnat 1958, Egerton 2007:53). Semper was a well-respected zoologist, and his book was read by other zoologists, but without serving as a Kuhnian paradigm that led others down paths which he had blazed.

More focused and also significant for early animal ecology was a study by German zoologist Karl August Möbius (1825–1909) on oysters (Querner 1974, Kölmel 1981, König et al. 1981, Nyhart

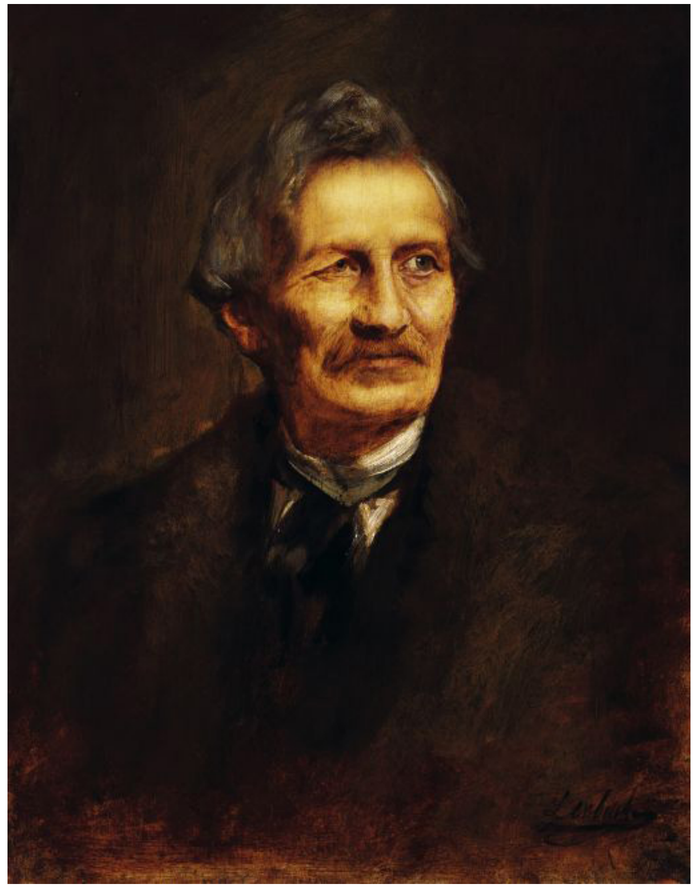

Fig. 1. (a) Carl Gottfried Semper. From web site. (b) Karl August Möbius. From web site.

2009:125–160). He was born into a poor family and worked his way up from teaching primary school in a small town to teaching high school in Hamburg. He soon worked at the Hamburg Museum of Natural History, co-founded the Hamburg Zoo, and planned Germany's first public aquarium. He studied under Johannes Müller at the University of Berlin and in 1853 became a teacher in a school in Kiel. He co-authored a treatise on three classes of Mollusca (sea slugs, marine snails, and clams) in Kiel Bay (Meyer and Möbius 1865–1872, two volumes) that had a general introduction in volume 1 that is ecological in scope and methodology, and used the term "Biocönose" to indicate forms of life having something in common (Querner 1974:432, Nyhart 2009:140–143). The introduction described five regions (zones) extending from sandy beach to mud at 10 fathoms. It also compared Kiel Bay's fauna with fauna in other parts of the North Sea. This treatise helped Möbius become Professor of Zoology at the University of Kiel in 1868.

In 1869, the Prussian government commissioned him to study French and English oyster culture, in order to promote that culture in German waters. In *Die Auster und die Austernwirthschaft* (1877, English 1880), Möbius explained in section 10 that "An Oyster–Bank Is a Biocönose, or a Social Community" (1880:721). Oyster beds occur in shallow sea water with sandy bottoms (Möbius 1880:727)

> *If the dredge is thrown out and dragged over the sea-flats between the oyster-beds, fewer and also different animals will be found upon this muddy bottom than upon the sand. Every oyster-bed is thus, to a certain degree, a community of living beings, a collection of species, and a massing of individuals, which find here everything necessary for their growth and continuance, such as suitable soil, sufficient food, the requisite percentage of salt, and a temperature favorable to their development. Each species which lives here is represented by the greatest number of individuals which can grow to maturity subject to the conditions which surround them, for among all species the number of individuals which arrive at maturity at each breeding period is much smaller than the number of germs produced at that time.*

To name such groups, he coined the term "Biocöenosis," meaning community. He emphasized both relationships between individuals and between individuals and environment and that the biocoenosis could change due to changing conditions. His term gained currency in Germany and elsewhere (Reise 1980), though "community" prevailed in English-language usage. Clements and Shelford (1939:5–6) questioned whether Möbius intended biocenose to include plants as well as animals, since his discussion of plants was limited to stating that only *Zostera* and some Florideae grew upon oyster banks and that desmids and diatoms were oyster food. However, I think that limited discussion was because his treatise was not on biocenose, but on oysters. Consider these more general comments (Möbius 1880:727)

> *The individual number of cultivated plants and animals has been immensely increased because man has artificially extended their biocönotic territory; and this artificial increase in the number of plants and animals by means of cultivation is the foundation for the increased fecundity of the human species and the greater number of individuals which arrive at maturity—that is, for the extension of the biocönotic territory of* Homo sapiens.

Since Möbius published his first discussion of "biocoenose" in the introduction to *Fauna der Kieler Bucht*, a year before Haeckel coined the term "oecologie" (1866), a recent student (Kölmel 1981) considers Möbius a founder of both the biocoenose concept and of modern ecology, even though Möbius' more definitive discussion of biocoenose appeared in 1877. A modern critic judges Möbius' concept to be mythic (Reise 1990:150)

> *Möbius' community concept was synthesized from three major lines of thought, popular at his time. Möbius combined Charles Darwin's theory of natural selection within the "web of life" with Alexander v. Humboldt's recurrent associations of plants as entities in our landscape, and added to these the ancient belief in natural harmony or balance of nature, called equilibrium in his mechanistic parlance.*

In Italy, entomologist Lorenzo Camerano (1856–1917) was educated at the Royal University of Torino (now Università degli Studi di Torino) and subsequently worked at the Museum of Zoology of the University (Cohen 1994:351–352). He also would become president of the Accademia delle Scienze di Torino. Camerano was a very productive scientist: he published 341 works, 1877–1917, some of which were well illustrated, for he had originally studied art, and became fascinated by zoology when, as a student, he had been recruited to illustrate zoological demonstrations. Many of his papers were descriptive and published in the Museum's bulletin, but in 1880 he published a theoretical paper, "Dell'

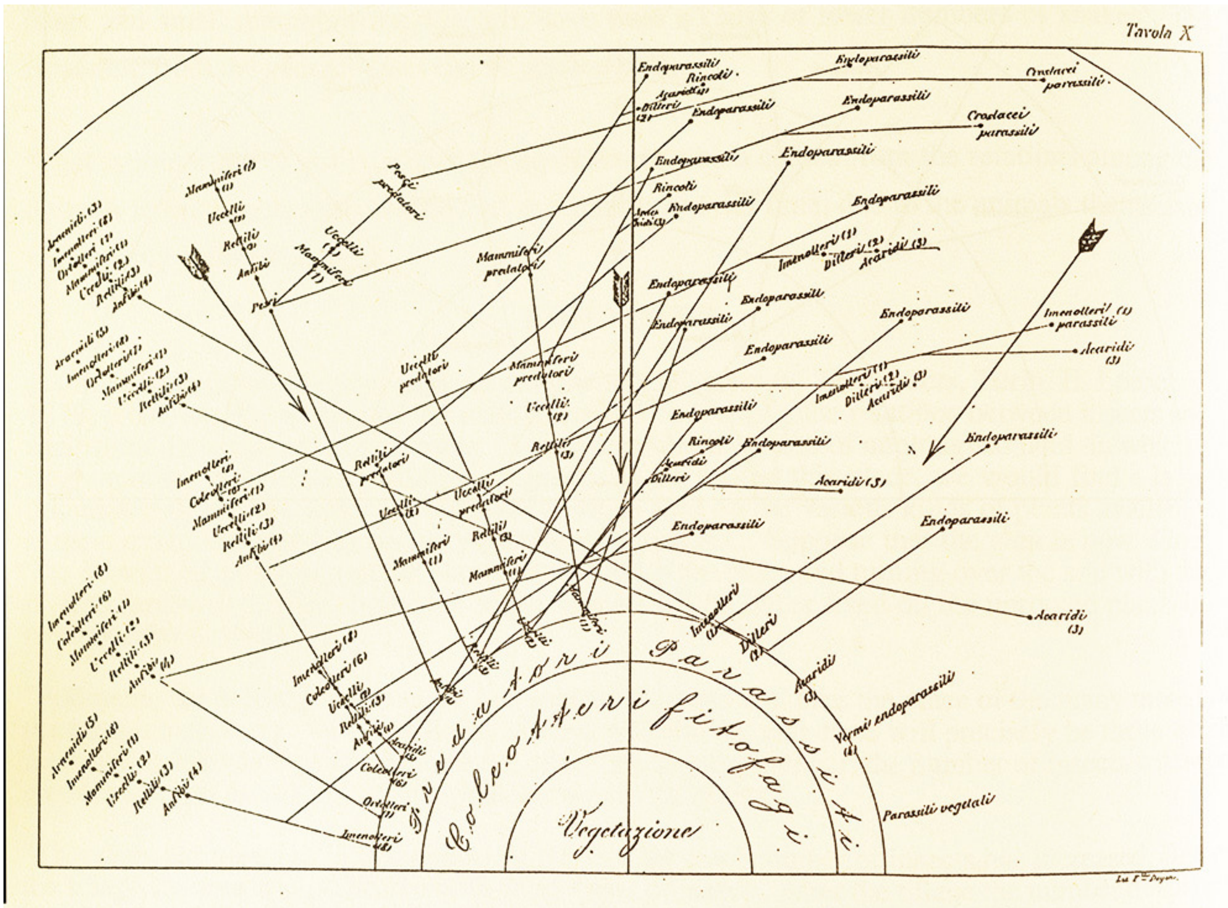

Fig. 2. The second of two food web diagrams. Camerano 1994:378.

equilibrio dei viventi mercè la reciproca distruzione" (English version, Camerano 1994), which contains four complex food web diagrams, the first such diagrams known (Egerton 2007:53). The quality of his seven conclusions is indicated by these two (Camerano 1994:375):

> *...causes of disequilibrium tend either to suppress each other, or an increased and to decrease one another alternately.*
>
> *The causes of disequilibrium produced by man in any animal group, such as deforestation, agriculture, etc., have many times insignificant effects because they are counterbalanced by other causes coming from the various groups of animals themselves*

His paper stimulated neither controversy nor other studies to test his conclusions.

With the works of Beneden, Espinas, Semper, and Möbius having displayed what a science of animal ecology might encompass, it seems surprising that afterwards the path grew dimmer rather than brighter. There was no well-defined tradition in zoology comparable to that in botany (Egerton 1976:340–342, 2013*c*), which spontaneously evolved into animal ecology. This lack of a well-defined animal ecology tradition is evident in a survey of relevant works published in Sweden, 1880s–1910s, showing no trend and no dominant leadership (Söderqvist 1986:58–69). Ecological traditions were developing in entomology and parasitology (Egerton 2013*a*, *b*), but without much broader influence.

British plant ecologists organized the British Ecological Society in 1913—the world's first ecological society—and its *Journal of Ecology* was oriented toward plant ecology (Egerton 2013*c*:357). Englishman Lancelot A. Borradaile published *The Animal and Its Environment: A Text-book of the Natural History of Animals* (1923) that was ecological in content, but without using the word "ecology." By then, Charles Elton was completing his education but had not yet made his reputation.

North America

Like American plant ecology (Egerton 2013*d*:358), American animal ecology arose mostly in the upper Midwest (Merriam and Lotka being exceptions), and for the same reason: universities there were still growing and could add ecologists to their faculty, which faculty recruited students to ecology.

Stephen A. Forbes (1844–1930), whom we met in part 45 (Egerton 2013*a*:72–73), was a very successful zoologist, who maintained good relations with the Illinois university, legislature, professional colleagues, students, and the public (Howard 1932, Mills 1958:94–97, Egerton 1976:339–342, Kingsland 1985:12–17, Hagen 1992: see index, Golley 1993:36–37, Lovely 1995, Burgess 1996:42, Schneider 2000, Croker 2001). It was due to intelligence, diligence, social innovations (organizing societies, public projects, converting a museum into a biological laboratory), and constant publication, though his only "book" is a collection of 17 articles and his bibliography (1977). He was probably first to make systematic studies on the food of birds and fishes, and he was capable of rising above his massive data to ecological generalizations. To horticulturists who considered encouraging beneficial birds and suppressing harmful birds, in 1878 he cautioned: "That the balance of nature should be disturbed only after full knowledge and searching reflection should be evident to any one who realizes the complicated relations of living things and the consequent numerous and remote results of any changes in these relations" (in Croker 2001:70). His study of crop pests revealed that the worst damages came from strongly oscillating insect populations, by which he meant that their populations fluctuate between plagues and scarcity: locusts, potato beetles, chinch bugs, and army worms (Crocker 2001:76–77).

Forbes is remembered most for his 1887 published talk, "The Lake as a Microcosm" (reprinted 1925, 1977, 1991). However, some ideas in it he had earlier expressed in "Some Interactions of Organisms" (1880:3, 1977)

> *The serious modification of any group, 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.*

A lake is a natural ecosystem (a later term; 1935), a concept which Forbes grasped with his nontechnical "microcosm" and its relationship to a "water-shed" (Forbes 1925:539). He apparently appreciated Möbius' concept of biocöenose, but did not use that term (Croker 2001:126). Although he mentioned "diatoms and other microscopic algae" and "the weeds and lily-pads upon the shallows

Fig. 3. (a) Stephen Alfred Forbes. Mills 1958:95. (b) Clinton Hart Merriam. Osgood 1947:2.

and around the margin,the Potamogeton, Myriophyllum, Ceratophyllum, Anacharis, and Chara, and the common Nelumbium" (Forbes 1925:542), only once did he explore a relationship between plants and animals, focusing instead upon relationships among different species of aquatic animals. Only 37 of Illinois' 132 fish species lived in its interior lakes, and the sunfish family was dominant. When common Lake Michigan fish species were transferred to inland lakes, they did not flourish (Forbes 1925:543). These lakes were poor in bivalve mollusks and rich in univalves. The lakes contained about 40 species of crustaceans, several worms, and common insect larvae. He discussed in most detail the Entomostraca, minute crustaceans that were common fish food. Black bass ate both Entomostraca and insects. But the crustaceans that it ate themselves consumed Entomostraca, algae, and protozoa. "At only the second step, therefore, we find our bass brought into dependence upon nearly every class of animals in the water" (Forbes 1925:548). Forbes' example of a relationship between plant and animal was unusual: bladderworts (*Utricularia*) are flowering plants that have hundreds of little bladders that trap minute animals which it digests, and therefore bladderworts compete with fishes for food (Forbes 1925:548). He concluded (rather perversely) that "beneficent order is maintained in the midst of a conflict seemingly so lawless" (Forbes 1925:549). The beneficent order is that if a species consumes more than the surplus individuals of its food source, it will then decline in numbers due to food scarcity.

In 1887, the Federal Hatch Act provided for agricultural experiment stations in every state, and the Illinois station opened in 1888, with Forbes serving as its entomology consultant (Croker 2001:102). During the 1880s, Forbes began studying a bacterial and a fungal disease of insects. He found a fungus, *Beauvaria globulifera*, that was fatal to chinch bugs, and during the early 1890s he distributed both infected bugs and the fungus to Illinois farmers, with some success, though he eventually concluded the fungus spread on its own well enough. "The legacy of Forbes's pioneer work in insect diseases for use in biological control of insect pests would appear later in the twentieth century" (Croker 2001:107–108). In 1895, the University of Illinois' College of Agriculture had a new dean, Eugene Davenport, who obtained increased funding for both the college and the experiment station, and, consequently, Forbes' work in agricultural entomology received increased support (Croker 2001:114–116). In his *Nineteenth Report of the State Entomologist on the Noxious and Beneficial Insects* (1896), Forbes "described ecology as 'lately distinguished as a separate subject and economic entomology as 'a division of this science of oecology'" (McIntosh 1985:32). Forbes doubted Dr. Louis W. Sambon's argument that *Simulium* biting flies transmitted microorganisms that caused pellagra disease. Forbes found no correlation between July abundance of these flies and new cases of pellagra (Forbes 1913, Croker 2001:122–123). (That pellagra is a niacin deficiency disease, not caused by microorganisms, was shown in 1934–1938.). In 1894, Forbes persuaded the state legislature to provide funds for a research station on the Illinois River. The story of that station will be told in part 50 of this history, on formalizing limnology. Forbes served as president of the Ecological Society of America in 1921 (Burgess 1977:7).

As an aside, the founder of neo-Lamarckian evolutionism in America, Alpheus Packard (1839–1905), began studying the cave fauna at Mammoth Cave, Kentucky, in 1874, for the Geological Survey of Kentucky (Bocking 1988, Egerton 2013a:53–54). He later studied other cave fauna and published "The Cave Fauna of North America, with Remarks on the Anatomy of the Brain and Origin of the Blind Species" (Packard 1888, 1977). His main focus was on evolution (Norland 1974), but his work was also a valuable resource for cave ecology, at a later time.

C. Hart Merriam (1855–1942) was from a prosperous family, living on a farm at Locust Grove, New York, which spent winters in New York City (Osgood 1947, Shor 1974, Sterling 1977, 1997*b*, Burgess 1996:76–77). He grew up with a strong interest in wildlife. In 1871, during the two terms in which his father was a Congressman, his father took him to chat with Spencer Baird at the Smithsonian. Baird examined birds and mammals Hart had stuffed and urged his father to have a taxidermist in New York train him, which was done. In spring 1872, Baird arranged for him to join Ferdinand Hayden's U.S. Geological Survey of the Rocky Mountains (Sterling 1977:8–13). Merriam published a "Report on the mammals and birds of the expedition" (Merriam 1873). Merriam studied zoology at Yale University for three years, then received an M.D. degree from the New York College of Physicians and Surgeons in 1879, then practiced medicine for six years. In 1885 he became head of a division in USDA to study birds and mammals and remained there until 1910, after which he continued private research into 1939. Merriam was among two dozen ornithologists who organized the American Ornithologists' Union in 1883 (Barrow 1998:50–54). When he, as chairman of the Committee on the Migration of Birds, sought federal funds for his committee's work, he got his funds through Congress in 1885 by becoming head of a division in USDA's Bureau of Entomology to study birds and mammals (his division's name changed four times) and remained there until 1910 (Sterling 1977:56–90, 1989, Kohler 2006:94–99).

Although his division mainly studied life histories of species having economic significance (Hamilton 1955:664–668), and provided a pest control service for farmers, Merriam had theoretical interests, some of which had ecological significance. Most notably, in 1889 his division conducted a survey of the San Francisco Peak and nearby Little Colorado River, Arizona (Sterling 1977:204–240). As Merriam explained (Merriam 1890:1)

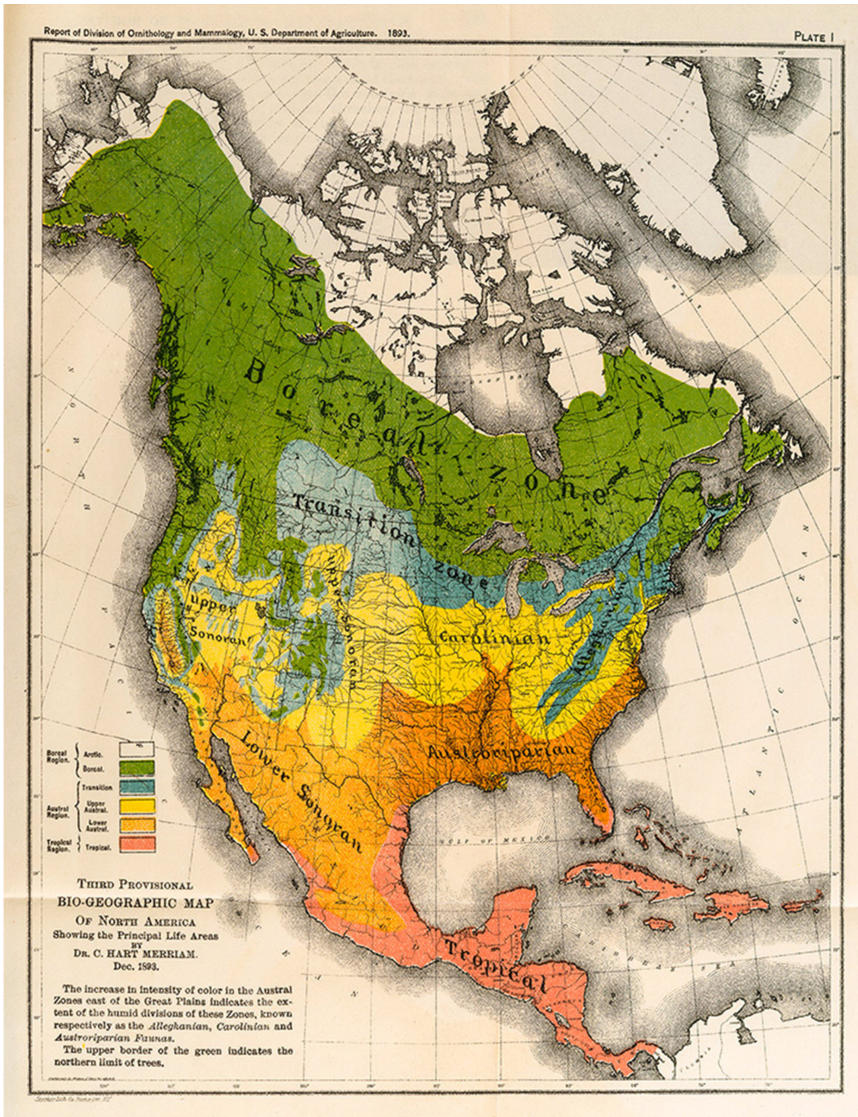

Fig. 4. Third provisional bio-graphic map of North America showing the principal life areas. Merriam 1894:facing 228.

Recent explorations in the West, conducted by the Division of Ornithology and Mammalogy of this Department, led to the belief that many facts of scientific interest and economic importance would be brought to light by a biological survey of a region comprehending a diversity of physical and climatic conditions, particularly if a high mountain were selected, where, as is well known, different climates and zones of animals and vegetable life succeed one another from base to summit.

The Secretary of Agriculture had confidence in Merriam's judgment and gave permission to proceed. Merriam explained that

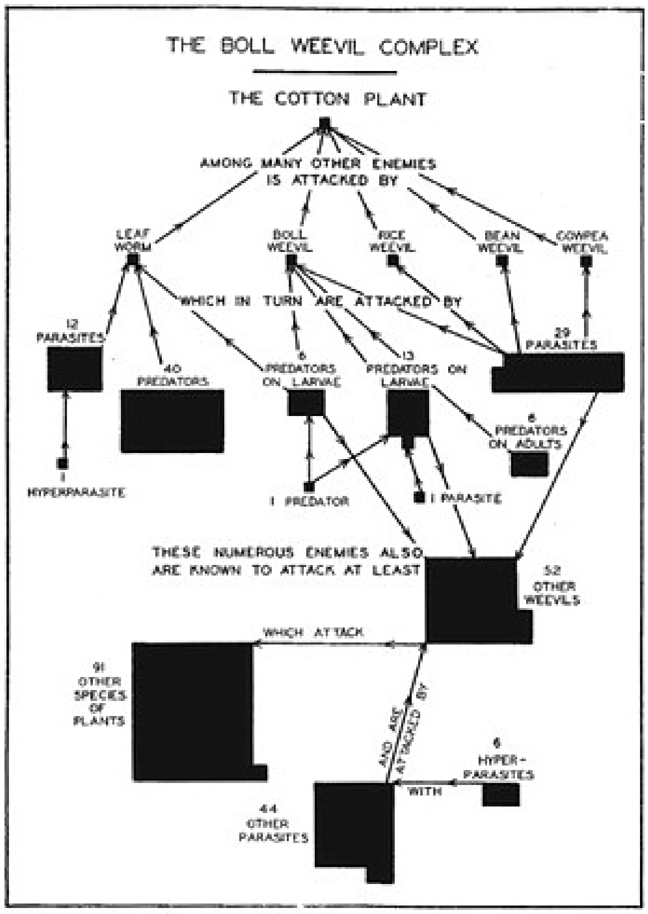

Fig. 5. The boll weevil complex. Pierce, Cushman and Hood 1912.

San Francisco Mountain was chosen because of its southern position, isolation, great altitude, and proximity to an arid desert. The area carefully surveyed comprises about 13,000 square kilometers (5,000 square miles), and enough additional territory was roughly examined to make in all about 30,000 square kilometers (nearly 12,000 square miles), of which a biological map has been prepared.

After he had studied the specimens and data collected, he reached "unexpected generalizations concerning the relationships of the life areas of North America, necessitating a radical change in the primary and secondary divisions recognized." The data he published, however, were on the elevation of the land at different points and measurements and descriptions of biological specimens; there were no climatological data. Even without such data, however, one could see as one ascended the mountain that the vegetation changed with elevation, and many animal species were limited to particular elevations and vegetation. He therefore identified seven "life zones" in the area (1890: plate 1), from Alpine Zone, above 3500 m (11,500 feet) down to Desert Zone at 1200–1800 m (4000–6000 ft.), and mapped them on four maps. Although he defined these particulars for that region for the first time, the concept itself was familiar, and had been mapped by Humboldt in his famous tableau of Chimborazo and Cotopaxi in 1807, which did include climatological, as well as elevation data (Egerton 2009:268–269). What is remarkable, however, is that Merriam then used his vegetational data to construct a "Provisonal Biological Map of North America Showing the Principal Life Areas," as his Map 5. As he collected more data from other

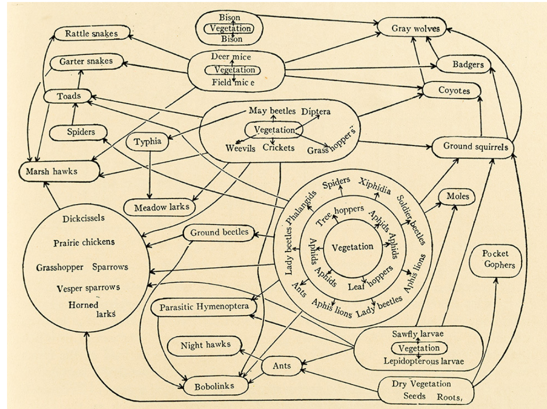

Fig. 6. (a) Victor E. Shelford. From web page. (b) Food web of land animals. Shelford 1913, 1937:167.

sources, he modified his map of North American Life Areas. Interestingly, in the same annual USDA report (1894) as Merriam's third version of his continental map, U.S. Chief Forester Bernard E. Fernow published a fold-out map of the forest lands and lumber regions of the United States. One might expect some overlap in the regions of Merriam's and Fernow's maps, and there is some, but not much. By the 1920s, ecologists criticized Merriam's scheme as simplistic (Shelford 1932, Sterling 1978:25), though Rexford Daubenmire (1938) praised his use of both animal and plant data in constructing his life zones, which continue to be pragmatically useful in the West.

Another aside: Merriam's sister, Florence (1863–1947), was a lifelong student of birds who encouraged studying them with opera glasses rather than with guns (Kofalk 1989, Bonta 1991:186–196, Norwood 1993:43–46). She married Vernon O. Bailey (1864–1942), her brother's most valued assistant at the Biological Survey (Cox 1997, Kohler 2006:185–187), and some of her extensive publications were coauthored with him. In their *Wild Animals of Glacier National Park* (1918), he wrote on mammals and she on birds. However, her *Birds through an Opera Glass* (1890), *My Summer in a Mormon Village* (1894), *A-Birding on a Bronco* (1896), *Birds of New Mexico* (1928), *Among the Birds in the Grand Canyon Country* (1939), and numerous articles were by her alone (a sample from her books: Bonta 1995:95–105). Vernon Bailey published *Mammals of New Mexico* (1931), a companion to her bird volume.

Fig. 7. (a) Vitto Volterra. Web site. (b) Alfred Lotka. Web site.

The first book to use the English-language term "animal ecology" might be David S. Jordan and Vernon L. Kellogg's textbook, *Animal Life: a First Book of Zoology* (1901:1) which was "an elementary account of animal ecology—that is, of the relations of animals to their surroundings and their responsive adaptations to these surroundings" (quoted from Cox 1979:76). Ichthyologist Jordan was president of Stanford University and entomologist Kellogg was a professor there (Shor 1973*a*, *b*).

Victor E. Shelford (1877–1968), from rural New York State, entered the University of West Virginia in 1899 for premedical studies (Kimler 1990*b*, Croker 1991:7, Mitman 1992:37–45, 1997, Burgess 1996:99, Egerton 1999). He lived with an uncle, William Rumsey, Assistant State Entomologist at the state agricultural experiment station, and he worked as student assistant in the laboratory of the university's Zoology Department. That environment failed to produce a physician; instead, Shelford transferred to the University of Chicago in 1901, and graduated with a S.B. in zoology in 1903. He continued in graduate work there, under zoologists Charles Child and Charles B. Davenport, and plant ecologist Henry Cowles—which was a perfect combination for turning Shelford toward becoming an animal ecologist. He studied tiger beetles in the same Lake Michigan dunes that Cowles had studied vegetation succession. He found that each species was associated with particular breeding environments and types of vegetation (Shelford 1908, Croker 1991:15–17).

Shelford could have become an ecological entomologist, but instead he embarked upon three studies on succession among fish in streams and ponds and then two on succession in land communities (Shelford 1911–1912), all of which he folded into his *Animal Communities in Temperate America: as Illustrated in the Chicago Region* (Shelford 1913, 1937), which drew upon both experimentation and observation. It appeared in the same year as Adams' *Guide to the Study of Animal Ecology*, both books being by University of Chicago graduates. Shelford's studies thus far added an animal layer to Cowles'

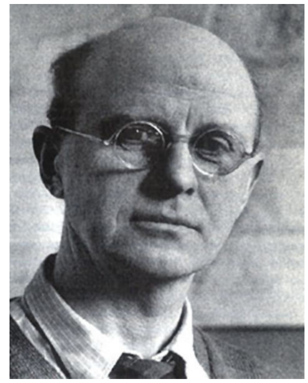

Fig. 8. (a) Charles Christopher Adams. Web page. (b) Charles Sutherland Elton. Web page.

successional studies on the vegetation of the Lake Michigan sand dunes (Croker 1991:24–29, Mitman 1992:44–45).

In 1912, three agricultural entomologists, W(illiam) Dwight Pierce, R. A. Cushman, and C. E. Hood, produced an outstanding diagram of a food web of enemies of cotton boll weevils in a USDA bulletin (1912, Egerton 2007:54–55). Pierce was listed in the first ESA directory of members (*ESA Bulletin*, March 1917:43). Born in Champaign, Illinois in 1881, he earned his B.A. and M.A. degrees (1904, 1907) at the University of Nebraska, and his Ph.D. at George Washington University in 1917. He worked at USDA in 1904–1919. Robert Asa Hood (1880–1957) was born in Taunton, Massachusetts and studied at the University of New Hampshire and Cornell University and in 1906 became a field agent at the USDA's Bureau of Entomology. He worked on parasites of the cotton boll weevil, 1906–1911, and when that work ended, he was assigned work on fruit insects in Virginia (Muesbeck 1957, Mallis 1971:372–373).

Shelford did not cite their bulletin and was unlikely to have seen it before his book went to press. His book diagramed both aquatic and terrestrial food webs (Shelford 1913, 1937:70:166). His book was well illustrated with both photographs and drawings, and with tables, maps, and diagrams. His concluding discussion rejected the emphasis on single factors to explain species distributions (Merriam emphasizing temperature; A. C. Walker, atmospheric moisture; A. Heilprin, food) but instead defended a "law of toleration," that species are most abundant where the factors that limit their lives are optimum, and less abundant where these factors are less favorable (Shelford 1937:302–304). One historian characterized the book as (Cox 1979:15)

> *…the first comprehensive description of temperate animal communities, and was also the first attempt to classify those communities. His was a broad survey that encompassed a range of habitats—scrub and woodland, grassland, rivers and streams, ponds and lakes, marshes, shores and bogs—stressing in each case the relations between the plant and animal communities. Though it lacked detail, as a general reconnaissance with a clearly defined underlying plan, it was a remarkable achievement.*

Cowles and Shelford taught a joint seminar on ecology, 1908–1914, at the University of Chicago. Shelford shared Cowles' conviction that ecology should include experimentation, and Shelford's first doctoral student, Warder Allee, became oriented toward experimental ecology, emphasizing physiology in his dissertation research. Shelford received a raise in 1913 and "*Animal Communities* generated much interest and excitement among biologists" (Croker 1991:35), yet by late fall, 1913, he decided he needed to leave the University of Chicago. Two ecologists recommended him to the University of Illinois. Here is what Cowles wrote (Croker 1991:38)

> *I have known him very intimately for more than a decade, and have, perhaps, been more closely associated with him than has anyone else.*
>
> *I regard Dr. Shelford as one of the ablest men in the world along the line of animal ecology.*

The other ecologist who recommended him was Forbes; he liked Shelford's publications. Shelford's three-year contract was for three-quarter time as an assistant professor and one quarter as assistant biologist at the State Laboratory of Natural History.

When the school year ended in Chicago in 1914, Shelford left not for Urbana but for Washington State. A former colleague at Chicago, Theodore C. Frye (1869–1962), Director of the Puget Sound Biological Station, had invited Shelford to teach a summer ecology course. He would spend nine summers there between 1914 and 1930 (Benson 1992:81). Those summers gave him an opportunity to extend his understanding and techniques from freshwater to saltwater animal communities, which he found more difficult than expected. Instead of experimentation, he finally settled for descriptions of intertidal and subtidal animal communities (Shelford 1932, 1935, Benson 1992:82–88). Shelford was active in the formation of the Ecological Society of America in 1915 and served as its first president in 1916 (Burgess 1977:2, Croker 1991:120–121).

Warder Clyde Allee (1885–1955) grew up on his family's farm near Bloomingdale, Indiana (Emerson and Park 1955, Schmidt 1957, Kimler 1988, Croker 1991:31–34, Mitman 1991, 1999, Burgess 1996:11, Sterling 1997*a*). His family was Quaker, and he earned his B.S. degree (1908) at Quaker-supported Earlham College, and his M.S. and Ph.D. degrees (1910, 1912) at the University of Chicago under Shelford. Allee taught at four other academic institutions before settling at the University of Chicago, 1921–1950, where he developed an informal school of animal behavior (Banks 1985). He also taught summer courses in invertebrate zoology at the Marine Biology Laboratory, Woods Hole, 1914–1921. He was a very productive ecologist, using extensive laboratory experiments, focused mostly on social behavior in social insects. Although the three books which brought him prominence appeared during the 1930s, they built upon his extensive publications during the 1920s. Allee's doctoral students included the Park brothers, Orlando (Ph.D. 1929) and Thomas (Ph.D. 1932), both of whom served as presidents of the Ecological Society of America. The second issue of the 1956 volume of *Ecology* was an Allee Memorial Number.

As if they had suddenly arrived from another planet, two mathematically sophisticated scientists, Vitto Volterra (1860–1940) and Alfred Lotka (1880–1949) realized at about the same time that animal ecologists had not developed mathematical tools that could facilitate their studies. The Italian Volterra was an extremely versatile mathematical physicist (Volterra 1976, Kingsland 1985: see index). Although he was the older of the two, it was not until 1925 that his ecologist daughter, Luisa, interested Volterra in commercial fish population dynamics. But that was the same year in which the American (born in Austria to American parents and educated in England) mathematical physicist, Lotka, published his landmark *Elements of Physical Biology*, which was intended to found a new discipline of physical biology (Gridgeman 1973, Kingsland 1985: see index). However, it takes more than a book to establish a new discipline, and Lotka had little contact with biologists. The biologist–demographer Raymond Pearl (1879–1940) had brought him to Johns Hopkins University on a fellowship in 1922 to write his book, and Lotka had seen the usefulness of Pearl's logistic curve for his own computations (Kingsland 1982:41–43). Biologists responded positively to Lotka's book, but since no physical biology discipline emerged, Lotka turned his attention to human demography. Volterra, with no knowledge of Lotka, published his first contribution to his new interest in English in 1926 (reprinted in 1991): "Fluctuations in the abundance of a species considered mathematically," appearing in *Nature*. Both scientists continued publishing on their new interest during the 1920s and 1930s, and their work did attract serious attention during the 1930s and later. However, there was much work to do once ecologists realized the possibilities these mathematical scientists had revealed before their tools could be fully accepted, and it took four decades to work through those problems (Kingsland 1985:116–206).

Formal synthesis

Charles C. Adams (1873–1955), from Illinois, wrote the first comprehensive (though brief) book on animal ecology: *Guide to the Study of Animal Ecology* (Adams 1913, 1977). He informs us that it is a guide, not a treatise like Warming's *Pflantesfund*. Adams was among the first explicit animal ecologists (Palmer 1956, Burgess 1996:10, Harmond 1997), with an M.S. degree from Harvard (1898) and Ph.D. from Chicago (1908). The author most frequently cited in Adams' *Guide* was Stephen Forbes, the most prominent early American founder of animal ecology; the second most frequently cited was Shelford, the most prominent American founder of a later generation. Adams was a professional colleague of both, while he was in Illinois (Kingsland 1985:see index, McIntosh 1985:86–87, Mitman 1992:36–37, Kohler 2002: see index, 2006: see index).

The close ties that American and British plant ecologists established (Egerton 2013*c*:357, 365–366) was not duplicated by animal ecologists, though Charles Elton was impressed by Shelford's *Animal Communities* (Croker 1991:37). Adams (1913) provided an interim guide to animal ecology, and syntheses appeared in two 1920s textbooks, by Pearse (1926) and Elton (1927). Park (1949:57) compared their books and found Pearse's primarily descriptive and Elton's more quantitative and dynamical.

Arthur Sperry Pearse (1877–1956), born in a sod shack on the Nebraska frontier, received his B.S. and M.A. degrees from the University of Nebraska and his Ph.D. (1908) from Harvard University (Pearse 1952, Gray 1957, Huff 1957, Burgess 1996:86). He held a variety of positions before joining the Duke University faculty in 1927. He was president of the Ecological Society of America in 1925 (Burgess 1977:7). Pearse's book was competent and would have been more important than it was (edition 2, 1939) if it had not been rivaled by Elton's, a classic.

Charles S. Elton (1900–91), son of an English professor at Owens College, Manchester, had been introduced to natural history by his older brother, Geoffrey (Cox 1979, Southwood and Clarke 1999). Charles received his bachelor's degree at Oxford University, where he studied under Julian S. Huxley. In summer 1921, while still an undergraduate, Elton was Huxley's assistant during the Oxford University Spitsbergen Expedition. He read Shelford's book before the journey. Shelford's inland terrestrial and aquatic food webs were essentially independent of each other, yet in Spitsbergen Elton was impressed by transfer of matter from ocean to land, as foraging sea birds brought back fish to their young. He made a sea–land food web showing this (Shelford 1913: diagrams 3 and 6 [cited from edition 2, 1937], Summerhayes and Elton 1923, Elton 1927:58, Egerton 2007:54–58). Elton joined two further Oxford expeditions to Spitsbergen in 1923 and 1924 (Summerwood and Clarke 1999:135–136). These experiences plus reading Charles G. Hewitt's *The Conservation of Wildlife in Canada* (1921) before his first trip, with discussion of lynx and snowshoe hare population cycles, focused Elton's interest on Arctic ecology (Cox 1979:8–38). However, his *Animal Ecology* (1927) attempted to provide a balanced understanding, not tilted to the Arctic, except for using Arctic examples to illustrate some ecological principles (Cox 1979:73–139, Chew 2006:106–111).

In addition to the introduction of the book, there are 11 topical chapters, but the book's lasting influence was based on a few distinctive themes: animal communities, food chains and food-cycles (webs), niche, and the pyramid of numbers (Cox 1979:77–105). Three chapters are specifically devoted to animal communities (chapters 2, 5, 7), and chapter 3 on "Ecological Succession" also deals with communities. They cannot be summarized here, but each chapter begins with a summary. Food chains and webs had been discussed since the early 1700s (Egerton 2007:50–58), but usually in isolation, though the "economy of nature" had provided some context. Elton could relate food chains and webs to both niche and pyramid of numbers. Joseph Grinnell (1877–1939), director of the University of California's Museum of Vertebrate Zoology (Shor 1972, Burgess 1996:49), used the term "niche" in reference to place, as in "The niche-relationships of the California thrasher" (1917).

Thomas Park, in his history of animal ecology, 1900–1940 (1949:57), compared Pearse and Elton's textbooks. Pearse "laid a general background of physical and biotic factors and then classified animals ecologically according to their major habitats. The treatment was primarily descriptive." Elton, on the other hand (Park 1949:57), was concerned more with organizing ecology around principles, and most of his principles centered around the animal community and the natural population. Unlike Pearse, he was interested, not so much in whether an animal was found in a desert or a lake, but rather in the environmental factors limiting the distribution of such a form. Elton stressed also the quantitative aspects, particularly in connection with the number of animals that occupy any community and the impact that these numbers make on their total environment. He viewed food chains as the most important integrating factor of the community, and his treatment of this subject is outstanding.

In other words, Elton's book was much more theoretical than Pearse's. For that time, it seems fair to see these differences as a reflection of differences in educational focus of the two countries, with America's focus being more empirical and descriptive and England's being more theoretical. A stock example has been the niche: Grinnell's concept (Grinnell 1917) emphasized place, and Elton's concept (Elton 1927:63–68) emphasized function. However, Thomas Schoener (1989:79–80) spoiled this simplistic contrast by reviewing five Grinnell publications concerning niche, 1913–1928, and he judged the differences between Grinnell's and Elton's concepts were rather slight, and that the significant contrast is rather between Grinnell's and Elton's vs. Hutchinson's (1957) concepts.

Conclusions

The formalizing of animal ecology began well with European works of broad scope by Espinas (1878) and Semper (1880), and Möbius' treatise on oyster communities (1877), but then momentum stalled. Adams' *Guide to the Study of Animal Ecology* (1913) provides a guide to the diverse progress made until 1912. The American, Stephen Forbes, developed an ecological perspective in his studies on food of Illinois birds and fishes, and he generalized on his findings in his well-known "The Lake as a Microcosm" (1887). He began using the term "ecology" in 1896. Animal ecology as an academic discipline arose at the University of Chicago in 1901, when Shelford arrived as a junior undergraduate and studied under two ecologically aware zoologists and botanist Cowles. Shelford wrote a doctoral dissertation on tiger beetles in the Lake Michigan sand dunes, then broadened the scope of his research to include fishes and land animals as a basis for his book, *Animal Communities* (1913), which appeared in the same year as Adams' *Guide*. Animal ecologists participated in founding the Ecological Society of America (1915), and in 1916, Shelford was its first president. Englishman Borradaile's *The Animal and Its Environment* (1923) was ecological, but without using the word. Yet, animal ecology textbooks soon appeared: from Pearse (1926) in the United States and from Elton (1927) in England. They culminated the formalizing of animal ecology. Lotka (1925) and Volterra (1926) did not build directly upon the accumulation of animal ecology literature. They were outsiders who merely saw that animal ecologists had not developed the mathematical tools that could assist their researches, and so they stepped forward and offered it to them. However, their contributions did not appear in the animal ecology syntheses of the 1920s.

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