Meeting Reviews

External Influences on Ecological Theory: Report on Organized Oral Session 80 at the 100th Anniversary Meeting of the Ecological Society of America

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The 100-year history of the Ecological Society of America spans most of the major advances in the field of ecology, from the "niche" of Grinnell and others, to Lotka and Volterra's models of predation and competition based on the logistic growth equation, to the concept of competitive exclusion developed from experimental ecology, to genetics and evolutionary ecology and all the ramifications and specializations of these topics over the rest of the 20th and into the 21st century.

The objective of this session, sponsored by the Historical Records Committee of the ESA, was to explore how ecological concepts have been shaped and changed by influences that are external to the scientific method, such as funding priorities, ideology, politics, personalities, and differences between the ecosystems where influential ecologists developed their ideas. Among the many memorable quotations of the philosopher/poet George Santayana (1863–1952) is the often quoted and misquoted observation, "Those who cannot remember the past are condemned to repeat it."

With more than a century behind us, it seems appropriate to look back on the history of our field to examine how the important concepts have developed and changed over time so that we can move forward to solve the major new problems facing our planet, rather than reinventing the old ideas that have been (or perhaps should not have been and were not) included in our canon.

A powerful new technique for addressing this type of question is the digitization of much of the scientific literature, and specifically the publications of the ESA. Aaron Ellison, Xichen Jiang, and Matthew Lau (OOS 80-1) opened the session with an analysis of nearly 100 years of papers published in *Ecology, Ecological Monographs*, and *Ecological Applications* that explored the hypothesis that ecology developed as a critical response to the rise and dominance of Modernism. Modernism encompasses the major economic, social, and cultural transformations to Western civilization that occurred in the late 19th and early 20th centuries associated with extensive industrialization and the growth of large cities, and emphasized the power of science and technology to control and transform the environment. Ellison et al. quantified changes over time in the frequency of 45 ecological concepts grouped in four clusters: "stability/equilibrium," "succession," "resilience," and "landscape" and found that 12 concepts dominated across the 94-year period, with their rank-order being virtually invariant through time and between the journals. They concluded that "ecologists see the world as we wish it were, not as it actually is. Ecologists working in the mainstream of ecology appear to work in a conceptual space that was intellectually conditioned and constrained when ecology emerged as a formal discipline over 100 years ago." While these analyses certainly do not suggest that ecologists have forgotten their past, they do raise the question of why there seems to be no reprioritization of old concepts or any emergence of new concepts. Perhaps, the old concepts are evolving and being redefined, responding in different parts of the world to different environmental and political influences, as discussed in subsequent presentations.

Coincident with the "Rise of Modernism" was an overly optimistic announcement of "The End of History," marking the end of the political conflicts and violence of WWI and the preceding centuries, and the beginning of a new era of rational management based on sound science. John Vandermeer (OOS 80-2) noted that the textbook history of the development of ecology, proceeding from Clements' superorganisms to Tansley's ecosystems to Gleason's continuum to Whittaker's structured landscapes to MacArthur's theories (with mid-course corrections by Tansley and Gleason), is not only an inadequate oversimplification but also more significantly ignores the powerful political forces that shaped the ideas of competing schools of ecology. Political and financial support for the developing fields of ecology and anthropology came initially from the British Empire, with the motivation to use expert knowledge to allow imperialism to achieve its maximum potential to rationally manage the British Empire (Anker 2002, Tilley 2011), which involved reaching out to Oxford ecologists, including Tansley. While there were vigorous debates, the general framework of imperial management of the Empire was agreed to by almost all ecologists involved, including the proper ecological place of the native peoples who occupied the subaltern places of the colonies, suggesting an ecology based upon, not in opposition to, modernism. The counterpoint to the

Imperialism project was articulated by some of the well-known Marxist academics, most notably Lancelot Hogben who, during his stay in South Africa (1927–1930), welcomed black Africans into his classes and helped fugitive black political organizers evade the racist British system. The Marxists were more inclined to frame the problem in a dialectical framework with the model of force, counter-force, and resolution (or thesis, antithesis, and synthesis), which, in addition to historical application to political struggles, could also be used as a framework for understanding nature. This intellectual approach to understanding interactions and feedbacks likely played a role in Lewontin's attempt to use dialectics to unite Development, Ecology and Evolution, most notably at the 1967 Syracuse Symposium, attended by Dobzhansky, Harper, Levine, Levins, Lewontin, Slobodkin, Waddington, MacArthur, and others (including Vandermeer). The dialectical approach in biology, synthesized by Levins and Lewontin in their 1987 book, "The Dialectical Biologist," has arguably been influential in the development of several lines of thought in both evolution and ecology. Vandermeer concluded with a paraphrase of Marx, "Dialectical philosophers have thus far only explained science. The problem is, however, to CHANGE it."

Differences in the natural environment of geology, soils, climate, and evolutionary history have led to contrasting sets of ecological concepts in different parts of the world. Patricia Werner (OOS 80-3), who has extensive field experience in both North America and Australia, discussed some of the dramatic differences in the development of ecological science between the northern hemisphere and "Down Under." The harsh and unpredictable natural environment created by Australia's ancient, infertile soils, extensive aridity and extremely variable precipitation, and frequent disturbances (especially fires) led to ecological concepts that focused on adaptations of plants and animals and landscape patterns of the distribution and abundance of species relative to natural abiotic conditions. In contrast, the dominant ecological concepts developed in North America and Europe, with young, fertile, mainly glacially derived soils and abundant or at least less-variable rainfall, focused on density-dependent interactions such as predation and competition among plant and animal species that were often quite abundant. Although some Australian ecologists contributed to the development of density-dependent theoretical models, the mathematical models developed in the north temperate zone seemed marginally relevant to understanding Australian ecology, and were little used or cited by most Australian ecologists. Australian ecologists developed sophisticated technical methods to quantify spatial and temporal patterns of precipitation and soil moisture, soil fertility, plant growth, and fire behavior in order to explain the Australian biota. These tools, along with their computer models based on environmental unpredictability and landscape-scale variation in environmental conditions, have played a major role in conservation planning, ecosystem restoration, and adaptation to climate change, both in Australia and globally.

Stephen Jackson (OOS 80-4) discussed the deep historical roots of the "biological interaction vs. environment" conceptual frameworks described by Patricia Werner, adding a third approach based on "chance" and history. The chance-based framework for understanding ecological structure was most recently articulated as "neutral theory," but has historical roots going back to ESA member H.A. Gleason (1920s) as well as the Australians Andrewartha and Birch (1950s), and not surprisingly to the historical contingency of Darwin and other early naturalists. "Neutral theory" assumes that all organisms (with most examples related to plants) are functionally identical and that the patterns observed in nature result primarily from random processes of immigration and extinction, rather than from ecological interactions such as competition. This contrasts most strongly with the deterministic environment–biota relationships along altitudinal and latitudinal gradients noted by von Humboldt and other early naturalist travelers. Jackson argues that all three of these approaches are necessary, but not sufficient to explain community composition and structure and cautions that all three approaches must be integrated if ecologists are to provide accurate and useful forecasts of ecological responses to ongoing and future environmental change. He illustrated the perpetual tension between theoretical/conceptual science and applied/empirical science with a quotation from Pierre Duhem contrasting continental physics (abstract and conceptual) with British physics (deterministic and practical), "there are nothing but strings which move around pulleys, which roll around drums, which go through pearl beads, which carry weights… We thought we were entering the tranquil and neatly ordered abode of reason, but we find ourselves in a factory."

The effects of humans on the environment in which they live and conduct research, specifically the effects of thousands of years of human occupation and land use, provide the context for Ernst-Detlef Schulze's discussion of conservation and land-management issues in Germany (OOS 80-5). Despite (or perhaps because of) the intensity of human land uses for agriculture and forests in Germany, as well as across Europe, Schulze reports that the number of plant species has increased exponentially since the Neolithic period. Although numerous invasive species from North America have spread across Europe, this increase in the number of plant species is not due to invasions, but rather to *in situ* speciation by hybridization, strong mortality selection, and other mechanisms producing large numbers of new species, many of which are apomictic (producing viable seeds asexually). This has produced a large group of poorly characterized species existing in various marginal habitats in the intensively utilized landscapes, but with little or no conservation focus. While there have been few documented plant extinctions in the remnant natural habitats, and only 3 of 178 forest specialist species are designated as of conservation concern, there is a large group of recently evolved species which are not protected. Under the new EU transboundary approaches to biodiversity conservation, Germany must take responsibility for species that are neither listed as endangered nor protected, indicating that evolutionary processes have not entered into conservation planning. Land management practices play a critical role in the survival of both the historical species and the new species, with the loss of traditional management practices such as grazing, hay-cutting, and coppicing threatening the survival of many of the original native species, particularly of grasslands. Schulze concludes that conservation theory is not adequately addressing the roles of land management and speciation in novel man-made environments in shaping the biodiversity of these anthropogenic landscapes.

Just as major ecological concepts did not change in relative ranking over time, the relative rankings of ecological concepts apparently do not change much regionally either. William A. Reiners and his collaborators took a spatial and disciplinary approach to the same types of ecological concepts that were examined over time by Ellison et al. (OOS 80-1). Reiners et al. analyzed the opinions of 1182 ESA members who responded to an online survey conducted over 2 weeks in the autumn of 2014. Each respondent was asked to rank 70 concepts based on the utility of each concept to their professional lives (from unimportant to important on a 5-level scale). A total of 82% of the respondents were from the United States, with another 16% from elsewhere in North and Central America, Europe, and Australia. The top 10 most highly ranked concepts by the U.S. respondents were, in descending order: scales, ecosystem, habitat, species, disturbance, organism, population, community, competition, and species life history. Preliminary analyses of this complex data set did not reveal major differences between the U.S. and non-U.S. subsets, nor were there differences among the various regions within the United States, perhaps indicating the ecological community was quite homogeneous with regard to the ecological concepts considered most important. There did seem to be some differences between states with high population densities and states with low population densities, but confirmation of significant differences will require further analyses. Preliminary analyses also suggested that concepts related to evolution were less important to scientists in applied government agencies than they were to academic scientists. Curious ecologists are eagerly awaiting further results from this interesting study.

Competitive equilibrium, with alternative states of monodominance vs. multispecies coexistence, has been a major concept in ecology since the time of Lotka, Volterra, and Gause, and continues to have a strong influence on both ecological theory and conservation biology. Michael Huston (OOS 80-7) traced philosophical interest in the "balance of nature" back to the Greek historian Herodotus (c. 484–425 BCE). Herodotus' explanation for the apparent stability of predator-prey dynamics provides what may have been the first description of what we now call r-K theory. Two millennia later, Darwin and Wallace's insights gave rise to a new question, "Why are there so few species?" By the sixth Edition of his book, Darwin (1872, p. 84) had come up with a simple explanation, based on the subdivision of a finite resource pool by a multiple species: populations must maintain some minimum size to avoid extinction due to natural fluctuations. However, within less than 50 years, the ecological focus returned to explaining how competitive exclusion and low diversity could be avoided. While mathematical models and laboratory experiments suggested that it was very difficult for multiple species to coexist under equilibrium conditions, theoreticians from Lotka to Chesson noted that there were a variety of processes and types of interactions that could promote coexistence, even under stable conditions. The dialectic between coexistence and competitive exclusion eventually led to recognition that the relative influence of these two processes changed along environmental gradients. Few species can survive under unfavorable conditions, while competitive exclusion and dominance by a few species often occurs under the most favorable growth conditions. The "balance of nature," as manifested by high species diversity resulting from high rates of coexistence, occurs most conspicuously under intermediate conditions, which seems an appropriate dialectical conclusion, and is particularly conspicuous in plants and other sessile organisms.

The intensifying environmental crises of the late 20th century, including accelerating climate change and apparent increases in extinction rates across the planet, have provided a powerful motivation for new ecological approaches to address these challenges. David Frank (OOS 80-8) pointed out the rapid increase in the use of the term "biodiversity" in the early 1990s following the 1988 "National Forum on BioDiversity" sponsored by the U.S. National Academy of Sciences and the Smithsonian Institution, the UN "Convention on Biological Diversity" signed at the 1992 "Earth Summit" in Rio, and the 1994 publication of the book "Biodiversity and Ecosystem Function" (Schulze and Mooney 1994), based on the 1991 Bayreuth Conference. A rapid increase in funding for research on the value of biodiversity produced a series of published experiments that captured scientific, public, and political attention with their claims that loss of biodiversity would inevitably lead to decreases in the rates of critical ecosystem processes essential for maintaining healthy ecosystems and supporting human well-being. However, a small group of ecologists (none of them funded by the major biodiversity research programs) criticized the validity of the experimental results based on supposed flaws in experimental design and interpretation. The "war between ecologists" came to a head when the Ecological Society of America published a glossy report in their "Issues in Ecology" series for policy makers that the critics attacked as "a propaganda document" that stated "opinions as facts." The protagonists came together in 2000 at the "Paris Peace Talks" and hammered out a consensus document that satisfied few of the authors, but has been heavily cited. Nearly, 20 years later, countless additional "biodiversity-ecosystem function" experiments have been published, definitions have been altered, and meta-analyses confirmed the consistency of all the experimental results, but the major areas of disagreement remain unresolved.

The field of ecology has grown and developed dramatically over the past century, with new analytical and statistical methods and increasing specialization into subfields, many of which have formed their own societies and now publish journals independently of the ESA. The field still has the "activist edge" that once responded to Modernism, and is now trying to respond to the multiple converging crises that are altering and degrading ecosystems and societies across the planet. A major question is whether the field of ecology, with its concepts and methods accumulated and refined over the course of the 20th century, can respond effectively to the new challenges facing our planet. While our historical overview has clearly documented development and change in ecological concepts, it has also revealed a somewhat surprising stasis and homogeneity of outlook. We should not be surprised that the information age has led to a global dissemination of ecological ideas that may have reduced regional differences that once reflected dominant processes in contrasting environments, as the survey by Reiners et al. seems to suggest. Similarly, the time-series textual analysis by Ellison et al. has only scratched the surface of what we can learn from this approach to understanding our history, but it is certainly significant that these preliminary results reveal an unexpected consistency in the conceptual framework of ecologists. The same twelve top-ranked concepts (out of a total of 45 concepts evaluated) have dominated ESA journals for nearly 100 years, with no significant change in rank order of usage.

How can we explain the observation that the most important concepts in ecology, as reflected in the publications of our society journals, have not changed in 100 years? Certainly, the types and spatial extents of environmental issues addressed by ecologists have changed dramatically in 100 years, with rapid expansion and acceleration of change in the past 50 years. Perhaps, these "time-tested" concepts can address the new and growing set of problems, but perhaps not.

One possible explanation for the apparent stability of our conceptual hierarchy is that our concepts have evolved over time, responding not only to the internal dynamics of science but also to external forces, such as the rise of Marxism in the Soviet Union, the Great Depression, WWII, the advent of public funding for research, the atomic age, new instrumentation, the rise of computers and systems analysis, the onset of both the Civil Rights and environmental movements, new paleoecological insights that things were not as we liked to imagine them, GIS and remote sensing, etc. Some fundamental aspects of ecology have remained intact, but the overall fabric of ecology has been distorted into different shapes over time, but still maintaining some sort of topological integrity.

An additional factor contributing to this consistency may be the citation practices of ecologists. Many of us regularly review manuscripts for various journals, and it is difficult to overlook the fact that most of the papers cited in submitted manuscripts were published within the past 10 or 15 years. Out of the 100-year history of our field, most current ecologists are only looking at the most recent 15 years of the literature. The danger is that hot new ideas in ecology may not be that new, but may have been discovered and published more than 20 years ago, which is beyond the standard "window of scholarship." Perhaps, ecologists are simply reinventing the same wheels over again every 15 or 20 years, believing that they are making major conceptual advances.

Another possibility is that new concepts are being developed and reprioritized most fully within the framework of the many specialized societies and journals that have "spun off" the Ecological Society of America. Is the ESA interacting sufficiently with those ecologists who work more closely with their biological subdiscipline or with the newer societies? The ecological and environmental problems facing the world are clearly changing. Is the field of ecology itself changing fast enough to solve today's major environmental and ecological problems?

Session program

OOS 80-1. Aaron Ellison, Xichen Jiang, and Matthew Lau. The emergence of ecology and the challenges of modernism.

OOS 80-2. John Vandermeer. Effects of politics on development of ecological theory: From Clements' organism to Dialectical Ecology.

OOS 80-3. Patricia Werner. Australian vs. North American ecological research: Contrasting environmental influences.

OOS 80-4. Stephen Jackson. Biology, chance, and environment: Three contrasting perspectives on community structure and composition.

OOS 80-5. Ernst-Detlef Schulze. Land management and plant evolution: biodiversity and conservation in anthropogenic landscapes.

OOS 80-6. W. A. Reiners, D. S. Reiners, S. D. Prager, and J. A. Lockwood. Do valuations of ecological concepts by contemporary ecologists vary with geography?

OOS 80-7. Michael Huston. Evolution of the equilibrium concept: seeking balance in nature.

OOS 80-8. David Frank. From "war among ecologists" to uneasy consensus: Science and conservation values in the biodiversity-ecosystem function debate.

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