Commentary

A History of the Ecological Sciences, Part 23: Linnaeus and the Economy of Nature

Carl Linnaeus (1707–1778) was a leading naturalist of the 1700s (Lindroth 1973, 1983, Morton 1981:259–276, 281–285, Goerke 1993, Broberg 2000, Spary 2002). All ecologists know he founded modern nomenclature and systematics (Larson 1971, Stafleu 1971, Mayr 1982:171–180, Eriksson 1983), but he is less well known for inventing an ecological science he called the economy of nature. He explained it in 1749, but the overly broad science of natural history, which he had pursued since childhood, was already ecological in outlook and content. In 1749 he generalized and formalized what he had been recording specifically and informally. A series of 186 essays, largely by Linnaeus, were defended by his students as dissertations for their doctoral degrees (Jackson 1913, Ramsbottom 1959:151–153, Smit 1989:118–119, Kiger et al.1999:231), and one of these was *Specimen academicum de oeconomia naturae* (1749), defended by Isaac J. Biberg. Linnaeus republished these dissertations in 10 volumes entitled *Amoenitates Academica* (Academic Pleasures, 1749–1790), though the last two volumes appeared posthumously. The *Amoenitates Academica* has been reprinted several times, and 19 dissertations are translated into English (Linnaeus 1775, 1781, 1977*a*, *b*). There is a helpful *Index to Scientific Names of Organisms cited in Linnaean Dissertations* (Kiger et al. 1999), with a guide to collected editions. Linnaeus' earlier natural history observations are recorded in travel books and other writings. All of his travel books and the dissertations are listed in B. H. Soulsby's catalogue of Linnaeus' works (1933:23–26, 99–151). Florence Caddy (1886–1887) provides two good maps on Linnaeus' travels, though the caption to the one at the end of volume I is misdated 1735–1738 (read 1732–1738).

Fig. 1. Linnaeus in his Lapland clothes (or costume). Drawn in Holland by Martin Hoffman, 1737.

Fig. 2. Crane fly (*Pedicia rivosa*). Linnaeus 1811, I:186, 1971.

Wilfrid Blunt (1971) includes maps and summaries of the trips in his biography of Linnaeus. Linnaeus' travel books show his broad interest in plants, animals, geology (Merriam 2004), and economic uses of natural history (Linnaeus 1766, 1781:1–67, 1977, Koerner 1999, Müller-Wille 2003, Rausing 2003). David Black selected natural history extracts from Linnaeus' books on the 1732 and 1741 trips, which he published with a map and modern illustrations by Stephen Lee (Linnaeus 1979).

Linnaeus' first expedition was undertaken in 1732, begun on 12 May, his 25th birthday, and lasted until 10 October. He traveled north to Lapland and then west to the Norwegian coast. On the return journey he traveled in Finland down the eastern side of the Gulf of Bothinia to Åbo and then crossed to Stockholm. It was his longest journey—he estimated 633 Swedish miles or about 3800 English miles (1811, II:270, 1971)—and the subject of his longest travel book. It was also the one travel book that he illustrated. A historian of Swedish botany judged this trip "the most productive exploratory expedition ever undertaken in Sweden" (Fries 1950:18). It was sponsored by the Royal Academy of Sciences at Uppsala, which declined to publish his manuscript, and an English translation was published (1811) long before the Swedish version (1913). Linnaeus' most recent biographer, who reads Swedish, judges some of his behavior and writings on this trip rather harshly (Koerner 1999:59–65). She says he doubled the actual distance he traveled in his report (her figure is 4500 miles) because he was to be paid per mile, that he drew a map indicating travel to places he had not visited, and that he later claimed to have stayed in Lapland much longer than he had. While I cannot check all her claims, this statement is doubly wrong: "He never passed the sixtieth degree north Latitude, which marks the Arctic Circle" (Koerner 1999:61). The Arctic Circle is actually at 66°30', and he did cross it. He visited Jokkmokk (29 June) just north of that line, and more than half a dozen other places north of Jokkmokk (see map in Blunt 1971:41). She does not accuse him of inventing any of his natural history observations.

When he visited the cataract of the Elf-Carleby River on 13 May, he described the salmon fishery below the cataract, the foam and spray that the cataract generated, and surrounding plants. But he did not merely describe; he also pondered how species lived (Linnaeus 1811, I:13, 1971):

> *Oak trees grow on the summits of the surrounding rocks. At first it seems inconceivable how they should obtain nourishment; but the vapours are collected by the hills above, and trickle down in streams to their roots*.

Linnaeus's illustrations did not always represent what he discussed in most detail. For example, he made an

Fig. 3. Hawk Owl (*Surnia ulula*). Linnaeus 1811, I:205, 1971.

excellent drawing of a crane fly but only recorded that he collected it at Umeå on 9 June.

Remarkably, he shot a hawk owl from his horse, "going on at a good rate" (Linnaeus 1811, I:204, 1971), at 12:15 am. Regrettably, it was too damaged by the shot to be stuffed, but at least he drew its picture.

For two insects collected at Lulea on 21 June, he provided both illustrations and discussion (Linnaeus 1811, I:233, 1971)

> *1. A large Capricorn Beetle, variegated with a lighter hue.* (Cerambyn Sutor, the female.) *The horns were longer than the body, black, consisting of ten joints, each joint ash-coloured at its base. Body black, rugged, its wing-cases besprinkled here and there with clustered dirty spots. Abdomen cylindrical, covered towards the thorax with beautiful red lice,* (Acarus coleoptratorum).

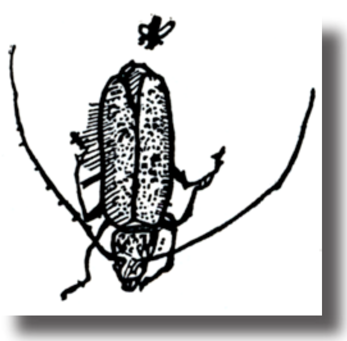

Fig. 4. Capricorn Beetle (*Cerambyx sutor*) and black fly (*Culex equines*). Linnaeus 1811, I: 232, 1971.

Fig. 5. *Rhododendron lapponicum.* Linnaeus 1811, I:301, 1971.

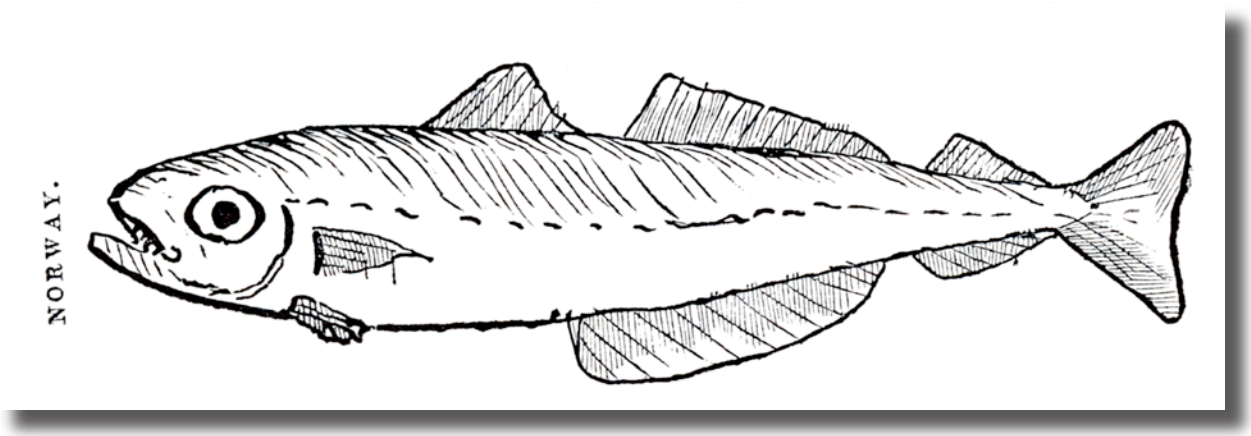

Fig. 6. Sey-fish (*Gadus virens*). Linnaeus 1811, I:342, 1971.

2. A minute black fly, with a roundish body and white wings, (Culex equines). *This infested the horses in infinite multitudes, running under the mane, and attacking them with great fierceness, being not easily driven off*.

The scientific names of species he discussed or illustrated were added by the editor, James E. Smith, from Linnaeus's *Flora Lapponica* (1737) and *Fauna Svecica* (1746). He also discussed at length a rhododendron he drew on 8 July in the Lapland Alps (Fig. 5), but only to describe it and to evaluate whether it belonged in the azalea genus (Linnaeus 1811, I:299–301, 1971).

On the Norwegian coast at Torfjorden he went fishing in a boat and caught with hook and line "plenty" of Sey-fish (*Gadus virens*), which he drew (Fig. 6). He found remora sticking to some of these 10-inch fish.

He also observed, collected, and drew four different kinds of medusa (jellyfish), but made no observations on their behavior or food (Linnaeus 1811, I:336–339, 1971). Two later Linnaean dissertations were on marine subjects: *Noctiluca Marina* (1752) on minute phosphorescent "insects," and *Natura Pelagi* (1757) on fish, turtles, and cetaceans (Smit 1979:120–123).

Reindeer were important draft and milk animals to Laplanders, and Linnaeus discussed them repeatedly in *Lachesis Lapponica* (1811), but only illustrated bridle, harness, and antlers (Linnaeus 1811, I:103–110, 135, 1971). He illustrated reindeer themselves in the frontispiece of *Flora Lapponica*, 1737). Their antlers were beginning to sprout in June, initially covered by soft skin which was often bloody from mosquito bites.

Females have smaller antlers than males. Squirrels gnawed antlers from previous years (Linnaeus 1811, I:127–128, 1971). Linnaeus' discussion of what reindeer eat is interesting (Linnaeus 1811, I:161–162, 1971):

The reindeer suffers great hardship in autumn, when, the snow being all melted away during summer, a sudden frost freezes the mountain Lichen (L. rangiferinus)*, which is his only winter food. When this fails, the animal has no other resource, for he never touches hay. His keepers fell the trees in order to supply him with*

Fig. 7. Frontispiece of Linnaeus, *Flora Lapponica* (1737), showing reindeer. The man seated in the foreground is Linnaeus. The steep mountains in the background do not represent the topography he found in Lapland.

the filamentous Lichens that clothe their branches; but this kind of food does not supply the place of what is natural to him. It is astonishing how he can get at his proper food through the deep snow that covers it, and by which it is protected from the severe frosts.

The reindeer feeds also on frogs, snakes, and even on the Lemming or Mountain Rat (Mus Lemmus)*, often pursuing the latter to so great a distance as not to find his way back again. This happened in several instances a few years ago, when these rats came down in immense numbers from the mountains.*

Fig. 8. Linnaeus' wedding portrait, 1739, by J. H. Scheffel, now at Hammarby, Linnaeus' summer home, managed by Uppsala University. Color reproduction courtesy of Hunt Institute for Botanical Documentation.

But he also reported that they ate nothing in hot weather, when mosquitoes were very troublesome (Linnaeus 1811, I:308, 1971). Later, he commented that the Lapps were negligent not to gather *Lichen rangiferinus* and horsetail (*Equisetum fluviatile*) in summer for winter fodder (Linnaeus 1811, II:107–108, 1971). Females give birth in May and fawns grow simple antlers their first year (Linnaeus 1811, I:313, 1971). In warm weather reindeer are tormented by the bites of gadflies (*Oestrus tarandi*), which leave so many scars that one author mistakenly thought they were caused by smallpox. (For more details on this fly and reindeer, see Linnaeus 1739, 1746*b*; part of the latter is translated by Susan Novikoff in Usinger 1964:5–6.) One insect, "probably a species of *Tabanus*" (Linnaeus 1811, I:280–281, 1971) bores into reindeer and lays its eggs under the skin, and the young leave by the same hole. The Lapps squeeze out the larva from their pustules to lessen the reindeer's pain. Another fly (*Oestrus nasalis*) lays eggs in reindeer nostrils (Linnaeus 1811, II:45, 1971). Reindeer also suffer from an epidemic disease that Laplanders called Pekke Kattiata that could be fatal (Linnaeus 1811, II:39–40, 1971). These observations were also included in a 1754 dissertation, *Cervus Rheno*, defended for a doctorate degree by Charles F. Hoffberg, and is translated into English (Linnaeus 1781:167–214, 1977).

On 17 July 1732, Linnaeus had a chance to see lemmings, which he described, and said they ate grass and reindeer moss. They lived mainly in the Scandinavian alps, but (Linnaeus 1811, II:19, 1971):

> *in some years thousands of them come down into the woodland countries, passing right over lakes, bogs, and marshes, by which great numbers perish. They are by no means timid, but look out, from their holes, at*

passengers, like a dog. They bring forth five or six at a birth. Their burrows are about half a quarter (of an ell?) deep.

(The parenthetic question about burrow depth was inserted by the book's editor.) Later in the book, Linnaeus raised his estimate of their numbers from thousands to millions and admitted that "nobody knows what becomes of them" (1811, II:82–83). In a still later article (Linnaeus 1740; partly translated in Blunt 1971:60), he rejected the belief that lemmings fall from clouds.

Without publishing his travel journal, Linnaeus still publicized his achievements, and the governor of Dalecarlia province offered to fund a survey of that province. Linnaeus agreed, and seven medical students gained permission to come along at their own expense. They first traveled to Falun, the provincial capital (where Linnaeus met his future wife), and then departed on their expedition on 3 July 1734, taking along the governor's two sons. Linnaeus was an organizing genius, and he delegated specialized tasks to each student: geography; climate and soils; stones, minerals and fossils; plants; animals; economics; and logistics. Every night each student added

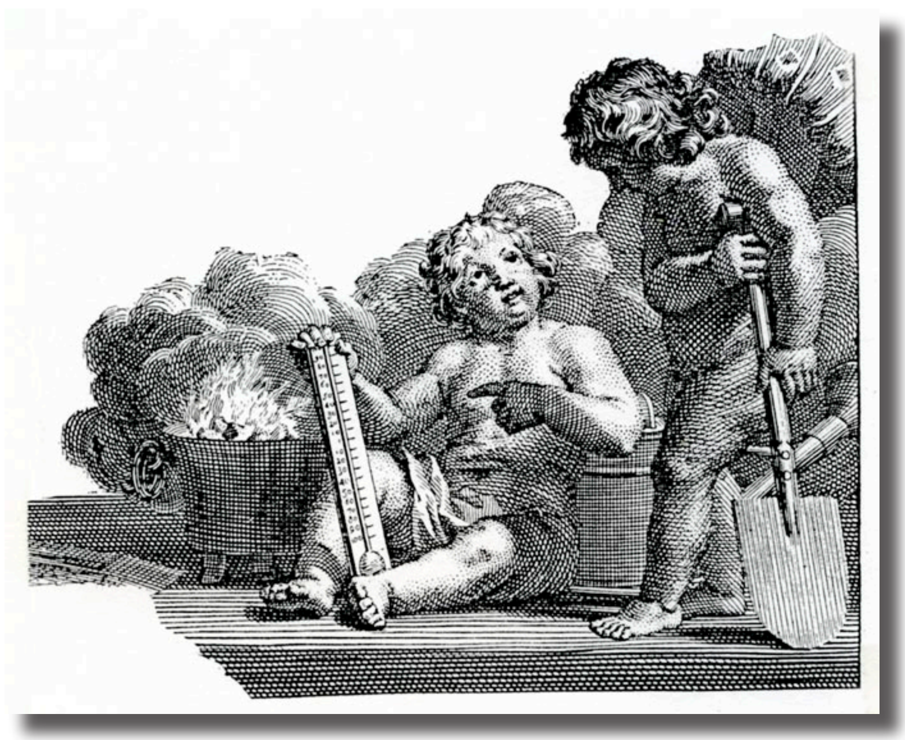

Fig. 9. Detail from frontispiece of Linnaeus, *Hortus Cliffortianus* (1737).

his report to whatever Linnaeus wrote. The last entries were dated 17 August, and when they returned to Falun, Linnaeus gave their *Iter Dalecarlium* to the governor. It was never published, but some account of the trip appeared in a Hamburg newspaper, and Linnaeus used some of their notes in later publications (Caddy 1886–1887, I:213–249, Blunt 1971:76–79).

Linnaeus did publish observations from subsequent field trips, and the book on his trip to Öland and Gotland in 1741 is also translated into English. The government (Swedish Estates of the Realm) asked him to make an economic survey, including natural history, of these islands. Accompanied by six young men, he departed from Stockholm on 15 May. It was quite cold, and Linnaeus suggested that "Spring should be measured according to climate and temperature rather than by the calendar" (Linnaeus 1973:23), and he then gave what we call phenological observations on the progress of the leaves and flowers or buds of several trees and herbs. Back in 1737 he had publicized a thermometer in the frontispiece to his *Hortus Cliffortianus*.

The thermometer was probably one he had obtained during three months spent in England, and he may have suggested to his friend Anders Celsius (1701–1744) that he reverse the scale he had developed, having boiling water at zero and freezing at 100 (Nordenmark 1935), because on 30 October 1758 Linnaeus wrote to a Montpellier botanist, Boissier de la Croix de Sauvages (English translation in Middleton 1966:100):

> *I was the first who decided to construct our thermometers in which the freezing point is 0, and the heat of boiling water 100; and this for the greenhouses of our garden*.

Two subsequent dissertations were phenological: *Vernatio Arborum* (1753) and *Calendarium Florae* (1754), and are translated into English (Linnaeus 1775:133–158, 233–286, 1977).

When our explorers reached the copper smelter at Adelfors on 23 May 1741, Linnaeus noticed that the junipers looked like "trimmed cypresses" (Linnaeus 1973:34), which he attributed to smoke from the blast furnaces. Workers and residents at Adelfors complained about the air pollution. They reached Öland on 1 June, and Linnaeus made an inventory of its plants and animals. A gamekeeper told him the time of mating and the gestation periods of red and fallow deer, wild boar, and bear, which he recorded (Linnaeus 1973:48). He examined the nest of a Rook (*Corvus frugilegus*) containing three nestlings and numerous mites (*Simulium reptans*) bloated with nestlings' blood. He counted annual rings of an oak stump and found it was 260 years old. Some rings were wider than others, which he thought was due to different severities of winters (Linnaeus 1973:58). Although modern botanists correlate annual ring width with summer moisture, this was a beginning of paleoclimatology. He knew that Francesco Redi had described 30 kinds of bird mites, which inspired Linnaeus (1973:69) to describe oystercatcher mites (*Saemundssonia haematopi*) and avocet mites (*Vanellus vanellus*). Along the seashore, he discovered that all plant species had succulent leaves, but that the majority of them growing elsewhere had ordinary dry leaves (Linnaeus 1973:72). *Potentilla anserine* grew on the sand and *Senecio vulgaris* on rotting seaweed. Cinnabar moths (*Hipocrita jacobeae*) were numerous on shore, and their larva ate the *Senecio* (Linnaeus 1973:86). He found that other plant species also had their own particular caterpillars, which he described and named, probably assisted by the entomologist Charles de Geer (Landin 1972), whom he visited at Medevi on 23 August (Linnaeus 1973:89, 199). Near the Lummelunda church he studied a marsh in which the sedge *Cladium mariscus* grew. This species had not previously been reported in Sweden; he emphasized the facts that cattle ate it in early spring and that it made good thatch for roofs. Since he learned that it grew in a former lake, he suggested that it be planted in Sweden's many "sterile and useless bogs" that could not be drained (Linnaeus 1973:113). Beyond Stenkyrka, he found under stones in water a white oval leech (*Hirundo [Nephelis] octoculata*) that could also be found in the stomachs of small fishes, and he thought that the liver worms of sheep were probably the "spawn" of this leech, which the sheep swallowed when grazing in marshy places (Linnaeus 1973:118–119). After transcribing runic inscriptions in the Hangvar churchyard on 27 June, he commented that a white lichen (*Kecabira cakcarea*) grew on the limestone tombstones but not on granite ones (Linnaeus 1973: 119).

They reached Fårö Island, just north of Gotland and much smaller (see map, Linnaeus 1973:facing page 109), on 28 June. Its inhabitants hunted seals but not porpoises. They also ate eider and their eggs, but Linnaeus

Fig. 10. Linnaeus in 1747 by Jean E. Rehn.

thought that "The time will probably come when the excellent down of these birds will save them from being shot" (Linnaeus 1973:126), but he did not explain how to collect it (possibly from their nests). He described in some detail the growth of "sandhafre" (*Ammophila arenaria*) on the sand dunes, and explained how it stabilized the dunes. He also found ant lions on the dunes that were "far more multicoulored than on Öland" (Linnaeus 1973:130). He referred the reader to Réaumur's memoir on ant lions for details.

Five years later, from 12 June to 11 August 1746, Linnaeus traveled through West Gothland and published his findings in *Wästgöte-Resa* (1747). Caddy (1886–1887, II:165–206) summarized this book, turning it into a Linnaean travelogue (she followed his route). Among the translated extracts quoted by Blunt (1971:163) is this generalization:

> *…when animals die they are converted into mould, the mould into plants. The plants are eaten by animals, thus forming the animals' limbs, so that the earth, transmuted into seed, then enters man's body as seed and is changed there by man's nature into flesh, bones, nerves, etc.; and when after death the body decomposes, the natural forces decay and man again becomes that earth from which he was taken.*

These thoughts were not especially original (Isaiah 40:6 "All flesh is grass."), but they are of interest as a prelude to the 1749 dissertation on the economy of nature.

Meanwhile, in 1744, the dissertation *Oratio de telluris habitabilis incremento* (On the increase of the habitable earth), defended by Johann Westmann, offered a novel geological theory (Frängsmyr 1983) and explanation of how the world had become populated with species (Linnaeus 1781:71–127, 1977*b*): (1) God created one pair of each sexual species and one individual of each hermaphroditic species; (2) since Adam named all species, the Garden of Eden must have been a mountain island; (3) each species increased in numbers every generation; (4) as they increased, they enlarged the geographical area they inhabited; and (5) the habitable land increased as the numbers of organisms increased. To support this argument, Linnaeus had to demonstrate the potential of all species to increase their populations. He listed the numbers of seeds reported for different flowers: *Helenium* 3000, *Zea* 2000, *Helianthus* 4000, *Papaver* 3200, and *Nicotina* 40,320. He then calculated correctly that an annual plant that only produced two seeds per year, if preserved from animals and accidents, would have 1,048,576 descendants in 20 years. That dissertation was only one of several publications that entitle Linnaeus to be called the founder of plant geography (Hofsten 1916:243–247, Browne 1983:16–23). Du Rietz (1957*a*) summarized his contributions to alpine phytogeography, paludology (on which see also Du Rietz 1957*b*), indicator plants, plant succession, limnology, and forest geography.

A fundamental difference between Linnaeus' conception of an ecological science and ours is that in his, biotic interrelationships were designed by God to work harmoniously and permanently and for the benefit of humanity (Hofsten 1957:90–102), whereas in ours, interrelationships evolve and can lead to extinction of species. His conception was part of a general outlook in science: for example, in astronomy, celestial bodies were unchanging in substance and orbits; and in geology, ongoing changes in the landscape were considered minor compared to the changes caused by God in the Flood of Noah. Scientists' study of a "static" universe gradually revealed that it is not static. This even happened to Linnaeus. In his *Systema Naturae* (1735, 1964) he confidently claimed that all species had been created by God at the beginning and no new ones had since appeared. However, the discovery of *Peloria* in 1741—so similar to *Linaria*, yet an apparently different species—shook his belief in the constancy of species. He eventually suspected that God had created only a few species, which later hybridized to form the great variety now seen (Hagberg 1952:196–205, Hofsten 1957:65–86, Larson 1971:94–121, Bowler 1989:64–68). On 18 August 1764, he explained this idea in a letter to Johannes Burmann (in Nicolas 1963:53).

> *Let us suppose God made a* Ranunculus [and that] *this species is crossed with a* Helleborus*, and* Aquilegia*, or a* Nigella *in hybrid generations. Through Divine Law the descendants of these hybrids will have, as in animals, the mother's medulla and father's cortex. As a result, there are so many of* Ranuncula *with either aquilegous leaves or nigellous ones that you could not separate them into arbitrary genera…*

Linnaeus' term "*oeconomia naturae*" (1749) is rather similar to the contemporary term for animal physiology, "animal economy," which involved studying how the parts contributed to the functioning of the whole. He may have implied an analogy between organs in an animal and species in a biotic community (Linnaeus 1775:39, 1977*a*):

> *By the Oeconomy of Nature we understand the all-wise disposition of the Creator in relation to natural things, by which they are fitted to produce general ends, and reciprocal uses.*

Having a passion for system, Linnaeus approached the economy of nature systematically. For each of the three kingdoms—stones (and soils), plants, and animals—he discussed a cycle of propagation, preservation, and destruction.

Surveying different kinds of stones under "Propagation," he suggested that one or more kinds had organic origins (Linnaeus 1775:51, 1977):

> *…testaceous bodies and petrifactions resembling plants were once real animals or vegetables; and it seems likely that shells being of a calcareous nature have changed the adjacent clay, sand, or mould into the same kind of substance. Hence we may be certain, that marble may be generated from petrifactions, and therefore it is frequently seen full of them.*

Under "Preservation," he speculated, inaccurately, on how stones are generated and augmented by water, but under "Destruction" he was more accurate in describing the actions of weather and water in the gradual erosion of rocks. He also noted that certain animals also helped erode some kinds (Linnaeus 1775:57, 1977):

> [Testaceous worms]…*eat away the hardest* rocks*. That species of* shell fish *called the* razor shell *bores thro' stones in Italy, and hides itself within them; so that the people who eat them are obliged to break the stones, before they can come at them. The* cochlea *F*[auna] *S*[vecica number] *1299. a kind of* snail *that lives on craggy* rocks*, eats, and bores through the chalky hills, as worms do through wood. This is made evident by the observations of the celebrated de Geer.*

God allegedly designed living beings to both survive and regulate each other (Linnaeus 1775:40, 1977):

> *…all living creatures should constantly be employed in producing individuals; that all natural things should contribute and lend a helping hand to preserve every species; and lastly, that the death and destruction of one thing should always be subservient to the restitution of another.*

This explicit statement was an important contribution to the balance of nature concept, though Linnaeus did not name it (Egerton 1973:335–337).

Under plant propagation, he discussed sexual reproduction, then seed dissemination (Linnaeus 1775:64–65, 1977):

> Berries *and other* pericarps*, are by nature allotted for aliment to animals, but with this condition, that while they eat the pulp they shall sow their* seeds*; for when they feed upon it they either disperse them at the same time, or, if they swallow them, they are returned with interest; for they always come out unhurt. It is not therefore surprising, that if a field be manured with recent mud or dung not quite rotten, various other plants, injurious to the farmer, should come up along with the grain, that is sowed.*

Under "*Preservation*," he claimed that God had decreed (Linnaeus 1775:67–68, 1977): "that the whole earth should be covered with plants, and that no place should be void, none barren." He had heard of deserts but had never seen one, so he confidently asserted that they have their own unique trees and herbs (which they do, but there is still bare ground). All environments—alpine, grassland, marshes, aquatic, deserts—have characteristic species, and he discussed examples. The graesmasken moth inhibits the spread of grass, leaving room for other plants. However, plants die, and their destruction is also part of God's plan. Black mould, which nourishes new plants, comes from dead plants, and that cycle really begins with the liverworts that grow on bare rocks; when they die, they leave mould for mosses, and as mosses die, they leave mould for herbs and shrubs. This dissertation contains one of the earliest descriptions of plant succession (which Clements, 1916:10, credited to Biberg, the defendant). Insects contribute to the death of plants by eating parts, which make them vulnerable to other hazards (Linnaeus 1775:76–80, 1977).

Under animal propagation, Linnaeus surveyed all the known reproductive habits of different species, and although he rejected spontaneous generation, he admitted that (Linnaeus 1775:89),

> *The laws of generation of* worms *are still very obscure, as we find they are sometimes produced by eggs,*

sometimes by offsets, just in the same manner as happens to trees.

He pointed out that smaller animals tend to produce more offspring than larger ones: mites can increase to a thousand in a few days, but elephants only produce one offspring in two years. However, some hawks are smaller than the poultry they eat, and he acknowledged that hawks layer fewer eggs, without attempting to explain why. He calculated that two pigeons breeding nine times a year could produce 14,672 young in four years, but his translator pointed out that Linnaeus had mistakenly added in the original pair to reach this figure (Linnaeus 1775:90, 1977); however, the numbers 6 and 7 were accidentally transposed in the English edition; Linnaeus' figure should have been 14,760 (Egerton 1967:174). In *Politia Naturae* (Latin, 1760, cited from the English translation, 1781:162, 1977*b*), he added that long-lived animals propagate slowly.

Under animal preservation, he discussed which species care for their young and which do not. Among polygamous species, "males scarcely take any care of the young" (Linnaeus 1775:93, 1977*a*), and cuckoos lay their eggs in the nests of wagtails and hedge-sparrows. Because of the great diversity of species, God assigned each one certain places to live and certain foods to eat. Linnaeus gave a brief survey of examples from the animal kingdom, but only provided details concerning the mutualism between the bivalve, *Pinna*, and the crab, *Pinnotheres* (Linnaeus 1775:111–113, 1977*a*). This relationship had been reported by Aristotle (*Historia Animalium* 547b16–17), but had been neglected by more modern naturalists until Linnaeus' disciple, Fredrik Hasselqvist (1722–1752), traveled to the eastern Mediterranean (where he died) and confirmed it. Since this *Oeconomia naturae* dissertation was published in March 1749, and Hasselqvist did not leave Stockholm until 7 August 1749 (Blunt 1971:183–185), Linnaeus obviously added these comments on *Pinna* and *Pinnotheres* before the dissertation was republished in *Amoenitates Academica*, volume 2 (1751), the source of Benjamin Stillingfleet's English translation.

Linnaeus' survey of the destruction of animals included two food chains, one terrestrial and one aquatic (Linnaeus 1775:114, 1977*a*):

…the tree-louse *lives upon plants. The fly called* musca aphidivora *lives upon the* tree-louse. *The* hornet *and* wasp fly *upon the* musca aphidivora*. The* dragon fly *upon the* hornet *and* wasp fly. *The* spider *on the* dragon fly. *The* small birds *on the* spider. *And lastly, the* hawk *kind on the* small birds.

In like manner the monoculus *delights in putrid water, the* knat *eats the* monoculus*, the* frog *eats the* knat*, the* pike *eats the* frog*, the* sea calf *eats the* pike.

Next, he emphasized the importance of predators to prevent their prey from over-running everything, and the importance of scavengers to prevent the earth from being overwhelmed with carcasses (Linnaeus 1775:114–122, 1977*a*).

In 1734, while exploring Dalecarlia, Linnaeus had watched his expedition's horses grazing certain plants and avoiding others. Both John Ray and René Réaumur had reported insects having very specific food plants (Egerton 2005:303 and 2006:), but in the late 1740s Linnaeus and some students (eight named, plus others) ran 2314 experiments on livestock to determine their plant preferences. Their findings were reported in a dissertation entitled *Pan Svecius* (Latin 1749, cited from Stillingfleet translation: Linnaeus 1775:361, 1977*a*):

Oxen eat	*276*	*refuse*	*218 plants*
Goats	*449*		*126*
Sheep	*387*		*141*
Horses	*262*		*212*
Swine	*72*		*171.*

This was one of the earliest, if not the earliest, series of experiments on an ecological question, and surely the earliest such large-scale quantitative experiments. (Stillingfleet's translation did not include all details in the original; more is translated in Ramsbottom 1959:162–167.) The reason for so many experiments was that, unlike the insects observed by Ray and Réaumur, these mammals were not limited to eating one or two species, but nevertheless were somewhat selective. Allegedly, God's reason to make various animal species eat different plant species was to prevent some plant species from becoming extinct due to overeating and others from becoming too abundant because they were not eaten (Linnaeus 1775:347–349, 1977*a*). Also, in "Oeconomy of Nature" (1775:99–100, 1977*a*) Linnaeus mentioned "an oeconomical experiment well known to the Dutch," of which he perhaps learned while he was in the Netherlands in 1735,

> *that when eight cows have been in a pasture, and can no longer get nourishment, two horses will do very well there for some days, and when nothing is left for the horses, four sheep will live upon it*.

In 1774 a dissertation comparable to *Pan Svecius* appeared on the subject of plants and animals eaten by chickens, ducks, and geese, *Esca Avium Domesticarum* (Smit 1979:122).

Linnaeus' second most important dissertation for ecology is *Politia Naturae* (1760), translated into English as "On the Police of Nature" (1781:129–166). It is on the struggle and survival of species, including humans. A pessimistic conclusion that he drew about humans seemed also to apply to some extent to plant and animal species. Unfortunately, F. J. Brand, the English translator of this dissertation, omitted it. Fortunately, Alan Blair translated it in Kurt Hagberg's biography of Linnaeus (1952:183).

> *...where the population increases too much, concord and the necessities of life decrease, and envy and malignancy towards neighbours abound. Thus it is* a war of all against all!

The point of the dissertation was to explain why a war of all against all (competition) did not lead to extinction. A major reason was what we call ecological diversity: each species is confined to its own "station" (habitat). Sweden had about 1300 plant species, but only about 50–100 are in any one place (Linnaeus 1781:133, 1977*b*). Linnaeus argued that although it is received opinion that plants were created for the use of animals, actually, animals were created to regulate plants' abundance. As proof, he cited numerous insect species that only eat a single plant species, doves eat surplus seeds, and other birds, bats, and anteaters eat insects to prevent them from consuming all of the plants they eat, and so on.

Linnaeus had a lifelong fascination with insects. Five of the dissertations translated by Brand were on insects and their interactions with other species of plants and animals (Linnaeus 1781:309–456, 1977*b*). Smit (1979:125) even claimed that Linnaeus made a major contribution to entomology, as evidenced by his *Fundamenta Entomologiae* (1767). If so, that dissertation was important because it synthesized briefly the works of others. Linnaeus praised as “immortal” the treatise by Réaumur, whom he had met in Paris, and he once sent Réaumur the eggs of the alpicola butterfly (*Papilio Apollo*). Réaumur’s thank-you note is published in Linnaeus’ correspondence (Smith 1821, II:477–479). However, Linnaeus also pointed out the necessity of providing official names for the species Réaumur had studied (Linnaeus 1772:13). Despite Linnaeus’ strong interest in both insects and plants, he never fully appreciated the role insects play in pollination, except for fig trees. He first named the nectary of flowers in 1735, and he did move from a belief that bees harm flowers by collecting nectar, to a belief that they help pollinate flowers, but never realized their crucial importance for flowers that are not wind pollinated (Miall 1912:322–324, Usinger 1964:6, Lorch 1978:518, 523, Eriksson 1983:105). He did, however, appreciate the danger of accidentally introducing American insect pests when American plants were brought to Europe. In 1739 he confessed to having brought American trees from England to the Netherlands in August 1736; these harbored aphids, which multiplied in a greenhouse and then escaped into botanical gardens in Amsterdam and Leiden (1781:325, 1977*b*). Pehr Kalm brought pea seeds when he returned to Sweden in 1751; he discovered that they contained live *Dermestes pisorum* insects, which he captured. However, Linnaeus warned against the danger of artificial introductions (Linnaeus 1781:386–387, 1977).

Linnaeus, physician and sometime professor of medicine, followed Richard Bradley (Egerton 2006:124–125) in arguing that minute organisms, “even smaller than the motes dancing in a beam of light” (Linnaeus quoted in translation from Smit 1979:123) transmit contagious diseases. He developed his argument in two dissertations, *Exanthemata viva* (1757) and *Mundus invisibilis* (1767). He also discussed and described parasitic worms. His speculations (1973:118–119) about some free-living worms being a different stage of internal parasitic worms was a reasonable hypothesis, but he supported it with unverified (and incorrect) examples (Foster 1965:32, Grove 1990:4, 40, 106, 386).

Linnaeus clearly deserves a prominent place among the founders of ecology, but was this a case like Mendel’s, in which his findings were only appreciated after others had rediscovered his basic ideas? No—many of his writings and the student dissertations were reprinted and translated into other languages, and contemporary and later naturalists, including Gilbert White and Charles Darwin, read them (Stauffer 1960, Limoges 1980).

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