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Chapter 1

The Tallgrass Prairie:

Raymond Lindeman, a Minnesota Bog Lake, and the Birth of Ecosystems Ecology

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. . . he was a field ecologist at heart, a limnologist from the prairie.

Under the summer sun of the late 1930s, as the world emerged from economic depression and reeled toward war, a graduate student would inflate his "pneumatic boat" and set out on a small lake in east central Minnesota to gather samples for his ecological studies.* One of his academic advisers at the University of Minnesota had spotted the lake during a reconnaissance flight years earlier and regarded it as a good subject for research. The student, Ray Lindeman, went about his sample collecting beneath the source of the energy that animated the ecological system of the bog-like lake he sought to understand in bold and original detail. About the same time, a Cornell University nuclear physicist, a Jewish émigré from Nazi Germany, was trying to solve the mystery of that very energy source, the sun. And solve it he did, publishing the "Energy Production in Stars" in the months before the sun set on Europe with the outbreak of war. Both the graduate student and the physicist were theoretical systems thinkers by nature. Both used thermodynamic calculations. Both were interested in energy flow, one through ecosystems and the other through stars. They had something else in common: the graduate student, naturally enough, got his hands and feet dirty doing his work; students of physicist Hans Bethe couldn't help but notice his muddy shoes when he came to class.[1]

Unlike Bethe, who was productive almost until the end of his ninety-eight years, the pioneering ecosystems ecologist Raymond Lindeman exercised his nascent yet powerful scientific imagination over the course of just a few years. He had no choice. As he collected his samples, recorded his data, wrote his dissertation, and drafted and re-drafted "The Trophic-Dynamic Aspect of Ecology,"[2] the manuscript whose publication would make him famous, he was dying. As death approached he appeared to treat the prospect as a distraction to his research and moving his ideas through scientific peer review into print, which was proving to be difficult.

Lindeman had a passion for discovering how the natural world works as a complex dynamic system. He possessed a mind well equipped to find out and work habits that enabled him to deliver the goods. The ideas about ecological energetics, food webs, and ecological succession encompassed in his paper fueled research for two generations of ecologists. The British ecologist and botanist Arthur Tansley had introduced the term "ecosystem" just as Lindeman launched his boat on Cedar Bog Lake, located north of Minneapolis, but it was Lindeman himself who gave birth to ecosystems ecology. Eugene Odum's classic textbook *Fundamentals of Ecology* (1953)[3] helped to make Lindeman's model of energy flow the key approach for studying diverse biological processes and comparing diverse ecosystems. More than seven decades after its publication, Lindeman's paper continues to be listed among essential readings in natural resource and species management and in ecosystem conservation.[4]

If the average human life expectancy worldwide is seventy-one years, in human terms the sun is about thirty-five years old. It will keep Earth habitable for life as we know it a couple more billion years by energizing Earth's ecosystems. As Hans Bethe observed in his Nobel lecture, stars have a life cycle much like animals: "They get born, they grow, they go through a definite internal development, and finally they die, to give back the material of which they are made so that new stars may live."[5] So it is with the ecosystems that sustain life on planet Earth, based on the natural metabolic processes Lindeman articulated in an aquatic system. Organisms die and decompose into simpler inorganic molecules in what he inventively termed "ooze." Subsequently these inorganic molecules in ooze are incorporated into living plants through photosynthesis and transferred through aquatic food webs, just as the sun incorporated heavy elements from earlier stars that died and became supernovas.

In ecosystems, these molecules cycle through Earth's biotic and abiotic worlds. "The *ecosystem* may be formally defined as the system composed of physical-chemical-biological processes active within a space-time unit of any magnitude, i.e., the biotic community *plus* its abiotic environment," Lindeman wrote, citing Tansley and his breakthrough idea. "The concept of the ecosystem is believed by the writer to be of fundamental importance in interpreting the data of dynamic ecology."[6] In short, the ecosystem is the key ecological unit in the natural world and an accessible avenue for the quantitative analysis of productivity and energy in ecological space.

Ecosystems are often described as self-organizing, self-regulating, and homeostatic. They are resilient to temporary changes in conditions, tending to keep them more or less in equilibrium. But what happens when people disrupt ecosystems? As Lindeman was struggling to get his transformational ideas published in the journal *Ecology*, ideas he would not live to see in print, few people aside from conservationists were concerned about environmental damage from human activity. Few talked about biodiversity loss. No one talked about human-caused climate disruption. And the debut of the term "the Anthropocene," the human age, was six decades away.

Up from the Farm

Lindeman's brief journey through life commenced on a farm set amid the gently undulating glacial-drift plain of southwestern Minnesota that the Des Moines lobe of the Wisconsin glaciation forged at the end of the last ice age. The glacial drift consists mainly of till overlaying a foundation of Precambrian bedrock. The Minnesota River, a descendant of the glacial River Warren, forms most of the northern border of Redwood County, which was home to the Lindeman farm.[7] This world, the land beneath Lindeman's feet, fired his imagination. Years later, as a graduate student, he would describe the geology and paleoecology of the Anoka Sand Plain north of Minneapolis in his article "The Developmental History of Cedar Creek Bog, Minnesota" published in the *American Midland Naturalist* in 1941, a year before his death. The Anoka Sand Plain was something of an aberration, a deflection of the Des Moines lobe as the lobe extended southward like a pseudopod creating the soil conditions on the Lindeman farm. The bog upon which Lindeman expended his graduate-student energy, as he himself described it, "was formed as an ice-block lake in a pitted sand-outwash topography."[8]

The soil upon which the farms of Redwood County rested was well suited for raising wheat, corn, oats, barley, potatoes, and prairie hay, the preferred crops of the German and Norwegian settlers there. The Lindeman 320-acre farm was next door to one of many farms in the area owned by Richard W. Sears, the founder of Sears, Roebuck & Co. who started as a railroad station agent in Redwood Falls in the early 1880s. Both Lindeman's parents, Otto and Julia (Ash), were 1910 graduates of the University of Minnesota's Agriculture School, where they met.[9] An entry in their senior yearbook's "Class Alphabet" reads (with its misspelling of Lindeman):

L is for LINDERMAN,
The chemist so rash,
Who is always well versed
On the essentials of ASH.

Otto and Julia were married in 1913. Raymond was born in 1915. He never took to agriculture despite his parents' college degrees in the field and his father's advanced practices. A family farmhand recounted that he never saw Raymond on a tractor. According to Robert W. Sterner, who interviewed people who knew him, Raymond expended his abundant boyhood energy on nature, not agriculture. "A common and recurring theme among those who recalled Raymond was his intense and not easily satisfied curiosity about the natural world," Sterner wrote in an article published in the *Limnology and Oceanography Bulletin*.[10] Lindeman spent a lot of time outdoors observing the flora and fauna hosted by the tallgrass prairie, the area wetlands and woodlands, and the ravines and bedrock outcroppings characteristic of Redwood County. During his excursions he would capture butterflies and kept a collection of them in his bedroom. His visual acuity of the natural world suffered a setback when he accidentally damaged the cornea of his

Raymond Lindeman
Pioneering ecosystems ecologist Raymond Laurel Lindeman (1915-1942). *Courtesy University of Minnesota.*

right eye with iodine, leaving the eye able to distinguish only light from dark.

After attending a one-room schoolhouse and then graduating from Redwood Falls High School in 1932, Lindeman enrolled in Park College, a small liberal arts school in Missouri, graduating second in his class in 1936. In his college application he wrote that he wanted to become an experimental biologist. Lindeman was something of an idealist, and science was his first love. Science allowed one to "see and try to understand the majestic symmetry of the universe" while serving humanity.[11] Two events had a profound influence on Lindeman while he was a college student. He met his future wife, Eleanor Hall, the daughter of a professor at Albion College in Michigan. She was an indispensable partner for his scientific interests and became an algal specialist in her own right. Then in the summer of 1935 Lindeman pursued undergraduate studies at the University of Minnesota's Lake Itasca field station, where he met his future doctoral adviser Samuel Eddy, a professor of zoology and curator of fishes at the Bell Museum of Natural History. But Eddy's influence on Lindeman after he enrolled in the doctoral program the next year may have been less than that of William S. Cooper, head of the botany department, whose research centered on the postglacial history of the Anoka Sand Plain. It was Cooper who had spotted Cedar Bog Lake during a reconnaissance flight in 1930.[12]

On a December day in 1936 Lindeman traveled the thirty-five miles from campus to what was soon to be named the Cedar Creek Natural History Area and began five intensive years of collecting samples including benthos, the aquatic organisms on the lake floor. After they were married in 1938, the collecting was invariably a joint venture of Raymond and Eleanor, who were sometimes accompanied by colleagues and friends. Friends did the driving because the Lindemans didn't own a car. Sometimes their friends would loan them a car. Raymond's persistence and single-mindedness when it came to his research sometimes led him to skip his classes, which during the course of his graduate school years included protozoology, animal physiology and behavior, terrestrial animal ecology, plant ecology, aquatic ecology, entomology, parasitology, histology, ichthyology, rotifer research, aquatic biology research, and, critically, biostatistics.[13] His $600 annual stipend as a teaching assistant meant that he and Eleanor could just get by. They lived in a trailer a few minutes' walk from a basement room in the zoology building where they did their research using the analytical instruments available. Large tubs accommodated aquatic organisms and biomaterials from the lake bottom. Sieves were employed to sort the contents into two-quart canning jars for subsequent spectroscopic analysis and data collection.

Cedar Bog Lake

View of Cedar Bog Lake with experimental plots in the rear. Cedar Creek Ecosystem Science Reserve, East Bethel, Minnesota. *Courtesy University of Minnesota College of Biological Sciences.*

A Theory Takes Flight

Ecology as an academic discipline was a half-century old when Lindeman commenced his revolutionary study of "the physical-chemical-biological processes active within a space-time unit," an effort focused on a bog lake, which according to ecological succession theory was destined to become woodland. The German biologist Ernst Haeckel coined the word "ecology" ("Ökologie") in 1866. He conceived of ecology as an anti-mechanistic, holistic approach to biology, a web that linked organisms with their surrounding environment. Haeckel's holistic view played a key role in the early intellectual development of ecology, infusing Nature with vitalism, the virtuous properties of "Mother Earth," and giving biology the upper hand over physical processes.[14] Frederic Clements, an influential Carnegie Institution plant ecologist, kept the focus on biology, the description and distribution of species, and ecological communities as communities of organisms until Arthur Tansley came along.

The botanist Tansley, a champion of landscape conservation, insisted that ecological studies needed to take into account "the whole *system* (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome—the habitat factors in the widest sense," he explained. "Though the organisms may claim our primary interest, when we are trying to think fundamentally we cannot separate them from their special environment, with which they form one physical system."[15]

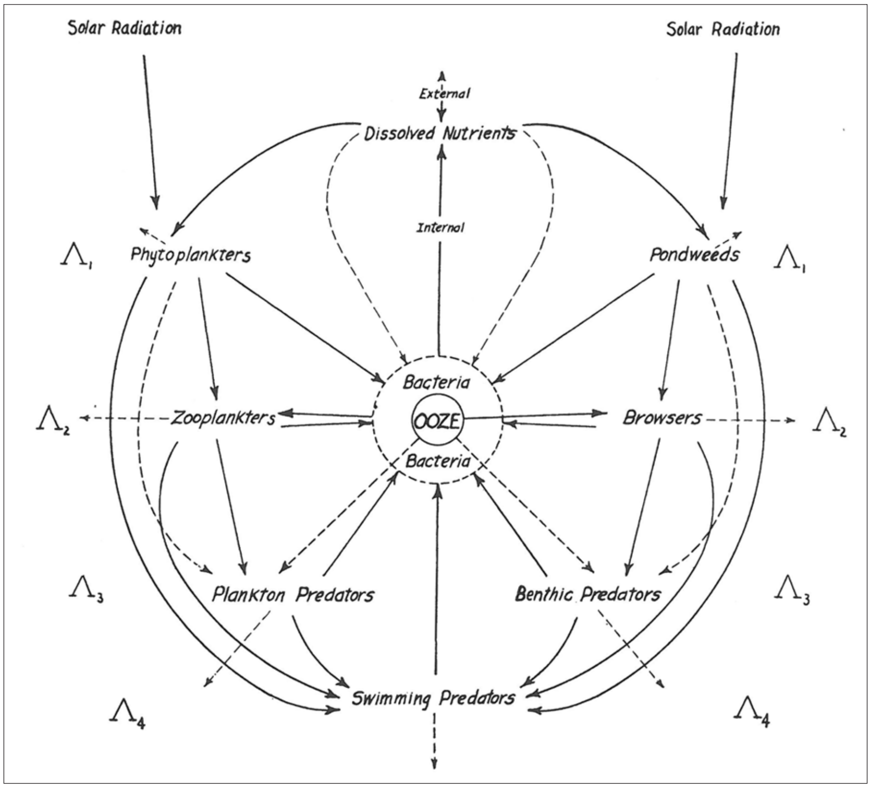
After Tansley, Lindeman was the key figure in reorienting ecology from its traditional biological emphasis, writing that "the discrimination between living organisms as parts of the 'biotic community' and dead organisms and inorganic nutritives as part of the 'environment' seems arbitrary and unnatural." The organic-inorganic cycling of nutritives "is so completely integrated that to consider such a unit as a lake primarily as a biotic community appears to force a 'biological' emphasis upon a more basic functional organization."[16] Unlike Tansley, Lindeman supported his theoretical leap with copious, well-organized data systematically derived from one specific, relatively well-delineated aquatic body over five years. At the time the field of ecology was dominated by empirical science and fieldwork. Theory was fine for astrophysicists calculating how stars like the sun produce the energy that sustains biological communities, but it was regarded by traditional ecologists as questionable, if not illegitimate, as a framework with explanatory and potentially predictive power for how these communities change over hundreds or thousands of years.

Harvard University ecologist Robert Cook elucidated Lindeman's theoretical and research originality in his essay "Raymond Lindeman and the Trophic-Dynamic Concept in Ecology," published in *Science* in 1977.[17] A hydrosere is an ecological succession that occurs in an aquatic habitat. Over a period of hundreds or thousands of years, temperate zone deep lakes progress from low nutrient levels at the outset (oligotrophy) to healthy levels of nutrients (eutrophy) to deterioration and decline (senescence) to hosting mats of floating vegetation (mat stage) to bog forests and eventually to stable biological communities (climax). In Lindeman's view, to understand a hydrosere it is essential to understand both the nutritional relations of life in successive trophic (nutritional) levels of the food cycle in the aquatic environment *and* how energy dissipates through these trophic levels. Cedar Bog Lake was then as it is today a weedy, littoral body of water lying in the transition between late lake succession and early terrestrial succession. In Cook's account, Ray and Eleanor meticulously sampled the population of "aquatic plants and phytoplankton, the grazing and predatory zooplankton, the benthic fauna of worms and insect larvae, the crustaceans, and the fish." The association of an organism with a given trophic level was governed by what the organism eats and what eats it. The exercise gave Lindeman an intimate understanding of the movement of nutrients from one trophic level to another.

To integrate their data of food-cycle dynamics with current principles of community succession, Lindeman created the trophic-dynamic viewpoint, a unifying principle for understanding ecological succession. Lindeman wrote in the last chapter of his doctoral thesis: "The trophic-dynamic viewpoint, to be elaborated in this paper, emphasizes the relationship of energy-availing (food cycle) relationships within the community to the process of succession.''[17] Lindeman believed that short-term trophic functioning had implications for long-term dynamic functioning of the lake and ultimately lake succession, the hydrosere. The only way he could prove it was through rigorous quantitative assessment of the biological productivity at successive trophic levels and then integrating that information with estimates of energy expenditures at successive trophic levels. In the end what was important was not the relation of members of the same species with one another or of communities of species in a given trophic level, but the overall biomass productivity and energy use in a given trophic level and how the productivity and energy use values compared with those of the adjacent trophic levels in the food pyramid.

Pyramids and Webs

Lindeman entitled a subsection of his paper "The Eltonian Pyramid" referring to the "pyramid of numbers" conceived by the English animal ecologist Charles Elton in 1927.[18] In Elton's pyramid, simple organisms at the base of the food cycle (e.g. invertebrates) are relatively abundant. Moving toward the top of the pyramid organisms become progressively larger in size and fewer in number (e.g. mammals). Lindeman noted that the Eltonian Pyramid "may also be expressed in terms of biomass. The weight of all predators must always be much lower than that of all food animals, and the



Diagram

The food-cycle relationships diagram Lindeman drew for his landmark paper "The Trophic-Dynamic Aspect of Ecology." Lindeman modified the diagram he drew for his doctoral thesis, adding solar radiation input and Greek letters denoting energy and trophic levels. *Courtesy "Ecology," Ecological Society of America.*

total weight of the latter much lower than the plant production."[19] Conversely, the biomass weight of primary producers (plankton, plants) is greater than that of primary consumers (zooplankton, terrestrial herbivores) which in turn is greater than that of secondary consumers (small predators) which is greater than tertiary consumers (larger predators) and so on. Then Lindeman added: "To the human ecologist, it is noteworthy that the population density of the essentially vegetarian Chinese, for example, is much greater than that of the more carnivorous English."[20]

In today's environmentally stressed world of seven billion people, this "noteworthy" example stands out. Using Lindeman's "ten percent law" for the transfer efficiency of energy between one trophic level and the next–that is, only about ten percent of the energy is fixed in flesh and available for creatures in the next trophic level of the food web—French scientists calculated the global median human trophic level for the first time in 2013.[21] The trophic level for omnivorous humans is 2.21 on a scale in which plants and phytoplankton represent trophic level 1 and carnivorous predators like polar bears and killer whales represent 5.5, the highest trophic level in what Elton called the food cycle and what ecologists today call the food web. From 1961 to 2009 humans moved up three percent trophically from 2.15 to 2.21 "due mainly to the increased consumption of fat and meat." Populous developing countries are moving up the food web to a higher trophic level, with profound consequences for human and planetary health. No wonder, then, that the French scientists titled their study "Eating up the world's food web and the human trophic level."

Renowned ecologist David Tilman and his graduate student Michael Clark showed that demand for meat protein by Lindeman's "essentially vegetarian Chinese" surged beginning in the second half of the twentieth century.[22] Current dietary trajectories in China, India, and ninety-eight additional developing and developed countries "are greatly increasing global incidences of type II diabetes, cancer and coronary heart disease" and "are causing globally significant increases in GHG [greenhouse gas] emissions and contributing to land clearing." Tilman, who is a professor at the University of Minnesota and at UC Santa Barbara, directs the Cedar Creek Ecosystem Science Reserve, home to the Raymond Lindeman Research and Discovery Center, East Bethel, Minnesota, on the northern edge of metropolitan Minneapolis-St. Paul.

Lindeman's theoretical foundation for explaining how energy and materials move through food web trophic levels also brings together ecosystem function with biomass distribution and biodiversity. Today his descendants in ecological theory construction are developing food web models of trophic interactions between species and energy flows among species in an effort to bring together biodiversity and ecosystem function in a single conceptual framework. Quantitative analysis and modeling of food webs are already proving to be useful for managing marine and aquatic ecosystems. In its 2012 meta-review "Biodiversity loss and its impact on humanity,"[23] an international team of ecologists, including Tilman, observed that models and statistical tools can help ecologists move from experiments that detail local processes to "landscape-scale patterns where management and policy take place." One of the greatest challenges, they concluded, is to use what has already been learned to develop predictive models based on empirically quantified ecological mechanisms, models that can forecast changes in ecosystems at scales that are "policy-relevant" and that link to social, economic, and political systems. If the modeling ethos that Lindeman introduced into his field leads to reliable forecasting at such scales with such links, "we may yet bring the modern era of biodiversity loss to a safe end for humanity." The existence of a growing fraction of the approximately "9 million types of plants, animals, protists and fungi that inhabit the Earth" is at stake. What their loss means to the future well-being of the biosphere and its seven billion human inhabitants cannot be computed.

What biodiversity loss means for the productivity of the native Midwestern grasslands is something Tilman and his colleagues have analyzed and calculated following long-term field experiments performed at Cedar Creek.[24] They found that decreases in grassland plant diversity affect productivity at least as much as changes in nitrogen, carbon dioxide, herbivores, water, drought, or fire. In their natural state, the "lakes of grass," as the Lakota described the Prairie to the French explorer Joseph Nicollet, thrive as communities of grass plant relatives.

Biogeochemical Cycles and the Biosphere

Early in his paper, Lindeman acknowledges that the trophic-dynamic viewpoint he was about to describe "is closely allied to Vernadsky's 'biogeochemical' approach."[25] The Russian biologist, geochemist, mineralogist, and natural philosopher Vladimir I. Vernadsky was a remarkable figure in twentieth-century science. Vernadsky revived the term "biosphere" and secured its association with his name with the publication of *The Biosphere* in Russian in 1926. *The Biosphere* was published in French in 1929, in German in 1930, and in English not until 1998.[26] (The Austrian geologist Eduard Suess had coined the term "biosphere" in the nineteenth century. Suess defined biosphere as "the place on earth's surface where life dwells.")

In *The Biosphere* Vernadsky conceived and formulated Earth's physics as a living whole. He is regarded by many as the founder of biogeochemistry, the scientific discipline that involves the integrated study of the chemical, physical, geological, and biological processes and reactions that govern the composition of the natural environment. His was an expansive understanding of living space that involves all space that is affected by life—from Earth's atmosphere to its deep-sea vents and deepest subterranean life-supporting strata. Vernadsky imagined Earth as a structure of great concentric regions subdivided by envelopes or "geospheres." The biosphere forms the upper geosphere of one of these concentric regions—the Earth's outer shell of rock called the crust. He asserted that "a considerable amount of matter in the biosphere has been accumulated and united by the energy of the sun" and that "solar energy is transferred to the depths of the crust."[27] As Hans Bethe was calculating the energy production of stars and Lindeman was conceiving the trophic-dynamic view of ecology, Vernadsky was expanding his idea of geospheric envelopes and their biological, physical, and chemical cycles in his writings.

Lindeman may have found his way to citing Vernadsky independently, but the influence of his Yale University mentor in elevating Vernadsky in his estimation may well have been a factor because G. Evelyn Hutchinson was an early and enthusiastic supporter of Vernadsky's ideas.[28] The story of how Hutchinson used his persuasive powers as the country's most distinguished academic ecologist to midwife Lindeman's manuscript into print is well known and well told by Robert Cook in his *Science* article. Having been awarded a Sterling Fellowship to do postdoctoral research at Yale, Lindeman joined Hutchinson's laboratory in late summer 1941. With Hutchinson's guidance and his wife Evelyn's encouragement, he began to reshape the last chapter of his dissertation into a journal article for submission to *Ecology*.

Hutchinson was raised in Cambridge, England, where his father was a professor of mineralogy at Cambridge University, which he attended. While a young zoology instructor in South Africa, Hutchinson was inspired by Charles Elton's book *Animal Ecology* and his food cycle pyramid.[29] Unlike many of his colleagues, Elton among them, he embraced quantitative science, math, and model building, which he readily joined with his empirical research, setting the stage for ecosystems ecology and Lindeman's trophic-dynamic concept. Hutchinson had broad interests including chemistry, geology, and energy in addition to biology and limnology, the study of inland lakes. His studies of Linsley Pond in Connecticut helped establish his credentials as a limnologist without peer and persuaded him, as biologist and author Joel Hagen wrote, that the self-regulatory mechanisms governing the biogeochemical processes of Linsley Pond "were comparable to those operating in the biosphere as a whole."[30] Nancy Slack concludes her book *G. Evelyn Hutchinson and the Invention of Modern Ecology* writing that Hutchinson was "one of the twentieth century's most notable scientific polymaths" and "a polymath within his chosen field of ecology as well." By the mid-1930s, she notes, Hutchinson was requiring his graduate students to read Vernadsky's *Biosphere* (in French).[31]

After joining the Yale faculty in 1928, Hutchinson became acquainted with George Vernadsky, a Yale historian who introduced him to his father's writings. Later, George Vernadsky and Hutchinson collaborated to bring Vladimir Vernadsky's writings to English readers. Vernadsky died in early 1945 just before two of his translated articles, including "The Biosphere and the Noösphere," were published in *American Scientist*, of which Hutchinson was then editor.[32] Hutchinson wrote in the foreword: "The two articles together present the general intellectual outlook of one of the most remarkable scientific leaders of the present century." Three years later, in "On Living in the Biosphere," published in *The Scientific Monthly*, based on a paper he presented at an American Association for the Advancement of Science (AAAS) symposium "The World's Natural Resources," Hutchinson addressed the carbon cycle. "In the cycle of carbon we have a remarkable, possibly a unique, case in which man, the miner, increases the cyclicity of the geochemical process." The combustion of coal and oil "actually returns carbon to the atmosphere as CO_2 at a rate at least a hundred times greater than the rate of loss of all forms of carbon, oxidized and reduced, to the sediments." Here Hutchinson cited Vicktor Goldschmidt, a Norwegian geochemist considered along with Vernadsky to be a founder of the field. Then Hutchinson stated tellingly, "This particular process obviously cannot go on indefinitely."[33]

Leopold, Lindeman, and the Land

Had he been alive, Aldo Leopold undoubtedly would have been invited to address the AAAS natural resources symposium where Hutchinson read his paper "On Living in the Biosphere." But Leopold, a University of Wisconsin-Madison professor of game management, died tragically earlier in the year from a heart attack after trying to help a neighbor put out a brush fire that was heading toward a pine stand. It happened near his "shack," a converted chicken coop outside of Baraboo, Wisconsin, where he was awaiting publication of *A Sand County Almanac: And Sketches Here and There*. It was a book of his reflections about the natural world surrounding the shack, a book infused with the wonder of his youth as he wandered freely in the woods, prairies, and along the Mississippi River bluffs in Burlington, Iowa, at the turn of the twentieth century, a book destined to secure his place in the pantheon of the American conservation movement.

Hutchinson and Leopold had recently been among the ecologists who formed the Ecologists Union, the future Nature Conservancy. The union was "devoted to the preservation of natural biotic communities for scientific use." Protecting the wetlands of "primeval America" as "living museums" constituted Hutchinson's main interest; Leopold's main concern, as he expressed to the Union's chairman, was "the apparent raid on Western public lands" and the river damming by Army engineers "without due consideration of ecological penalties."[34]

A well-known scientist, ecologist, forester, environmentalist, and author, Leopold began writing *A Sand County Almanac* in 1942, the same year Lindeman's landmark article was published in *Ecology*. "In this influential article," wrote Leopold's biographers Richard Knight and Susanne Riedel, "Lindeman added an important element missing in Tansley's original characterization of ecosystems: energy."[35] Lindeman's trophic-dynamic viewpoint was "state of the art" when Leopold wrote "The Land Ethic," the concluding essay in *A Sand County Almanac*. Leopold laid out his environmental philosophy in the essay. A land ethic changes the role of *Homo sapiens* "from conqueror of the land-community to plain member and citizen of it." The first principle of an ethic for the land was straightforward: "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise." Leopold saw the extension of ethics beyond human environments to the natural world as "an evolutionary possibility and an ecological necessity."[36]

The philosophical roots of "The Land Ethic" can be found in the speech Leopold delivered to a joint meeting of the Society of American Foresters and the Ecological Society of America in Milwaukee in 1939. In it he called ecology "a new fusion point for all the natural sciences" and one that challenged the "balance of nature" approach to discovering where utility ends and conservation begins.

"If we must use a mental image for land instead of thinking about it directly, why not employ the image commonly used in ecology, namely the biotic pyramid?" he asked.[37] Leopold revealed a modified version of Charles Elton's food cycle pyramid to represent a soil-biota energy circuit. In the scheme energy flows up the food cycle from soil through plants, plant-eating insects, insect-eating birds and rodents, herbivorous mammals, bird- and rodent-eating mammals, to carnivores, with each group returning energy to the soil. "Land, then, is not merely soil; it is a fountain of energy flowing through a circuit of soils, plants, and animals."

But *energy* does not cycle. It arrives via the sun, flows, and dissipates into nature's entropic sinks. In his book *Thinking Like a Planet: The Land Ethic and the Earth Ethic*, environmental philosopher J. Baird Callicott wrote that if Lindeman was not in Leopold's audience when he read his plenary address, "G. E. Hutchinson would have been."[38] Callicott poses the question of whether Leopold's address directly influenced Lindeman or indirectly influenced him through Hutchinson. Leopold never adopted Lindeman's "field-defining" trophic-dynamic viewpoint of energy flow. Writing "The Land Ethic" as Lindeman's unifying concept was inspiring some key ecologists, Leopold repeated his "fountain of energy" error. He merely renamed his biotic pyramid the "land pyramid." It was a curious scientific blunder in an otherwise powerful environmental vision, a vision that lives on in natural resource conservation and ecosystems management.

Ecosystems, Earth's "critical zones," and the Anthropocene

From its earliest days knowledge integration was key in the intellectual development of ecology, serving a deep-seated desire to see "ultimate order, balance, equilibrium, and a rational and logical system of relations," in the words of ecologist Frank Golley. The rise of ecosystems ecology with Lindeman's unifying principle of energy flowing through a complex dynamic system that inextricably entwined the living and nonliving fed the prevailing ethos even though it was, in a sense, as Golley described it, "machine theory applied to nature."[39]

Unlike the early affiliation of conservation with academic departments of applied economics in schools of agriculture, ecology grew up in departments of biology "fractured into botany, zoology, and other taxonomic or functional 'ologies,'" as Golley put it.

Naturally the "biotic" dimension of the biotic-abiotic complex that Lindeman described was emphasized. Moreover, aquatic systems were preferred over terrestrial systems for study. Ponds, streams, lakes, and rivers have characteristics that lend themselves to metabolic study. The water column is relatively easy to sample, aquatic organisms can be retrieved more readily than terrestrial and soil-based organisms, and the instruments needed to analyze photosynthesis and respiration in aquatic systems were available in the 1930s.

Lindeman made numerous comparisons of aquatic systems to terrestrial systems in formulating his trophic-dynamic viewpoint. But in the end he built his theory from the study of an aquatic system, comparing his data mainly with that of Chancey Juday's study of Lake Mendota in Wisconsin.[40] Not until the 1960s was ecology able to produce reliable metabolic data sufficient to show how energy flows through trophic levels in marine and terrestrial ecosystems. A review of its application to food webs in marine ecosystems seventy years after Lindeman concluded that "trophodynamics as an organizing theme is robust and valuable for marine ecological research."[41] Terrestrial trophodynamic research also was on the move. By the 1970s ecologists were able to show that terrestrial ecosystems, including soil, were responsible for a large fraction of carbon dioxide in the atmosphere. Two decades later, with rising atmospheric CO_2 levels becoming a growing concern, the role of Earth's surface materials and their alteration from human activity came into sharper focus, culminating in the formulation of Earth's "critical zones" concept by geophysicist Thomas Jordan and sedimentologist Gail Ashley.[42]

A critical zone is defined by the National Science Foundation's Critical Zone Observatory program as "a living, breathing, constantly evolving boundary layer where rock, soil, water, air, and living organisms interact."[43] The term "critical" was used to highlight the human factor in the profound alterations occurring in structure and function of the Earth's outer skin. Critical zone observatories around the world coordinate observation, experimentation, and modeling of the dynamic processes that drive the atmosphere and tree canopy layers, the soil, and subsoil regions down to the deepest aquifers and regions of biogeochemical reactions in what Vernadsky termed the Earth's "crust." The communications system is a sort of Earth sciences "Internet of things," the interconnection of computing devices and sensors embedded on the Earth's surface and beneath its surface. The wireless system monitors the availability of life-sustaining resources, including food and water, and the interactions that regulate natural habitats.

One critical zone observatory, based at the University of Illinois, focuses on intensively managed landscapes in Illinois, Iowa, and Minnesota. The core site for Minnesota is the Minnesota River basin where Lindeman grew up. Land use in the basin has undergone profound changes since the beginning of European settlement in the 1830s. Settlers drained wetlands, cut down the hardwood forests, and converted the tallgrass prairie to row crop agriculture, which now covers more than three-fourths of the basin. Faculty and students from the Department of Soil, Water, and Climate at the University of Minnesota, Lindeman's alma mater, are studying how natural and human-induced landscape change can influence the movement of sediment and the water quantity and quality into the Minnesota River.[44]

Lindeman's trophic-dynamic approach to ecology is poised to help make comprehensible how critical zones and terrestrial ecosystems function, in the view of ecologists Daniel Richter of Duke University and Sharon Billings of the University of Kansas. They see metabolism and energy flow as fundamental to both terrestrial ecosystems and critical zones. Richter and Billings propose that deeper sub-surface regions be examined "to connect the biogeochemistry and hydrology of the above-ground ecosystem and its soils with groundwater, streams, lakes, and rivers."[45] They stress the words of Tansley and the spirit of Lindeman, Hutchinson, and Odum that an ecosystem is "one physical system." Lindeman could easily have substituted terrestrial systems into his text about lakes, which Richter and Billings imagine might read, "to consider such a unit as a forest, a grassland, or a wetland primarily as a biotic community appears to force a 'biological' emphasis upon a more basic functional organization."

Richter and Billings say terrestrial ecosystem metabolism can only be resolved by quantifying the full effects of respiratory carbon dioxide released by organisms at their deepest level. Measurements should proceed from soil to weathering geologic substrata—the layer where rocks are broken down into small grains and soil—to the base of the critical zone. That requires bringing the Earth sciences of hydrology, geology, geomorphology, geophysics, ecology, pedology, geochemistry, and biogeochemistry fully into terrestrial ecosystem science. "At a time when Working Group of the International Commission on Stratigraphy is evaluating 'the Anthropocene' as a new, contemporary unit of geological time," they write, how better to promote understanding of the human forcings of the planet than by accelerating interdisciplinarity across all the Earth sciences? Critical zone science "may become the science of the Anthropocene."[46]

Ecosystems, Life Code, and Conservation

In his account as Lindeman's classmate, lab partner and friend at the University of Minnesota, Charles Reif told the story of how Lindeman had built "a set of detachable rods and a piston-type coring device with which he sampled the subsurface layers of the bog."[47] He used the device to gather materials from the lake's benthic layer at specific sites across the length of the lake. Benthos is home to aquatic organisms that live on, in, or near the bottom, from algae, aquatic plants, zooplankton, and protozoa to microflora like bacteria and fungi to macroinvertebrates like clams, snails, worms, and crayfish. It represents both producing and consuming trophic levels in the food web.

When Lindeman was writing his doctoral dissertation based on his intensive study of Cedar Bog Lake, most scientists believed protein was the carrier of genetic information. Not until 1944, two years after his death and publication of his landmark paper, was deoxyribonucleic acid, DNA, found to be the molecule responsible for transmitting heritability.[48] In the decades that followed the code of life was deciphered, the chemistry of life was explained, and the transfer of genetic material from one organism to another gave birth to a new industry, biotechnology, now four decades old.[49]

The development and deployment of powerful new tools based on advances in physics, chemistry, and computer science beginning in the 1980s are transforming the study of the "biotic" component of Lindeman's biotic-abiotic complex. Ecosystem genomics is to the biosciences what the critical zone is to the Earth sciences. Both constitute rapidly emerging fields of inquiry enabled by new tools and by reframed visions about how to explore and conserve the natural world, including the substantial ecological services natural and modified ecosystems provide to human beings.[50] Both are enhanced by the information revolution and Moore's Law, the axiom that computing power per cost input doubles every two years. Whether it be the rising tide of "omics"–genomics, proteomics, transcriptomics, metabolomics, and microbiomics–or the ubiquitous wireless sensors, communications and imaging devices, and earth-bound and satellite networks, technological innovation is opening a big window on the biosphere.

The genome is an organism's complete DNA sequence including all of its genes. Genome sizes vary widely, for example, from a couple hundred thousand DNA base pairs in the smallpox virus to 3.2 billion base pairs in the human genome to 22 billion base pairs in the loblolly pine genome. Ecosystem and conservation genomics use new genomic techniques to solve problems in environmental science and conservation biology. Because genetic fitness is key to healthy populations, genomic approaches are currently being employed to study animals as diverse as wolves, bison, and bighorn sheep to inform care and breeding practices in captive or managed populations and monitor trends in wild populations.[51] In the unseen world, metagenomics is revolutionizing microbiology and related fields. Today Lindeman would be able to draw a sample from the benthic layer of Cedar Bog Lake, sequence the genomes of all species in the sample as a single community, and gauge the entire community's productivity and energy transfer potential.

The application of genomics to ecosystems "is an especially important advance as this field has not previously incorporated genetics into studies of fundamental processes such as energy flow or nutrient cycling," wrote an international team of scientists in "A Framework for Community and Ecosystem Genetics: From Genes to Ecosystems" published in *Nature*.[52] In a study providing a genetic basis for trophic-level interactions, researchers showed that small genetic changes in cottonwood trees along Utah's Weber River increased the density of aphid galls on the host trees, which in turn spurred birds preying on the aphids.[53] Does genetic variation influence the way energy flows among organisms in an ecosystem?

Knowledge of microbial genes and the organisms in which they are expressed can be used to develop screening instruments to assess how these genes and organisms fix carbon dioxide (photosynthetic micro-organisms), break down organic matter, reduce metals, remediate hydrocarbons, transfer energy, and otherwise influence biogeochemical cycles. Metagenomic studies in the Gulf of Mexico following the Deepwater Horizon oil spill, for example, showed that indigenous sediment microbes perform a valuable ecosystem service by degrading spilled oil through hydrocarbon-reducing genetic pathways.[54] Other microbial genetic pathways helped to make oil from decomposed food-web plant and animal matter over hundreds of millions of years. Microbes are versatile. They perform on the global stage and have a long run.

The genetic revolution has much to offer natural resource, energy and ecosystems conservation, remediation of environmental damage, sustainable photosynthetic harvests, and adaptation to climate change. The new genomic editing technologies can be used to create "gene drives," genetic systems that greatly enhance the odds that a specific trait will be passed on to offspring in sexually reproducing wild populations.[55] Gene drives have the potential to help protect endangered species and suppress or eradicate invasive species and disease-bearing insects. They and other genetic technologies are poised to become useful tools for twenty-first century ecosystems management and conservation practice, though their adoption by practitioners in the field will not occur unless their safety and value can be persuasively demonstrated.[56]

A Tribute and a Legacy

Lindeman died in June 1942 at age twenty-seven, two weeks after surgery to treat a rare form of hepatitis. He had written to Charles Reif in May that "there is a better than even chance I won't survive the summer."[57] If there was a consolation to his rapidly failing health it was the letter from *Ecology* editor Thomas Park he received in March. "I have carefully considered your revised manuscript and am herewith accepting it for *Ecology*," Park wrote. "I rather imagine that the original referees will still object to certain of its basic premises but I think it best to publish your paper regardless. Time is a great sifter in these matters and it alone will judge the question."[58]

As he would with the passing of Vladimir Vernadsky three years later, Lindeman's Yale mentor G. Evelyn Hutchinson wrote a tribute to him in an addendum to the trophic-dynamic paper, which was published in the October issue of *Ecology*:

> Knowing that one man's life at best is too short for intensive studies of more than a few localities, and before the manuscript was completed, that he might never return again

> to the field, he wanted others to think in the same terms as he had found so stimulating, and for them to collect material that would confirm, extend, or correct his theoretical conclusions. The present contribution does far more than this.

The "father of modern ecology" ended his tribute by calling his late postdoc "one of the most creative and generous minds yet to devote itself to ecological science."[59] That mind, born of the tallgrass prairie, could grasp and integrate questions about the length of food chains; the efficiency of trophic transfers; the rates of primary productivity; energy value adjustments for losses due to respiration, predation, and decomposition; and the role of bacteria and microorganisms in cycling dead organic matter.[60] Despite criticism of Lindeman's trophic level concept,[61] it has endured. "Lindeman was able to see beyond the immediate form of ecosystem relationships to perceive the underlying thermodynamic generator for much of organized behavior," wrote theoretical ecologist Robert E. Ulanowicz.[62]

The laws of thermodynamics operated exactly the same when fossil fuels were being formed from dead organic matter eons ago as when Hans Bethe discerned how the sun produces the energy that radiates to Earth and Lindeman proffered a unifying theory for energy flow in ecosystem food webs. The energy demand for life itself, for metabolism, respiration and reproduction, has not changed. The energy demand for human life, as humans prefer to live it, has changed enormously, running up against constraints posed by ecology and thermodynamics.[63]

In O*n the Origin of Species*, a book in which the word "energy" does not appear, Darwin wrote that "plants and animals, most remote in the scale of nature, are bound together by a web of complex relations." Lindeman figured out how energy flows through Darwin's web in a few short years, mostly when he was a graduate student and briefly as a postdoctoral fellow. He was a mere decade removed from life on a prairie farm, from his letter to Park College in which he expressed his interest in science because it allowed one to "see and try to understand the majestic symmetry of the universe." It was this orderly balance that Darwin understood, invoking Newton at the end of his book with the observation that endless forms have been and are being evolved while "this planet has gone cycling on according to the fixed law of gravity."

Yet Darwin's theory of evolution by natural selection lacks the symmetrical structure of Newtonian physical laws. Its apparent randomness and contingency were out of sync with science's prevailing "balance of nature" paradigm, the concept that an implicit order underlies the natural world and is just waiting to be discovered.[64] In ecology the balance of nature implies that ecosystems are normally in a stable equilibrium. Here Lindeman hedged, qualifying the natural symmetry he had hoped to confirm. "Natural ecosystems may tend to approach a state of trophic equilibrium under certain conditions, but it is doubtful if any are sufficiently autochthonous [indigenous] to attain, or maintain, true trophic equilibrium for any length of time," he wrote in his paper. The less-than-stable equilibrium was principally a function of local conditions, however, conditions that in his mind could be overcome when framed in a larger context, say as a single global biogeochemical mechanism. Under Hutchinson's influence, Lindeman reached again for the "majestic symmetry of the universe" that he had envisioned when he was a high school senior in Redwood Falls, Minnesota, writing, "The biosphere as a whole, however, as Vernadsky so vigorously asserts, may exhibit a high degree of true trophic equilibrium."[65] To view the biosphere as asymmetrical, intangible, contingent, and stochastic was to rob it of its harmony and beauty. That may have been the case as much for a pioneering ecosystems ecologist as it would surely be for a twenty-first century environmental activist.

The biosphere and its ecosystems are not zones of harmonious order, and neither is their energy source. As Lindeman collected his samples on Cedar Bog Lake beneath the summer sun and calculated energy flow through trophic levels of ecosystem food webs, Hans Bethe was calculating the energy production in stars using quantum mechanics, the very embodiment of scientific uncertainty in the invisible world of energy flow. Indeed, quantum effects are found in photosynthesis itself.[66] Yet ecologists are uncomfortable with indeterminacy, so the search goes on for a plausible explanation of ecological dynamics. More than a century after it first appeared on the scene, Robert Ulanowicz wrote in 2003, "ecology today still appears to many to be too diverse and conflicted to be able to coalesce around any one coherent theory."[67] What is needed, in his view and that of others, is a more encompassing metaphysics, one that can accommodate metaphor and bridge the divide between ecological science and environmental ethics.[68]

Lindeman likely would have agreed. Bethe did not see his thermodynamic calculations of nature's energy source as inconsistent with his being an outspoken critic of the world's prevailing post-World War II environmental threat, the buildup of thermonuclear weapons. Besides, although Lindeman is remembered chiefly for a breakthrough theoretical concept of energy flow in ecosystems, he was a field ecologist at heart, a limnologist from the Prairie. His description of the natural history of Cedar Bog Lake echoes his limnological forebears, with origins in Stephen Forbes's classic description of "The Lake as a Microcosm" (1887) and Henry David Thoreau's account of Walden Pond (1854). Indeed, the transcendentalist Thoreau, regarded by some as America's first limnologist, spent a day at the Indian agency in Redwood Falls while touring Minnesota in 1861, botanizing along the way.[69]

In his journal Thoreau described *Decodon verticillatus*, swamp loosestrife. "What stout, woody, perennial rootstocks!" he exclaimed.[70] Lindeman observed in his *American Midland Naturalist* article that most of Cedar Bog Lake "is bordered by an invading front" of *Decodon*, "a plant rare in Minnesota but very abundant in the Cedar Bog." *Decodon* is better adapted than *Typha latifolia* (cattail), its rival in the battle for invasion supremacy from the shoreline, particularly with high water, he wrote. Both *Decodon* and *Typha* are key contributors to the vegetative mat that, based on the ecological principles of lake succession, will be transformed into peat-like soil that can support the growth of trees including *Thuja occidentalis*, the white cedar after which Cedar Creek with its bog lake was named.

The ecological principles of lake succession are no longer the exclusive province of the natural world. Seen from the sky on a clear summer day, Cedar Bog Lake is like an oval mirror framed in green felt. We can imagine that the mirror reflects not just a summer sky beneath which a graduate student once collected samples but an atmosphere dramatically altered by human agency in ways we struggle to comprehend because we cannot see it. The sunlight that animated ecosystems eons ago, now effectively packed in organic materials from *Decodon* and *Typha* and other plants and animals, is being massively resurrected from Earth's subterranean vaults. These materials are burned at eight times the rate they were when Lindeman extended his sampling rod into Cedar Bog Lake.[71] Their combustion produces tens of billions of tons of waste compounds each year that cannot readily be gathered and stored or shipped. For now, living things and their ecosystems have little choice but to adapt to having these waste compounds in their midst.

In time, the relentless biotic encirclement and encroachment of the lake Lindeman came to know so intimately will transform it, as he envisioned the natural course of lake succession. The oval mirror will go dark, covered over by sedge mat succeeded by bog forest. Meanwhile, an unnatural ecological transformation flowing from laws governing energy and heat, breathtaking in scope, is well underway.

Modern ecology constitutes the interplay of science and conservation, an interplay reflected in the research of young investigators who receive the Raymond L. Lindeman Award for aquatic science.[72] Lindeman undertook his ecological and developmental studies of Cedar Bog Lake just as public attitudes towards prairie wetlands were shifting. In his book about the wetlands of the American Midwest, geographer Hugh Prince describes how growing interest in wildlife conservation, elevated by Aldo Leopold, dramatically slowed the massive draining of prairie wetlands for agriculture that came with Euro-American settlement.[73] Wetland ecosystems, he concluded, are culturally constructed representations of deep history.

The Cedar Creek upland forest-wetland mosaic that Lindeman came to know stretches across the heart of the Anoka Sand Plain. The ecological succession of the bog lake he explored proceeds largely as nature would have it proceed. In contrast, the prairie-wetland mosaic of Redwood County at the time of Thoreau's visit has been transformed into a food production grid. Like much of Earth, southwestern Minnesota no longer possesses a natural history unaltered by human design. But it produced Lindeman just as the wetlands preservation movement was beginning to flower on the Prairie. It gave the world a keen intelligence for imagining and describing the life-energy dynamic of an aquatic system, an ecosystems dynamic animated by energy from the sun.

Notes

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[1] Bethe's classic paper is H. A. Bethe, "Energy Production in Stars," *Physical Review* 53 (1939): 434-56. The reference to Lindeman's dirty hands and feet can be found in Robert W. Sterner, "Raymond Laurel Lindeman and the Trophic Dynamic Viewpoint," *Limnology and Oceanography Bulletin* 21 (May 2012): 47. The reference to Bethe's muddy shoes is from the account of his student and future famous physicist in his own right Freeman Dyson in his memoir *Disturbing the Universe* (New York: Basic Books, 1979): 47.

[2] Raymond L. Lindeman, "The Trophic-Dynamic Aspect of Ecology," *Ecology* 23 (1942): 399-417. Lindeman's paper was drawn from the final chapter of his doctoral thesis "Ecological Dynamics in a Senescent Lake" (1941). Gary W. Barrett and Karen E. Mabry in "Twentieth-Century Classic Books and Benchmark Publications in Biology," *BioScience* 52 (2002): 282-285, rank Lindeman's paper third among journal articles that biologists considered to have had "the greatest impact with respect to their career training" based on a survey of American Institute of Biological Sciences (AIBS) members. They wrote: "Lindeman's 1942 paper . . . not only set the stage for both Odum's classic text [see next note] but also provided a functional (energetic) basis for this emerging science."

[3] Eugene P. Odum, *Fundamentals of Ecology* (Philadelphia: W. B. Saunders Company, 1953). In his book *A History of the Ecosystem Concept in Ecology* (New Haven, CT: Yale University Press, 1993), ecologist and environmental historian Frank B. Golley wrote that "Eugene P. Odum's use of the ecosystem concept as an organizing concept . . . in his popular, widely used textbook, *Fundamentals of Ecology*, transformed a specialized technical idea into a concept with vast theoretical and applied significance."

[4] Paul R. Krausman and Bruce D. Leopold, eds. *Essential Readings in Wildlife Management and Conservation* (Baltimore: Johns Hopkins University Press, 2013): 213-33.

[5] H. A. Bethe, "Energy Production in Stars" Nobel Lecture, December 11, 1967, 233, accessed January 17, 2015, http://www.nobelprize.org/nobel_prizes/physics/laureates/1967/bethe-lecture.html. In his Nobel lecture, Bethe observed that in a supernova explosion much of the material of the star, probably containing heavy elements, is ejected into interstellar space and can then be collected again by newly forming stars. "This means that most of the stars we see, including our sun, are at least second generation stars, which have collected the debris of earlier stars which have suffered a supernova explosion."

[6] Lindeman (1942), 400.

[7] George R. Shiner and Robert Schneider, "Geology and Ground-Water Conditions of the Redwood Falls Area, Redwood County, Minnesota," U.S. Geological Survey Water-Supply Paper 1669R (Washington, DC: United States Government Printing Office, 1964), R1-R2. See also the contributions of Thomas Dilley on geology and Neal S. Eash on soils in Murray County adjacent to Redwood County in *Draining the Great Oasis: An Environmental History of Murray County, Minnesota*, Anthony J. Amato, Janet Timmerman, and Joseph A. Amato, eds. (Marshall, MN: Crossings Press, 2001). Contributors to Joseph Amato and David Pichaske, eds., *Southwest Minnesota: A Place of Many Places* (Marshall, MN: Crossings Press, 2000) explore the history, land, culture, and character of the Redwood Falls region.

[8] Raymond L. Lindeman, "The Developmental History of Cedar Creek Bog, Minnesota," *American Midland Naturalist* 25 (1941): 101-12.

[9] Franklyn Curtiss-Wedge, "The History of Redwood County, Minnesota," Volumes I and II (Chicago: H. C. Cooper, Jr. & Co., 1916). The verse citing Otto Lindeman and suggesting his future wife Julia Ash is from "The Senior," the 1910 senior yearbook of the University of Minnesota (University of Minnesota Archives).

[10] Robert W. Sterner, "Raymond Laurel Lindeman and the Trophic Dynamic Viewpoint," *Limnology and Oceanography Bulletin* 21 (May 2012): 38-51. Sterner's is the best account of what is known about Lindeman concerning his upbringing on the farm (40-41), his collegiate, graduate school and postgraduate experiences (41-44), and those who influenced him (44-46). Sterner also explains the conceptual background for Lindeman's trophic dynamic viewpoint and its development while Lindeman was a Yale University postdoctoral fellow working under G. Evelyn Hutchinson (46-49).

[11] Joel B. Hagen, *An Entangled Bank: The Origins of Ecosystem Ecology* (New Brunswick, NJ: Rutgers University Press, 1992): 87-88.

[12] Sterner, 45.

[13] Ibid., 44.

[14] Anna Bramwell, *Ecology in the 20th Century: A History* (New Haven, CT: Yale University Press, 1989): 41-42. Golley, n. 3 above, 2-3.

[15] A. G. Tansley, "The Use and Abuse of Vegetational Concepts and Terms," *Ecology* 16 (1935): 284-307.

[16] Lindeman (1942): 400.

[17] Robert E. Cook, "Raymond Lindeman and the Trophic-Dynamic Concept in Ecology," *Science* 198, 22-26. Lindeman's doctoral thesis is R. L. Lindeman, "Ecological Dynamics in a Senescent Lake," University of Minnesota (1941).

[18] Charles Elton, *Animal Ecology* (New York: Macmillan Co., 1927).

[19] Lindeman (1942): 408.

[20] Ibid.

[21] Lindeman proposed that about ten percent of energy is stored in organisms populating each ascending trophic layer of the food pyramid. Thus about ten percent of the net productivity of primary producers is incorporated by herbivores, about ten percent of the net productivity of herbivores is incorporated by first-level carnivores, and so on. J. L.

Chapman and M. J. Reiss, *Ecology: Principles and Applications* (Cambridge, UK: Cambridge University Press, 1999), 142. For an estimation of the median human trophic level in the food pyramid or food web, see Sylvain Bonhommeau, et al., "Eating Up the World's Food Web and the Human Trophic Level," *Proceedings of the National Academy of Sciences U.S.A.* 110 (2013): 20617-20620.

[22] David Tilman and Michael Clark, "Global Diets Link Environmental Sustainability and Human Health," *Nature* 515 (2014): 518-22.

[23] Bradley J. Cardinale, et al., "Biodiversity Loss and Its Impact on Humanity, *Nature* 489 (2012): 59, 65.

[24] David Tilman, Peter B. Reich and Forrest Isbell, "Biodiversity Impacts Ecosystem Productivity as Much as Resources, Disturbance, or Herbivory," *Proceedings of the National Academy of Sciences U.S.A.* 109 (26) (2012): 10394.

[25] Lindeman (1942): 399.

[26] Vladimir I. Vernadsky, *The Biosphere* (New York: Springer Science & Business Media, 1998). For accounts of Eduard Suess coining the term "the biosphere" and the publication of Vernadsky's *The Biosphere* in diff erent languages, see Nicholas Polunin and Jacques Grinevald, "Vernadsky and Biospheral Ecology," *Environmental Conservation* 15 (1988): 118.

[27] Ibid., 91.

[28] Nancy G. Slack, G. *Evelyn Hutchinson and the Invention of Modern Ecology* (New Haven, CT: Yale University Press, 2011). For Hutchinson's upbringing in Cambridge, see Chapter 2, 15-41. For Elton's influence, 144-45. For Vernadsky's influence, 171-73. In the foreword, Harvard biologist and author E. O. Wilson called Hutchinson "the last great Victorian naturalist, a pioneer of modern ecology and justifiably called its founder, the one who brought the discipline into the Modern Synthesis of evolutionary theory." Eville Gorham in "Biogeochemistry: Its Origins and Development," *Biogeochemistry* 13 (1991): 199-239, acknowledges "the inspiration of G. E. Hutchinson and his academic descendants" in his valuable overview of the biogeochemical concept with origins that preceded Vernadsky. Gorham conducted pioneering studies of the effects of acidic precipitation and carbon cycle perturbations on lakes, bogs, and peatlands as a University of Minnesota ecologist.

[29] Slack, 134-35.

[30] Hagen, 65.

[31] For Slack's concluding remarks about Hutchinson being a polymath, 371. For her reference to Hutchinson requiring his graduate students to read Vernadsky's *Biosphere*, 173.

[32] V. I. Vernadsky, "The Biosphere and the Noosphere," *American Scientist* 33 (1945): 1-12. The word "noosphere," the "sphere of the mind or intellect," was coined in Paris in the 1920s by the French scientist and Jesuit priest Pierre Teilhard de Chardin, the French philosopher Edouard Le Roy, and Vernadsky. See Paul R. Samson and David Pitt (eds.), *The Biosphere and Noosphere Reader* (London: Routledge, 1999), 4.

[33] G. E. Hutchinson, "On Living in the Biosphere," *The Scientific Monthly* 67 (1948): 393-97. For Hutchinson's acquaintance and collaboration with George Vernadsky, see Polunin and Grinevald, 119, n. 26 above.

[34] Permanent Constitution: Ecologist's Union, adopted December 31, 1947. The Aldo Leopold Archives, accessed January 17, 2015, http://uwdc.library.wisc.edu/collections/AldoLeopold. For Leopold's interest in protecting Western public lands, see his letter to Ecologist's Union chairman Curtis L. Newcombe, December 17, 1947. For Hutchinson's interest in protecting the wetlands of "primeval America" as "living museums," see Slack, 308-10, note 28 above.[35] Richard Knight and Susanne Riedel, *Aldo Leopold and the Ecological Conscience* (New York: Oxford University Press, 2002), 93.

[36] Aldo Leopold, *A Sand County Almanac, and Sketches Here and There* (New York: Oxford University Press, 1949), 203-04, 224-25.

[37] Aldo Leopold, "A Biotic View of the Land," *Journal of Forestry* 37 (1939): 727-30.

[38] J. Baird Callicott, *Thinking Like a Planet: The Land Ethic and the Earth Ethic* (New York: Oxford University Press, 2014), 84-86. Callicott argues that Leopold had anticipated both energy transfers and materials cycling before Lindeman integrated them in his paper. Leopold failed to understand that energy flows rather than cycles, "but he did understand that energy is more fundamental than food—that energy, not food is the burning question in the biotic community."

[39] Golley, 2-3.

[40] Lindeman (1942): 409.

[41] Simone Libralato, et al., "Trophodynamics in Marine Ecology: 70 Years After Lindeman," *Marine Ecological Progress Series* 512 (2014): 6.

[42] Jordan T, et al., *Basic Research Opportunities in Earth Science* (Washington DC: National
Academy Press, 2001).

[43] National Science Foundation's Critical Zone Observatory program, accessed January 17, 2015, http://criticalzone.org/national/.

[44] Minnesota River Basin, Intensively Managed Landscapes, National Science Foundation's Critical Zone Observatory program, accessed January 17, 2015, http://criticalzone.org/iml/infrastructure/field-area/minnesota-river-basin/.

[45] Daniel deB. Richter and Sharon A. Billings, "'One Physical System': Tansley's Ecosystem as Earth's Critical Zone," *New Phytologist* (2015): 1-13, doi: 10.1111/nph.13338.

[46] Ibid., 3.

[47] Charles B. Reif, "Memories of Raymond Laurel Lindeman," *Bulletin of the Ecological Society of America* 67 (1986): 20-25.

[48] Oswald T. Avery, Colin M. MacLeod, and Maclyn McCarty, "Studies on the Chemical Nature of the Substance Inducing Transformation of Pneumococcal Types: Induction of Transformation by a Deoxyribonucleic Acid Fraction Isolated from Pneumococcus Type III, *Journal of Experimental Medicine* 79 (1944): 137-58.

[49] William Hoffman and Leo Furcht, *The Biologist's Imagination: Innovation in the Biosciences* (New York, Oxford University Press, 2014).

[50] Cardinale et al., 60 (see n. 23 above). Ecosystem services include provisioning services such as the production of renewable resources (e.g. food, wood, fresh water) and regulating services such as those that lessen environmental change (e.g. climate regulation, pest/disease control). Concerning the latter, an international scientific team reported in 2015 that the carbon sink services provided by the Amazon rainforests have been in decline since the 1990s, suggesting these rainforests are becoming saturated just as their environmental services are needed most to modulate global climate change. R. J. W. Brienen et al., "Long-term Decline of the Amazon Carbon Sink," *Nature* 519 (2015): 344-48. Tropical rainforests account for roughly half of all the carbon scrubbed from the atmosphere by the land biosphere. Lars O. Hedin, "Signs of Saturation in the Tropical Carbon Sink," *Nature* 519 (2015): 295.

[51] Fred W. Allendorf, Paul A. Hohenlohe and Gordon Luikart, "Genomics and the Future of Conservation Genetics," *Nature Reviews Genetics* 11 (2010): 697-709.

[52] Thomas G. Whitham, et al., "A Framework for Community and Ecosystem Genetics:
From Genes to Ecosystems," *Nature Reviews Genetics* 7 (2006): 510-23.

[53] Joseph K. Bailey, et al., "Importance of Species Interactions to Community
Heritability: A Genetic Basis to Trophic-level Interactions," *Ecology Letters* 9 (2006): 78-85.

[54] Olivia U. Mason, et al., "Metagenomics Reveals Sediment Microbial Community Response to Deepwater Horizon Oil Spill," *ISME Journal* 8 (2014): 1464-75.

[55] Kevin M. Esvelt, Andrea L. Smidler, Flaminia Catteruccia, and George M. Church, "Concerning RNA-guided Gene Drives for the Alteration of Wild Populations," eLife (2014), 10.7554/eLife.03401.

[56] Aaron B.A. Shafer, et al., "Genomics and the Challenging Translation into Conservation Practice," *Trends in Ecology & Evolution* 30 (2015): 78-87.

[57] Letter from Raymond Lindeman to Charles Reif, May 16, 1942, Lindeman papers, Yale Archives. Reported in Robert W. Sterner, 43, n. 10 above.

[58] Cook, 24.

[59] Ibid., 25.

[60] Golley, 59-60.

[61] Steve Cousins, "The Decline of the Trophic Level Concept," *Trends in Ecology & Evolution* 2 (1987): 312-16.

[62] Robert E. Ulanowicz, "Ecosystem Trophic Foundations: Lindeman Exonerata" in *Complex Ecology: The Part-Whole Relation in Ecosystems*, Bernard C. Patten and Sven E. Jorgensen, eds. (New York: Prentice Hall, 1994), 559.

[63] James H. Brown, et al., "Energetic Limits to Economic Growth," *BioScience* 61 (2011): 19-26. Herman E. Daly, *Ecological Economics and*

Sustainable Development (Edward Elgar Pub, 2008), 143-45. Adam Frank, "Is a Climate Disaster Inevitable?" *The New York Times*, January 15, 2015. An astrophysicist at the University of Rochester, Frank notes that no matter on what planet they live "any species climbing up the technological ladder by harvesting energy through combustion must alter the chemical makeup of its atmosphere to some degree" because chemical byproducts from combustion "can't just disappear."

[64] Jason Simus, "Metaphors and Metaphysics in Ecology," *Worldviews* 15 (2011): 185-202.

[65] Lindeman (1942): 411. John Kricher discusses Lindeman and his revolutionary paper in the context of the "balance of nature" paradigm in his book *The Balance of Nature: Ecology's Enduring Myth* (Princeton, NJ: Princeton University Press, 2009): 75-77. According to Golley, 59, n. 3 above, one of the organizing principles of Hutchinson's theoretical work was "the familiar concept of system equilibrium or balance. He thought that systems evidenced processes of self-regulation that produced and maintained equilibrium conditions."

[66] Jessica M. Anna, Gregory D. Scholes and Rienk van Grondelle, "A Little Coherence in Photosynthetic Light Harvesting," *BioScience* 64 (2014): 14-25. The authors write that because biological systems are so complex, statistical approaches are employed to determine averages in cellular processes such as respiration and enzymatic activity. As a result, quantum mechanical (or *coherent*) phenomena are hidden. A new technology called two-dimensional electronic spectroscopy is being used to identify coherent [quantum] contributions to energy transfer dynamics in photosynthetic complexes.

[67] Robert E. Ulanowicz, "Some Steps Toward a Central Theory of Ecosystem Dynamics," *Computation Biology and Chemistry* 207 (2003): 523.

[68] Robert E. Ulanowicz, "Limits on Ecosystem Trophic Complexity: Insights from Ecological Network Analysis," *Ecology Letters* 17 (2014). See also Jason Simus, "Metaphors and Metaphysics," no. 64 above.

[69] For Thoreau's account of his visit to Redwood Falls, see Letter to F. B. Sanborn (at Concord) from Henry David Thoreau, Redwing, Minnesota, June 26, 1861 in Franklin B. Sanborn, *The Familiar Letters of Henry David Thoreau* (Boston: Houghton Mifflin 1894), 445-53. For Thoreau's visit to Minnesota in 1861 including his journey to Redwood Falls via the Minnesota River, see John T. Flanagan, "Thoreau in Minnesota," in *Minnesota* History, 16 (1935), 35-46, and Harriet M. Sweetland, "The Significance of Thoreau's Trip to the Upper Mississippi in 1861," *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* LI (1962): 267-86. For a short description of Thoreau's walking, botanizing, and description of American landscapes, see Joseph A. Amato, *On Foot: A History of Walking* (New York: New York University Press, 2006), 141-47.

[70] Henry David Thoreau, *The Writings of Henry David Thoreau: Journal*, edited by Bradford Torrey and Franklin Benjamin Sanborn (Boston: Houghton Mifflin, 1906), 308.

[71] Angus Maddison, *Contours of the World Economy 1-2030 AD: Essays in Macroeconomic History* (New York: Oxford University Press, 2007). See Chapter 7, Table 7.11, World Consumption of Primary Energy, 1820-2030 (metric tons of oil equivalent), fossil fuels (million tons).

[72] Information about the annual Raymond L. Lindeman Award can be found at http://www.aslo.org/information/awards.html. The award recognizes an outstanding paper written by an author who is no older than 35 years and published in a peer-reviewed journal in the aquatic sciences.

[73] Hugh Prince, *Wetlands of the American Midwest: A Historical Geography of Changing Attitudes* (Chicago: University of Chicago Press, 2008), 1, 347.