can serve as an exemplar for other interdisciplinary and emerging fields of science.

To date, the computer database has taken two pathways. The first piece is our web-based centralized "Big Canopy Database." This database holds information, field data, and images of use to canopy researchers, educators, and conservationists, including lists of researcher contacts, research projects, study area descriptions, images, canopy-dwelling taxa, visualization and analysis programs, meetings, training programs, equipment and safety descriptions, and scientific and popular citations. A prototype is available for viewing at <www.evergreen.edu/canopydb>

The second piece is a web-based program called "Emerald," which will allow canopy researchers to search for and download field data submitted by other researchers, design field databases and download them for their own use, and to document and archive their own databases. The system thus builds new databases from database components that "fit" canopy data. We term these components "templates."

"Emerald" currently contains data sets from six different canopy projects. To submit data to the database, a researcher from each study works directly with a database technician to provide metadata and to structure his/ her data to fit one or more existing field data templates, or to generate a new template for novel data types. We anticipate that after some number of studies are entered, a finite number of data templates will be available, and researchers joining the database will find what they need within the program, obviating the need for an intermediary. The current Emerald prototype is implemented in SQLServer, Microsoft's Active Server Pages (ASP) and HTML. We are currently enhancing that prototype, using SQL Serve, but with Java rather than ASP.

Our efforts to create a database for the canopy research community will help push forward this emerging field of science. We also believe that our efforts could be viewed as a model for other emerging areas of ecology, where data-linking and data-sharing can be effective in integrating results from different studies. We seek input from researchers in the field of canopy studies to contribute to the database, and from those outside the field who may have insights into making this process efficient and productive.

Literature cited

Lowman, M. D., and N. M. Nadkarni. 1995. Forest canopies. Academic Press, San Diego, California, USA.

- Lowman, M. D., and P. K. Wittman. 1996. Forest canopies: methods, hypotheses, and future directions. Annual Review of Ecology and Systematics **27**:55–81.
- Nadkarni, N. M., and G. G. Parker. 1994. A profile of forest canopy science and scientists—who we are, what we want to know, and obstacles we face: results of an international survey. Selbyana **15**: 38–50.
- Nadkarni, N., G. G. Parker, E. D. Ford, J. B. Cushing, and C. Stallman. 1996. The International Canopy Network: a pathway for interdisciplinary exchange of scientific information on forest canopies. Northwest Science **70**:104–108.
- Parker, G. G. 1995. Structure and microclimate of forest canopies. Pages 73–106 *in* M. Lowman and N. Nadkarni, editors. Forest canopies. Academic Press, San Diego, California, USA.
- Parker, G. G., A. P. Smith, and K. P. Hogan. 1992. Access to the upper forest canopy with a large tower crane. BioScience **42**:664–670.

Nalini M. Nadkarni and Judy B. Cushing The Evergreen State College Olympia, Washington 98505 USA

A History of the Ecological Sciences, Part 3. Hellenistic Natural History

The ancient Greeks called themselves "Hellenes," and historians use the adjective "Hellenistic" to refer to the period beginning with Alexander's conquest of the Persian Empire (334– 329 BC), when Greek culture started to spread throughout the eastern Mediterranean region. Although the Hellenistic Age is often said to end in 30 BC—when Rome conquered Egypt and Cleopatra committed suicide— Hellenistic culture, including science, persisted throughout the Roman period (Sarton 1959, Lloyd 1973). The previous essay summarized the contributions of the Lyceum under Aristotle and Theophrastos; this one surveys Greek writings of ecological significance from the 200s BC into the AD 200s.

Dominant economic and cultural activity shifted from Athens to Alexandria, Egypt, one of a dozen places that Alexander named for himself. Egypt's earliest Macedonian rulers, Ptolemaios I and Ptolemaios II, patronized learning and endowed at Alexandria a graduate research institute, the Museum, which collected the most important library of antiquity. Scholars attracted to Alexandria did outstanding literary, mathematical, and scientific research. The Lyceum's studies on the natural history of animals and plants were so impressive that the Museum's scientists turned to other subjects. The Lyceum's contributions to comparative animal anatomy provided a foundation for the Museum's detailed studies on human cadavers. Euclid (flourished 295 BC) synthesized the cumulative knowledge of three centuries in his Elements of Geometry, the first and most successful textbook ever published. It became a foundation for further advances in geometry and for the sciences of geography, optics, statics, hydrostatics, and astronomy.

Eratosthenes of Cyrene (c.276c.195 BC), who headed the Library of the Museum, demonstrated the power of geometry by applying it to the earth sciences-most spectacularly by calculating the circumference of the earth with just three simple measurements (Dicks 1971). Assuming the Euclidian proposition that angles created by a line connecting two parallel lines are equal, he needed to measure an angle created by the shadow of a sundial in Alexandria on the summer solstice at noon when another sundial at Syene, on the Nile near Aswan, did not cast a shadow. He had to assume that the sun rays striking both locations were parallel and that Alexandria and Syene were on the same meridian (the actual difference is 3 degrees, 4 minutes). He had the distance between the two locations measured. Because his figures appear to be rounded off, apparently he was satisfied with approximations. Nevertheless, his geometrical method was sound and his measurements were adequate to achieve a reasonably accurate result. He also developed mathematical geography, establishing the polar and tropical circles of Cancer and Capricorn. He pointed out that mountains and valleys were insignificant in relation to the size of the earth, and thus did not distort its spherical shape. He also discussed other matters such as prevailing winds.

Since he achieved a good figure for the size of the earth by a clear and sound method, it is unfortunate that the teacher-scholar Posidonios of Apameia (c.135-c.51 BC) recalculated it by another method that was also geometrically sound, but his measurements were not (Warmington 1975). Eratosthenes' figure for the earth's circumference was 252,000 stades and Posidonios' was 180,000. As a Stoic, Posidonios wanted a precise understanding of our place in the universe, and the smaller figure may have seemed more satisfying. Columbus naturally chose to believe Posidonios when defending his project of sailing west to the East Indies, but the Portuguese who turned him down were skeptical.

Interest in astronomy and geography led to interest in astrology. Mesopotamians had invented astrology, and the Greeks learned about it when Alexander conquered the Persian Empire (Tester 1987, Burton 1994). It was compatible with Greek thought, because most Greeks had followed Pythagoros in believing that heavenly bodies were gods. Mesopotamia devised the 12 signs of the zodiac as mnemonic devices to keep up with the calendar-each sign being visible for one month-but once invented, these signs took on a life of their own. Stoicism and astrology probably awakened Posidonios' interest in earthly phenomena such as meteorology, volcanoes, and earthquakes. He was not the first to notice a connection between the sun and moon, and tides, but he first explained that spring and neap times are caused by the conjunction and opposition of sun and moon, respectively. Apparently he made actual measurements to establish the correlation. People had long known that the female menstrual cycle is correlated with the lunar cycle, and the Aristotelian Generation of Animals attempted unsuccessfully to explain why (767a:3-6). The importance of the sun for all forms of life was a commonplace, and by analogy, other heavenly bodies also influence life.

The writings of Eratosthenes and Posidonios do not survive, but the encyclopedic Geography by Strabon of Amaseia (c.64 BC-c.AD 20) does, and it drew upon their works (French 1994: Chapter 3). Born in Greece, when he was about 20, Strabon went to live in Rome, where there was little interest in mathematics. That did not bother Strabon, who lacked Eratosthenes' enthusiasm for mathematical geography. Strabon believed Homer was the first geographer, and a great one, and thought that Eratosthenes was rash for having attempted to correct Homer. Although Strabon mentioned conspicuous species of plants and animals, such as palm trees and elephants, he went into less detail about the natural products of places than Herodotos had in his History. Strabon used the abundance of grapes,

olives, and figs in different countries as indicators of fertility.

One of the most important medical works of antiquity was a pharmacopoeia written by a Greek physician, Pedanios Dioscorides (active AD 60s-70s). He was from a picturesque town, Anazarbus (now in Turkey), and he studied in the neighboring cultural center, Tarsus. He traveled widely in the Mediterranean Basin; some of these travels probably occurred during his brief stint with the Roman army (Riddle 1985). His book, although written in Greek, was widely known during the Middle Ages and Renaissance in Latin translation, and it is still known by its Latin title, De materia medica. Its direct relevance for ecology is not conspicuous, but indirectly it was quite important. Most medicines or drugs in antiquity came from plants, and his pharmacopoeia is organized mainly around plant species. (A few chapters are on animals and minerals.) Most of its chapters on approximately 537 species of plants contain 12 types of information, including (1) name and illustration, (2) habitats, (3) botanical description, and (12) geographical locations. This was the first surviving work organized on a species-byspecies basis, and therefore his book was important for botany as well as pharmacy; it focused attention on the importance of determining particular species. At times, this challenge exceeded Dioscorides' capabilities, but he inspired others to take up where he left off. Later physicians were even more concerned than he about species identification and geographical distribution, because they had such faith in his medical recipes that they were anxious to make their preparations from the proper species. If one compares Polunin and Huxley's Flowers of the Mediterranean (1966) with Dioscorides' De materia medica, one finds that although the emphasis obviously has shifted from pharmacy to botany, the two books share similar concerns. Polunin and Huxley even mention species that once were valued medicinally, such as Paeonia mascula (L.), although their motive is no longer medicinal, but to alert readers to the fact that these species were widely transplanted beyond their original range.

Claudios Ptolemaios (c.AD100c.170) was the last great physical scientist of antiquity. By his time, Egypt's last royal family was long gone, and his name might only indicate that he was from Ptolemais, Egypt. The Museum still existed, and he was associated with it. His syntheses of astronomy, geography, and optics were enormous achievements, although his geography was handicapped by scant data on latitude and longitude. He undoubtedly understood the contributions that anatomy and physiology made to medicine, and he was convinced that astronomy could make a comparable contribution to astrology. Just as well-educated physicians complained about the quackery of poorly educated practitioners, Ptolemaios complained about poorly educated astrologers giving astrology a bad name. His Tetrabiblos ("Four Books") was intended to do for astrology what his treatises on astronomy and optics did for those subjects. Reasoning by analogy, if anyone could see the influence of the sun and moon upon earthly life as demonstrated by the seasons, tides, and menstrual cycles, then welltrained astronomers could go further and find the influence of planets. He acknowledged that the subject matter did not permit certainty (but neither did medicine, an art, permit it). He regarded the influence of heavenly bodies as only one of the determinants of earthly phenomena. "But, plausible as [his] introduction might appear to an ancient philosopher, the rest of the treatise shows it to be a specious "scientific" justification for crude superstition" (Toomer 1975:198).

Early hunting-gathering bands had extensive knowledge of many plants and animals on which they depended. After population growth forced people to switch to growing crops and tending livestock, much of that knowledge was lost, while tribal people gained new knowledge of domesticates. However, some people who owned slaves, and thus had leisure time, revived hunting and fishing as sports. This was true of royalty in Egypt, Mesopotamia, and Macedonia, where these activities were portrayed by artists; not much written natural history came from those civilizations. At a humbler level, hunting and fishing did stimulate Greeks to record observations, partly because the animals targeted seemed fascinating and partly to offer guidance for these activities. An early example was the Cynegeticos by Xenophon of Athens (c.430–355 BC), one of Socrates' students. Xenophon is best remembered for his memoir of life as a mercenary soldier, Anabasis. He advocated hunting as good training for war. Most of his advice was on choice of hunting dogs, techniques, and equipment. However, he apparently observed hares over many years, and he provided the earliest detailed account of any animal in his discussion of their habits and hunting them.

During the following four centuries, there were similar writings by other hunters and fishers, which survive in fragments if at all. Two surviving poems on marine fishing and hunting are based on these earlier writings, rather than on personal experience; both were attributed to Oppianos, but are no longer thought to have been written by the same person. The longer poem (3506 lines) on fishing, Halieutika, is attributed to Oppianos of Cilicia (flourished AD 170s); whereas the shorter one (2149 lines) on hunting, Cynegetika, is attributed to Oppianos of Apamea (flourished AD 210s). They both contain lore akin to ecology. Halieutika has attracted the most scholarly interest (Gow 1968, Bodson 1981), because its sources reflect actual experience, whereas Cynegetika is based upon uncritical folklore. Oppianos of Cilicia provides much information on habits, habitat, breeding, feeding, and parasites of both fish and shellfish. For example (I:92-110, slightly abridged, Mair translation):

> Fishes differ in breed and habit and in their path in the sea, and not all fishes have like range. Some keep by the low shores, feeding on sand

and whatever things grow in the sand: Sea-horse, the swift Cuckoo-fish, yellow Erythinus, Citharus, Red Mullet, the feeble Melanurus, shoals of Trachurus, Sole, Platyurus, the weak Ribbon-fish, the Mormyrus of varied hue, Mackerel and the Carp. . . . Others feed in the mud and the shallows of the sea: Skate, the monster tribes of the Ox-ray, the terrible Stingray, Cramp-fish, Turbot, Callarias, Red Mullet, Oniscus, Horse-mackerel and the Scepanus.... On the weedy beach under the green grasses feed Maenis, Goatfish, Atherine, Smaris, Blenny, and both sorts of Bogue...

Oppianos of Apamea was interested in relationships between vertebrate species, both predation and mutualism, but most of his material was inaccurate. His other interest was in breeding behavior of the larger mammals; this material was more plausible.

Another popularization from the same period is the anonymous Physiologos (Naturalist), which dealt with about 40 animals-real and mythical-a tree from India, and six stones. Its fate, however, was quite different from the Oppianos poems, because an anonymous Christian soon expanded it by adding religious interpretations, somewhat like Aesop's Fables (500s BC). This Christianized version became very popular during the Middle Ages, in the original Greek and in translations into Latin and other languages (Ley 1968:Chapter 4; French 1994:276-286).

Greek medicine flourished during Hellenistic civilization. Concern for healthy environments continued and awareness of parasites apparently increased. Galenos of Pergamum (c.AD 129–c.200) was the last important medical scientist–practitioner. He was a very industrious author and polemicist, although some writings attributed to him but not mentioned in his medical autobiography are probably not authentic (Scarborough 1981). He was a traditionalist who followed Hippocratic medicine and Aristotelian scientific theory. Galenos is the earliest known experimenter in physiology, although he was not diligent enough to establish experimentation as essential. He left no treatise on parasitology, but mentioned parasites in many of his medical works (Hoeppli 1959, Théodoridès 1966). He believed that helminths were generated spontaneously from intestinal contents, and that the liver hydatids arose from fascia surrounding the liver. Greek medicine explained disease, in general, as being caused by an imbalance of four humours: blood, phlegm, yellow bile, and black bile. Galenos suggested that scabies was caused by a disturbance of black bile. He did not realize that malaria is a parasitic disease, and he explained tertian fever as caused by deranged yellow bile, quartan fever by deranged black bile, and quotidian fever by deranged phlegm. In parasitology, his traditionalist mindset inhibited him from appreciating the significance of what he saw, and his unprecedented medical knowledge did not enable him to make any theoretical or therapeutic progress.

There was much philosophical ferment during Hellenistic times, some of which was ecologically relevant. I will discuss two examples, saving the others for my next essay on Roman natural history. Alexander of Aphrodisias (flourished AD100s-early 200s), who became head of the Lyceum and a commentator on the Aristotelian Corpus, mentioned in his Problemata (Book 2, Section 64) that differential longevity is a factor tending to preserve the balance of nature: species that can only produce a few young at a time tend to be long-lived so that they can keep reproducing, and species that can produce many young at a time tend to be short-lived. Plotinos (c.204-270), a Neoplatonic Egyptian philosopher who wrote in Greek and taught in Rome, achieved a somewhat dynamic view of the balance of nature within his theology (Lovejoy 1936, Blakeley 1997). He wanted to reconcile the existence of evil with belief in an omnipotent, benevolent creator. Predation was one such evil, which he decided was essential for the greatest diversity and quantity of life to exist: the positive good of life more than justified the suffering and death that predation causes (*Enneads* III, 2:15).

Hellenistic science, especially at the Alexandria Museum, progressed far beyond the achievements at the Lyceum in Athens. Yet little of this progress was ecologically relevant, and none matched in ecological importance the relevant writings from the Lyceum. From c.200 BC to c.AD 200, writings of ecological significance were diverse and there were no means, theoretical or practical, to bring them together.

Literature cited

- Alexander of Aphrodisias. 1488. Problemata. Latin translation by George Vallam. Antonius de Strata, Venice, Italy.
- Barton, T. 1994. Ancient astrology. Routledge, New York, New York, USA.
- Blakeley, D. N. 1997. Plotinus as environmentalist? Chapter 12 *in* L. Westra and T. M. Robinson, editors. The Greeks and the environment. Rowman and Littlefield, Lanham, New York, USA.
- Bodenheimer, F. S. 1952. Xenophon in the history of biology. Archives Internationales D'histoire des Sciences **5**:56–64.
- Bodson, L. 1981. L'incubation buccopharyngienne de *Sarotherodon niloticus* (Pices: Cichlidae) dans la tradition grecque ancienne. Archives Internationales D'histoire des Sciences **31**:5–25.
- Dicks, D. R. 1971. Eratosthenes. Dictionary of Scientific Biography 4:388–393.
- Dioscorides, P. 1906–1914. De materia medica libri quinque. Max Wellmann, editor. Three volumes. [In Greek.] Weidmann, Berlin, Germany.
- Dioscorides, P. 1934. The Greek herbal. Translated by J. Goodyer (1655). Edited by R. T. Gunther. Oxford University Press, Oxford, UK. 1959 reprint. Hafner, New York, New York, USA.
- French, R. K. 1994. Ancient natural history: histories of nature. Routledge, New York, New York, USA.

- Gow, A. S. F. 1968. On the Halieutica of Oppian. Classical Quarterly **18**: 60–68.
- Hoeppli, R. J. 1959. Parasites and parasitic infections in early medicine and science. University of Malaya Press, Singapore.
- Ley, W. 1968. Dawn of zoology. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
- Lloyd, G. E. R. 1973. Greek science after Aristotle. Chatto & Windus, London, UK.
- Lovejoy, A. O. 1936. The great chain of being: a study of the history of an idea. Harvard University Press, Cambridge, Massachusetts, USA.
- Merlan, P. 1970. Alexander of Aphrodisias. Dictionary of Scientific Biography **1**:117–120.
- Oppianos. 1928. Cynegetica, or the Chase, and Halieutica, or Fishing. [In Greek.] Translation by A. M. Mair. Harvard University Press, Cambridge, Massachusetts, USA.
- Plotinos. 1966–1988. Enneads. Seven volumes. [In Greek.] Translation by A. H. Armstrong. Harvard University Press, Cambridge, Massachusetts, USA.
- Polunin, O., and A. Huxley. 1966. Flowers of the Mediterranean. Houghton Mifflin, Boston, Massachusetts, USA.
- Ptolemaios, C. 1940. Tetrabiblos. [In Greek.] Translation by F. E. Robbins. Harvard University Press, Cambridge, Massachusetts, USA.
- Riddle, J. M. 1985. Dioscorides on pharmacy and medicine. University of Texas Press, Austin, Texas, USA.
- Sarton, G. 1959. A history of science: Hellenistic science and culture in the last three centuries B.C. Harvard University Press, Cambridge, Massachusetts, USA.
- Scarborough, J. 1981. The Galenic question. Sudhoffs Archiv für Geschichte der Medizin **65**:1–30.
- Strabon. 1917–1935. The geography. [In Greek.] Translation by H. L. Jones. Harvard University Press, Cambridge, Massachusetts, USA.
- Tester, S. J. 1987. A history of Western astrology. Boydell, Wolfeboro, New Hampshire, USA.
- Théodoridès, J. 1966. Les grandes étapes de la parasitologie. Clio Medica 1:129–145.

- Toomer, G. J. 1975. Ptolemy (or Claudius Ptolemaeus). Dictionary of Scientific Biography 11:186–206.
- Xenophon. 1925. On hunting. Pages 365–457 in Scripta minora. [In Greek.] Translation by E. C. Marchant. Harvard University Press, Cambridge, Massachusetts, USA.
- Warmington, E. H. 1975. Posidonius. Dictionary of Scientific Biography 11:103–106.
- Westra, L., and T. M. Robinson, editors. 1997. The Greeks and the environment. Rowman & Littlefield, Lanham, New York, USA.

Frank N. Egerton Department of History University of Wisconsin–Parkside E-mail: frank.egerton@uwp.edu

Baseline Theory of Biodiversity and Ecosystem Function

Understanding the relationship between species richness and ecosystem properties is critically important to ecology and conservation biology. Hart et al. (2001) attempt to unite several conjectures about the shape of the relationship between species richness and ecosystem function. I offer two extensions toward this goal of a simple, unified theory that might provide a baseline for evaluating data on species richness and ecosystem properties.

First, the general relationship between species richness and community function could be even simpler than presented. Hart et al. (2001) assumed that community function increases to an asymptote at some threshold level of richness, and does not change for further increases in species richness. I would throw out the threshold and assume a single curve that always increases with species richness, but at a decelerating rate (see Fig. 1). Apparent threshold effects could occur due to our P < 0.05 convention for statistics. Even though the same biological principles hold throughout, researchers working with different portions of the same asymptotic function might reach different conclusions. At low species richness, researchers would quite likely not detect statistically significant curvature, and assume a linearly increasing relationship. At high species richness, researchers would quite likely not detect statistically significant changes, and assume no relationship existed.

Second, I propose new tools for calculating how sampling effects could produce a relationship between species richness and ecosystem function. For an ecosystem property such as productivity, an extreme possibility is that a mix of species performs no better than the most productive, best performing species in that mix. Nevertheless, performance increases with species richness because, on average, the best value in a sample increases with sample size. Order statistics predict both the mean and variance for such sampling effects (Arnold et al. 1992), and vast tables of results have already been compiled for many distributions (e.g., Harter and Balakrishnan 1996). Often, the variance decreases as the mean increases with larger samples (Fig. 1). Although sampling effects have been vigorously debated, our theoretical expectations seem poorly defined (see Loreau 2000 for a review). To my knowledge, the sampling effect has only been calculated for a uniform distribution (Tilman et al. 1997: first model), and by simulated resampling of observed values (Huston 1997). Order statistics may help us refine our theoretical expectations for the relationship between species richness and ecosystem function.

Literature cited

- Arnold, B. C., N. Balakrishnan, and H. N. Nagaraja. 1992. A first course in order statistics. J. Wiley, New York, New York, USA.
- Hart, M. M., R. J. Reader, and J. N. Klironomos. 2001. Biodiversity and ecosystem function: alternate hypotheses or a single theory? ESA Bulletin **82**:88–90.
- Harter, H. L., and N. Balakrishnan. 1996. CRC handbook of tables for the use of order statistics in estimation. CRC Press, Boca Raton, Florida, USA.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluation of the ecosystem function of biodiversity. Oecologia **110**:449–460.
- Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos **91:**3–17.
- Tilman, D., C. L. Lehman, and K. T. Thomson. 1997. Plant diversity and ecosystem productivity: theoretical considerations. Proceedings of the National Academy of Sciences (USA) 94:1857–1861.

Peter A. Bednekoff Biology Department Eastern Michigan University Ypsilanti, MI 48197 E-mail: peter.bednekoff@emich.edu



Fig. 1. Sampling effects lead to a higher mean and lower variance for a normal distribution (mean = 0, variance = 1). See Harter and Balakrishnan (1996:Tables C1.1, C1.2).