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History of Ecological Sciences, Part 34: A Changing Economy of Nature

In 1749, when Linnaeus believed in unchanging species, he developed a static economy of nature concept, in which the organisms in nature interact with each other according to a designed plan (Egerton 2007). Later, he lost confidence that species never change, but did not rethink the economy of nature from his new perspective. After him, others did. A curious example was Scottish naturalist Rev. John Fleming (1785–1857), who discussed the limitations of Linnaeus' concept in his *Philosophy of Zoology* (1822), "but [Fleming's] commitment to natural theology and his ultra-conservatism in theoretical matters prevented him from constructing a coherent vision of nature's operations to replace the lost world of Linnaeus" (Rehbock 1985:137, England 2004). The focus here is on naturalists who were more theoretically daring than Fleming.

Is it coincidental that the theories of Erasmus Darwin and Lamarck about species changing over time arose in the midst of the French Revolution, with which both sympathized? Before the Revolution, Lamarck had not accepted Buffon's belief that species degenerate as they spread from their original home into new areas (Corsi 1988:46). Is it coincidental that the fiercest opponent of evolutionary theories was Cuvier, who hated the Revolution? There are no known statements from Darwin or Lamarck saying they developed their theories because they approved of the Revolution, nor any from Cuvier saying he opposed evolutionary theories because he hated the Revolution. During the 1930s and 1940s, in similarly politically charged environments, in Germany there was Aryan science (good) and Jewish science (bad), and in the Soviet Union, communist science (good) and capitalist science (bad). In the 1790s and early 1800s naturalists expressed no such explicit connections between political and scientific thinking. Nevertheless, the correlations between their political sympathies and their biological thoughts are striking.

There is, however, an irony here. E. Darwin and Lamarck saw only gradual change in nature. It was Cuvier who spoke of revolutions or catastrophes in nature. It is reasonable to assume that Darwin and Lamarck favored gradual political change, which is how the French Revolution began. Neither of them approved of the guillotining of Lavoisier, leader of the revolution in chemistry, in 1794. The Reign of Terror, 1793–1794, could be blamed on paranoia caused by threatening enemies of revolution at home and abroad. However, Cuvier was not one to split hairs. To him, the entire Revolution was a disaster, partially corrected by Napoleon's coup d'état in 1799, and fully corrected by the Restoration of 1815. For Darwin and Lamarck, political change came from the constant striving of many people; for Cuvier, there were occasional catastrophic revolutions of unspecified cause. One might imagine they were caused by God if one wished, but certainly not caused by striving individuals.

Jean Baptiste Pierre Antoine de Lamarck (1744–1829) was the youngest son of a minor nobleman who was a military officer. He followed in his father's footsteps, and while serving in frontier forts during peacetime, 1763–1768, he began studying the French flora (Packard 1901:11–14, Landrieu 1909:28–

Fig. 1. Lamarck in 1821. Packard 1901:facing 180.

29, Burlingame 1973:584). An accident led to his resignation from the army, and he went to Paris and studied medicine for four years. However, he became more interested in botany, chemistry, meteorology (Delange 1997), and conchology. He collected an important herbarium (Aymonin 1981, Jolinon and Raynal-Roques 1997), and his *Flore française* (three volumes, 1779) attracted favorable attention. It was very popular, partly because it introduced into botany the now indispensable keying method of identification, in which one makes choices from general to progressively more specific options until (if followed correctly) one reaches the match between one's specimen and the species name (Landrieu 1909:28–32, Adams 1969:120–121, Stafleu 1971:399, Corsi 1988:40–46, Laurent 1997:163–266, Spary 2000:81, Magnin-Gonze 2004:157, Drouin 2008:119–123).

It is revealing to compare Lamarck's interests, publications, and moderate successes with his very successful younger contemporaries, Humboldt and Cuvier. Lamarck's interests were about as broad as Humboldt's, and he published a substantial body of works, though not on Humboldt's scale. However, whereas Humboldt went from success to success, Lamarck's successes came from systematic publications describing plants and animals. Humboldt was a correlationist (Egerton 2009*b*), which was not controversial. Humboldt spoke of laws of nature, but his laws were usually so limited in scope that they were seldom, if ever, challenged. Lamarck was a theoretician, which proved to be very controversial. Lamarck was, like Humboldt, a diligent collector of data, and he even said that "All knowledge that is not the product of observation is altogether without foundation and truly illusory" (Wheeler and Barbour 1933:v). However, the gap between Lamarck's data and theories was usually so wide that few of his peers thought his evidence provided adequate support for his theories. Cuvier, who also diligently collected data, restricted his research to comparative anatomy, especially of living and fossil mammals, and he did not develop any theory about the cause of catastrophes (Adams 1969:138–164, Ruse 1979:12–15, 37–38, Mayr 1982:363–371, Bowler 1989:112–118, Packer 2000). Like Humboldt, and unlike Lamarck, Cuvier was also very successful in science and in society (Outram 1976, 1978, 1986, Gillispie 2004, Taquet 2006).

Buffon had gotten Lamarck elected to the Académie royale des Sciences in 1779. In 1793, at the former Jardin des Plantes, a Muséum d'Histoire Naturelle was established, and its professors quickly learned to place their teachings in a revolutionary context (Burkhardt 1970, Spary 2000:215–221). Others had priority for the botanical positions, and Lamarck was made professor of "insects and worms," which he redefined under the name "animaux sans vertèbres." Lamarck's last support for the stability of species was published in 1794, and his first support for species changing was in 1800 (Burkhardt 1977:94–95). The shift in his thinking only began in 1799, and it came from his thinking about geology and paleontology (Burkhardt 1972). He began developing his theory of geology in February 1799, and it was published in 1802 as *Hydrogéologie* (English 1964). Two important features of his theory and book were beliefs in uniformitarianism and in a very old earth (Carozzi 1964, Gohau 1997). He could have gotten both ideas from James Hutton's *Theory of the Earth* (1795), but apparently he was only influenced by French authors (Landrieu 1909:262–287, Burkhardt 1977:105–112). He claimed (Lamarck 1964:91) that only living organisms create chemical compounds, that all rocks and minerals are organic remains, and that all compounds eventually decay into simple elements (Stafleu 1971:413–415). All of these claims were based on observations, but were over-generalized. His uniformitarianism was forward looking, but his chemical notions were at odds with the prevailing chemical knowledge of the time, and the book had little, if any, influence (Goux 1997). In 1802 Lamarck also first published his theory of how species change, in the "Discours d'ouverture" to his *Systême des animaux sans vertebras* (translated into English in Lamarck 1984:407–433), though his most detailed account of it is in his *Philosophie zoologique* (1809; in English, 1914, 1984).

Meanwhile, Georges Cuvier (1769–1832) had come to Paris in 1795 and gave a talk on fossil and living elephants in 1796. He, like Lamarck, was the son of a retired army officer, but his interest in

Fig. 2. Cuvier at middle age. After a painting by Mme Lizinka de Mirbel, engraved by Richomme.

nature had developed while he was still a boy, and after college, while working as a tutor, he had studied zoology alone (Coleman 1964:6–11, Bourdier 1971, Outram 1984, Packer 2000, Taquet 2006). His talk on elephants was rather brief, but he was the first to argue that there were two living and two fossil species of elephants, using drawings of their skulls and teeth in his presentation (published in 1798 and 1799; see Smith 1993:21; English translation in Rudwick 1997:13–24). Cuvier believed that the fossil elephants had become extinct. Despite his belief in the extinction of species and their replacement by others, he also believed in the balance of nature (Bourdier 1971:525–526).

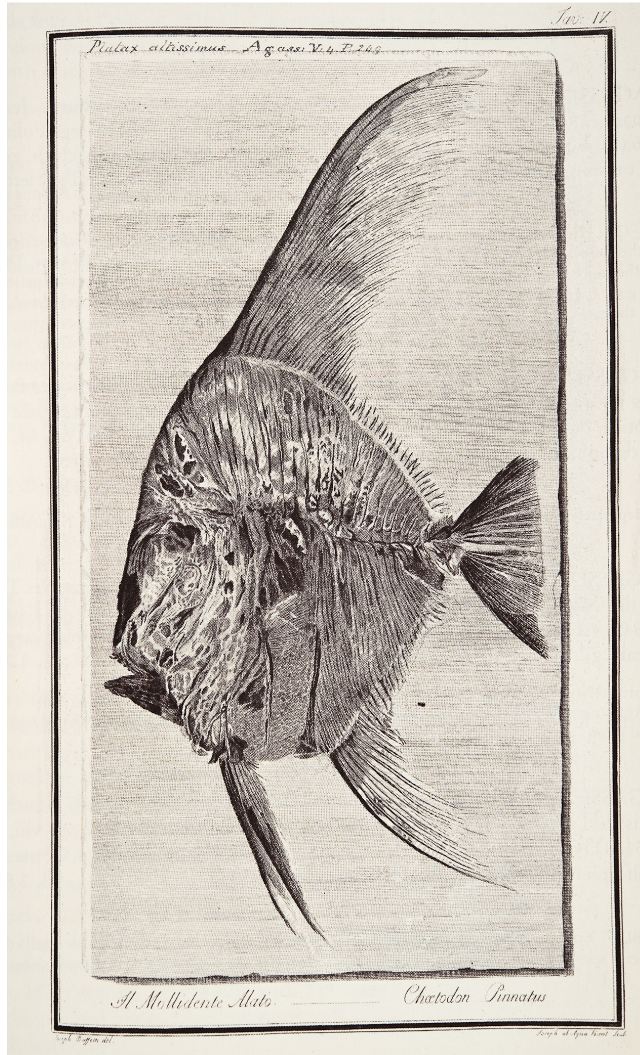

Fig. 3. Fossil fish *Chaeton pinnatus*. Volta 1796.

The question of extinction was one of the influences that pushed Lamarck into believing in the change of species over time (Hodge 1971, Burlingame 1973:592, Burkhardt 1977:130). He rejected the idea that fossils represent extinct species and instead postulated that fossils represent living species before they changed their form, with modern descendants no longer resembling their ancestors. He also assumed that the simplest forms of life arise by spontaneous generation, reopening a debate that Spallanzani had presumably settled in 1765 (Egerton 2008). Lamarck also believed in the balance of nature (Egerton 1968:227–228, 1973:338, La Vegata 1990*a*:216–226), and seems not to have worried about how it could be preserved while all species were evolving into something else. However, since he believed that spontaneous generation was always occurring, any species that became extinct could be replaced by evolution of simpler forms into the species that had disappeared (Ruse 1979:5–12, Mayr 1982:343–360, Bowler 1989:82–88). He opposed Cuvier's idea of catastrophic revolutions in nature in which species became extinct and were replace by others, and his *Systême des animaux sans vertèbres* (1802) showed that 41 species of shelled mollusks that were found as fossils were still living, casting doubt on Cuvier's claim of mass extinctions (Burkhardt 1977:128–131).

My previous conclusion on Lamarck's contribution to the understanding of the economy of nature was as follows.

> *Since he believed that organisms respond quickly to environmental changes, he concentrated on physiology and neglected ecology. His conclusion contained a part of the truth—some species do evolve into new species. However, since Lamarck had overestimated the adaptability of species to new environmental demands, his theory of evolution, unlike Darwin's, led to a worse rather than a better understanding of population biology.* (Egerton 1968:229)

Pascal Acot, a French historian of ecology, challenged my assessment (1997:191)

> *…Darwinism has not played an important part, if any, in the birth of scientific ecology; on the contrary, it is becoming more and more evident that the Lamarckian theory of direct adaptation has left, from its very origins, a deep and lasting impression on the new discipline.*

It may be more accurate to state that Lamarck's work is indirectly relevant to the history of ecology (Matagne 1999:119–124). Darwin (not Lamarck) convinced almost all biologists that evolution occurs, but he convinced only a minority that natural selection was the main mechanism. Many biologists became neo-Lamarckians, who believed in the inheritance of acquired traits (Mayr 1982:526–527, Bowler 1983:75–98, 1989:257–268). French botanists and zoologists in the later 1800s accepted the possibility of some change in species from acclimatization, which might reflect some influence of Lamarck and Darwin (Matagne 1997, Osborne 1997). Darwin became somewhat of a Lamarckian in the later editions of *The Origin*, when he was pushed into acknowledging that natural selection and sexual selection might not be the only causes of species change (Vorzimmer 1970:40, 90, 98, Hodge and Radick 2003:228). Probably few neo-Lamarckians outside France actually read Lamarck to understand his theory, and if they had, what did he write that would have influenced ecological thinking? Jean-Michel Dutuit (1997) found precursors of the idea of ecosystem in Lamarck's writings, but Lamarck did not develop that idea and neither did neo-Lamarckians. What Acot apparently had in mind is the fact that many early founders of a formal science of ecology were neo-Lamarckians, but that does not demonstrate that Lamarck made a significant positive contribution to understanding the economy of nature and the founding of a formal ecological science. We know that those who founded the formal science did read Darwin, even when they rejected natural selection, and there is much in his writings that relates to ecology.

Frederic E. Clements (1874–1945) was a prominent early American ecologist who wrote "Darwin's influence upon plant geography and ecology" (Clements 1909:151), showing various connections of Darwin's writings to ecology. He ended by claiming that Darwin's views were similar to his own views, and he minimized Lamarck's influence on ecology.

> *Darwin's later opinions upon adaptation, as upon the causes of variation, and upon the inheritance of acquired characters, did not differ essentially from those of Lamarck. More important than this, for Lamarck was a prophet, not an investigator, they are in accord with the first results of the application of exact ecological methods to the question of the origin of new forms in natural habitats* (Clements 1909:151).

Clements mischaracterization of Lamarck seems to indicate a lack of acquaintance with Lamarck's works.

Augustin-Pyramus de Candolle (1778–1841) was a Genevan who became one of the foremost botanists in Europe (Pilet 1971, Magnin-Gonze 2004:165, Drouin 2008). He first went to Paris in 1796 to study science and medicine. He looked forward to discussing botany with Lamarck, only to discover that Lamarck was absorbed with chemistry and meteorology (Burkhardt 1977:95, Candolle 2004:91). De Candolle returned to Geneva in the spring of 1797, but in March 1798 he went back to Paris and stayed for a decade. While there, he agreed to bring out a third edition of Lamarck's *Flore française* (Candolle

2004:206), but he was not tempted by Lamarck's theory of species changing (Drouin 1997). De Candolle taught botany in Montpellier, 1808–1816, but in September 1816 the Academie de Genève created a professorship of natural history for him and he returned home (Naef 1987:342–352). We have seen that Humboldt had created a paradigm for a science of plant geography in 1807 (Egerton 2009*b*), but his account was tied to his diagrammatic tableau of plant elevations correlated with measurements made with his instruments. De Candolle provided a more general treatment in his encyclopedia article, "Géographie botanique" (Candolle 1820, 1821, 1977, 1998, 2004*a*), which became the basis for a very similar article in English by William Jackson Hooker (1834, 1977), who cited de Candolle's article.

Fig. 4. Augustin-Pyramus de Candolle. Trembley 1987:388.

De Candolle began with what we today call ecology: a discussion of the influence of environmental factors—temperature, light, water, soil, atmosphere (atmospheric moisture, wind, and more)—on the distribution of species (1820:363–383). Next, he argued that plant geography had been hampered by confusing the Linnaean concepts of "station" (habitat) and "habitation" (range). Linnaeus himself (1754) had not been as clear in their distinction as was needed. On the former he wrote: "The native places or stations of plants respect the country, climate, soil, and situation, nature of the ground, earth, and mould" (Rose translation, Linnaeus 1775:368), and he also included these factors in his explanation of the latter, along with latitude, altitude, and topotgraphy (Linnaeus 1775:369–371). Nelson (1978:280–281), Rehbock (1983:124), and La Vergata (1990*a*:233–238) explore de Candolle's use of these two terms in some detail. De Candolle adopted Linnaeus' list of stations for plants (1820:387–390): maritime or saline; marine; fresh water; damp regions; prairie; cultivated; rocky; sand; sterile soil; rubbish piles; forest; bushes and hedges; subterranean; mountain; parasitic; and saprophytic. Unlike Humboldt, de Candolle emphasized the importance of competition (Candolle 1820:384, translated by Lyell 1830–1833:II, 131, but with a phrase dropped by Lyell added in brackets).

> *All the plants of a given country, [all those of a given place,] are at war one with another. The first which establish themselves by chance in a particular spot, tend, by the mere occupancy of space, to exclude other species—the greater choke the smaller, the longest livers replace those which last for*

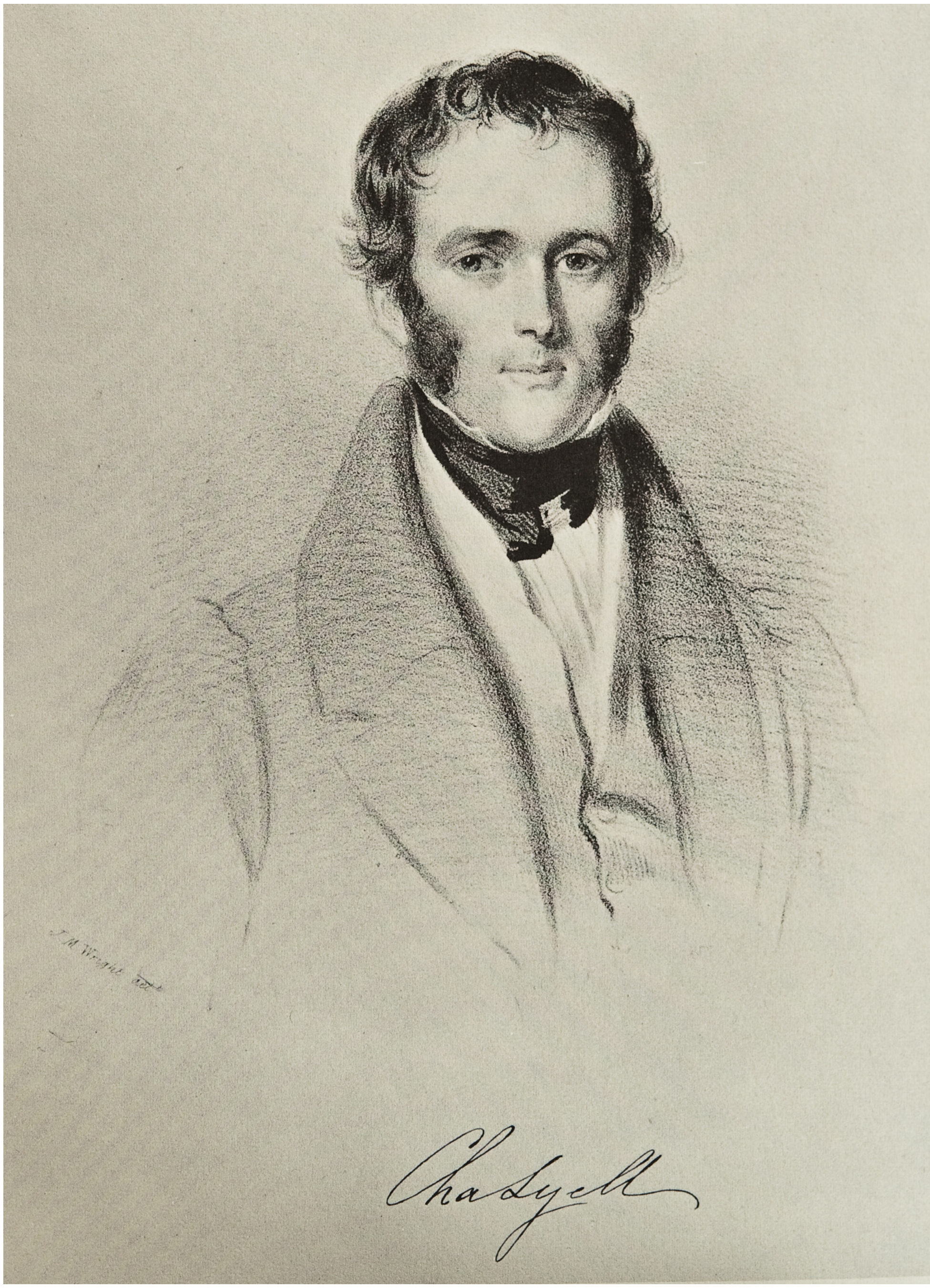

Fig. 5. Charles Lyell in 1836. Drawn by J. M. Wright. National Portrait Gallery, London.

> *a shorter period, the more prolific gradually make themselves masters of the ground, which species multiplying more slowly would otherwise fill.*

De Candolle was not the first to notice competition in nature—his "war one with another" is an echo of Linnaeus' *Politia Naturae* (Dajoz 1984:13–20, Egerton 2007:84)—but de Candolle first pointed out its dynamic significance. How might he have developed this idea? The second edition of Malthus' *Essay on the Principle of Population* had been translated into French (1809) by Pierre Prevost, who had taught philosophy to de Candolle, and de Candolle was quite familiar with that edition (Candolle 2004:318, Drouin 2010). In January 1816 De Candolle went to England, where Malthus was among the many whom he met. Perhaps his reading of and contact with Malthus and his ideas were influential on de Candolle's introduction of the concept of population pressure as a factor in understanding plant geography.

In *Stationes Plantarum* (1754), Linnaeus had argued that each species had been created with a definite station and played a definite role in nature. De Candolle agreed that the structure of a species is correlated with its station, but his explanation for the fit was no longer its prior design for the station, but merely that a species' traits enabled it to compete successfully in a particular station. The conditions for existence for each species (for example, tolerance of temperature changes) could be measured. Species with small tolerance to changes would live in restricted habitations, those with wider tolerances in larger habitations.

Well-written encyclopedia articles (Candolle 1820) do not always have an important impact, but de Candolle gave a copy to his friend, Charles Lyell (Corsi 1978:236). Lyell (1797–1875) was trained in law, but found it boring (Adams 1969:243–274, Wilson 1972, 1973, Oldroyd 2000, Dean 2004, Rudwick 2004). Instead of becoming a prominent lawyer, he became Britain's leading geologist and the author of the paradigm that brought that science to maturity, *Principles of Geology* (three volumes, 1830–1833). He, like Lamarck, was a uniformitarian, though his ideas on it came from James Hutton. Lyell rejected both Lamarck's theory of species change and Cuvier's catastrophism, but he needed to explain why most fossil species are no longer living. He did like Cuvier's idea of saying that some species became extinct and were replaced by others without explaining how the others arose. Lyell thought they arose naturally, but not by evolution. In his second volume (1832), Lyell argued at great length against Lamarck's theory and provided his own explanation for species extinction (Coleman 1962, Corsi 1978), which was heavily indebted to de Candolle's article.

Lyell acknowledged that variations exist among members of a species, and that the species in some genera are quite similar, but this did not signify evolution. Dogs are extremely variable, but still belong to one species (Lyell 1830–1833, II:23–25). Having argued for the reality of species, he turned to their geographic distribution to see "whether the duration of species be limited, or in what manner the state of the animate world is affected by the endless vicissitudes of the inanimate" (Lyell 1830–1833, I:66). The greatest mystery in biogeography was why species are found where they are but not in similar stations elsewhere. De Candolle (1820:402) had suggested that it was because environmental factors are never exactly the same in different places. Lyell doubted that de Candolle's explanation was the whole story. Climate alone could not explain the peculiar distributions of floras and faunas of islands (Lyell 1830–1833, II:70)

> *In islands very distant from continents, the total number of plants is comparatively small; but a large proportion of the species are such as occur nowhere else. In so far as the Flora of such islands is not peculiar to them, it contains in general, species common to the nearest main lands*
>
> .

He reviewed the evidence that Linnaeus and de Candolle had collected on plant dispersal by wind, ocean currents, animals, and humans. Human transport of species was sometimes important, but could also be offset by barriers that humans established by farming and other alterations of the landscape.

Next, Lyell examined factors affecting the distribution of mammals, birds, mollusks, and insects, showing that their movements could be due to lack of food, bad weather, overcrowding, and that mountains and bodies of water could be barriers, though water could also be a means of dissemination for some species (La Vergata 1990*a*:239–260). He rejected the suggestion that subterranean conduits could explain how cetaceans had migrated from the Mediterranean to the Caspian Sea (Lyell 1830–1833, II:96–99). It seemed to Lyell that species were created in different places and at different times, because there were many areas from which species of plants and animals extended their ranges (Lyell 1830–1833, II:123–126). Lyell accepted neither Lamarck's belief that fossil species had evolved into the living species, nor Cuvier's belief that periodic geological catastrophes exterminated species over a wide area.

Although Lyell could not explain the origin of species, he felt he could explain extinctions. The Italian naturalist Giovanni Battaista Brocchi (1772–1826), wrote an important study on fossil shells from the Apennines region (Gregory 1970), with a chapter on extinctions, in which he speculated that species might have a propensity to age and die, just as individuals do (Brocchi 1814, cited from edition 2, 1843, I: Chapter 6). Lyell drew heavily upon Brocchi's monograph, but he sought environmental causes of extinction. Climatic change and the increase in population of a competing species might lead to extinction. He cited as evidence the goat-and-dog struggle for existence on Juan Fernandez Island, which both Antonio de Ulloa and Joseph Townsend had discussed (Egerton 2009*a*:183), an article by John Fleming (1785–1857) on animals extirpated in Britain (1824), and de Candolle's discussion of competition among plant species. Influenced by Linnaeus (Egerton 2007:84), Lyell (1830–1833, II:134) stated that insects were specially adapted to regulate the growth of plants: when any plant species became overly abundant, insects have

> *power of suddenly multiplying their numbers, to a degree which could only be accomplished in a considerable lapse of time in any of the larger animals, and then* [after eating the available plants] *as instantaneously relapsing, without the intervention of any violent disturbing cause, into their former insignificance…no sooner has the destroying commission been executed, than the gigantic power becomes dormant.*

Adverse changes in weather, he noted, often decimated these insects.

Lyell's view of insects as regulatory agents in nature was, however, inconsistent with the account immediately following, in which he summarized accounts of devastations caused by plagues of aphids, ants, caterpillars, and locusts (Lyell 1830–1833, II:136–138). He thus attributed to insects the dual roles of preserving and disrupting the balance of nature. Alfred Russel Wallace (1823–1913) noticed this discrepancy in Lyell's argument and jotted down this rebuttal in his "Species Notebook" (pages 49–50, quoted in McKinney 1966:345–346, 1972:38)

> *Some species exclude all others in particular tracts. Where is the balance?* When the locust devastates vast regions *and causes the death of animals and man, what is the meaning of saying the balance is preserved?* [Are] *the Sugar Ants in the West Indies* [and] *the locusts which Mr. Lyell*

Fig. 6. Oleander hawk moth. John Curtis 1824–1839.

says have destroyed 800,000 men an instance of the balance of species? To human apprehension there is no balance but a struggle in which one often exterminates another.

Yet, factors that tend to preserve the balance of nature received Lyell's close attention. He described a buffering effect that allows stress in one part of nature to be dissipated to some extent by reactions in other parts. His analysis of this effect was mainly concerned with predation (1830–1833, II:138–139):

> *Although it may usually be remarked that the extraordinary increase of some one species is immediately followed and checked by the multiplication of another, yet this is not always the case, partly because many species feed in common on the same kinds of food, and partly because many kinds of food are often consumed indifferently by one and the same species. In the former case, where a variety of different animals have precisely the same taste, as for example, when many insectivorous birds and reptiles devour alike some particular fly or beetle, the unusual numbers of the latter may only cause a slight and almost imperceptible augmentation of each of those species of bird and reptile. In the other instance, where one animal preys on others of almost every class, as for example, where our English buzzards devour not only small quadrupeds, as rabbits and field-mice, but also birds, frogs, lizards, and insects, the profusion of any one of these last may cause all such general feeders to subsist more exclusively upon the species thus in excess, and the balance may thus be restored.*

Sometimes, he continued, this equilibrium is maintained by an interaction between species inhabiting different kinds of environments, as when amphibious animals eat either aquatic or terrestrial food, depending on which is more abundant. Fish that migrate from oceans into rivers provide a link between animals inhabiting land and those of deep seas.

After this digression into the interactions between species, Lyell returned to his earlier discussion of species distribution in time and space to apply his conclusions. To demonstrate that species were exterminated fairly frequently, he needed now to show further that the living and abiotic factors in the environment undergo steady changes, which can alter a station enough to eliminate a species occupying it. The crucial factor would often be the increase of some population (1830–1833, II:142):

> *when any region is stocked with as great a variety of animals and plants as the productive powers of that region will enable it to support, the addition of any new species, or the* permanent *numerical increase of one previously established must always be attended either by the local extermination or the numerical decrease of some other species.*

His hypothetical example was not well chosen, however: in an enclosed park stocked with all the deer it could support, one could not introduce sheep without removing some deer. (Since deer browse and sheep graze, they do not compete closely for food, unless food is scarce.)

The invasion of a new species into a region, he thought, would probably affect directly or indirectly most species already there. His hypothetical example in this case was a good illustration of interrelationships. Polar bears occasionally floated on ice from Greenland to Iceland, and he speculated on the impact of their becoming established there (Lyell 1830–1833, II:143–144):

> *The* [populations of] *deer, foxes, seals, and even birds, on which these animals sometimes prey, would be soon thinned down.*
>
> *But this would be a part only, and probably an insignificant portion, of the aggregate amount of change brought about by the new invader. The plants on which the deer fed being less consumed*

Fig. 7. Polar bear climbing an ice floe. Engraved by Joseph Wolf in Lydekker 1895.

in consequence of the lessened numbers of the herbivorous species, would supply more food to several insects, and probably to some terrestrial testacea, so that the latter would gain ground. The increase of these would furnish other insects and birds with food, so that the numbers of these last would be augmented. The diminution of the seals would afford a respite to some fish which they had persecuted; and these fish, in their turn, would then multiply and press upon their peculiar prey. Many waterfowls, the eggs and young of which are devoured by foxes, would increase when the foxes were thinned down by the bears; and the fish on which the water-fowls subsisted would then, in their turn, be less numerous. Thus the numerical proportions of a great number of the inhabitants, both of the land and sea, might be permanently altered by the settling of one new species in the region; and the changes caused indirectly might ramify through all classes of the living creation, and be almost endless

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The reality of extinction, however, inhibited Lyell from excessive emphasis upon interdependence of species. He noted that slight changes in climate or topography might eliminate a species from a region and cause readjustment in the remaining populations. A new equilibrium would eventually be reached.

Lyell realized that man has become an important factor in the alteration, and sometimes obliteration, of natural areas. He also noticed that where humans replaced a natural area with an agricultural crop, productivity of land often decreased. Some animals, like the dodo, had been exterminated by hunting, and as Fleming had noted (Fleming 1824:291), when farming eliminated the habitat of a species, that species also disappeared (Lyell 1830–1833, II:147–151). Besides these direct actions of humans, they had introduced into foreign lands domestic animals that reduced populations of native species (Chew 2006:23–25, Davis 2009:106–126). In less than three centuries, the few horses and cattle introduced to the pampas of Buenos Aires had increased to over 15 million, and the population of native species must have been reduced as a consequence. Goats and dogs had overrun Jean Fernandez Island. Human populations would likely increase continually, especially in America and Australia, and Lyell thought other species would consequently be exterminated. He disagreed with those who lamented this, since the natural spread of any other species would have the same effect (Lyell 1830–1833, II:154–156).

In concluding his discussion of species, Lyell speculated upon the rate of extinction and replacement. Over a million species of plants and animals existed, and more than a million years would be needed if one were exterminated and another created each year. At that rate, only one species would be replaced in Europe in 20 years, and 8000 years might go by before a new species of mammal was replaced in Europe. Therefore, he was undisturbed that no new species had been noticed in Europe within historical time (Lyell 1830–1833, II:181–182). Lyell did not introduce any new concepts into studies on the economy of nature, but his synthesis, though not as comprehensive as Sir Matthew Hale's had been in 1677 (Egerton 2005:35–36), nevertheless ranks with Hale's in importance. No one before Lyell had expressed as clearly as he the fluidity of natural populations. His account shows populations expanding or contracting in response to a variety of factors, the intensity of which vary randomly. He placed much less emphasis on the physiological control of populations than had Buffon, Lamarck, and Brocchi. Although influenced by Linnaeus' concept of the economy of nature, competition and the extinction of species were important for Lyell's synthesis.

Herbert Spencer (1820–1903) was a wide-ranging Victorian philosopher who speculated on a variety of biological questions (Spencer 1904, Peel 1975, Atmore 2000, Harris 2004, White 2004). He lacked a university education but read continuously and became a highly respected Victorian intellectual. Lyell's *Principles of Geology* converted him to a belief in evolution, despite Lyell's attack on Lamarck's theory. In "Remarks on the theory of reciprocal dependence in the animal and vegetable creations, as regards its bearing upon paleontology" (Spencer 1844), he argued that plants have increased the amount of oxygen available to animals throughout geological history, and the higher animals could only have arisen after sufficient oxygen had accumulated for them to thrive. He published "A theory of population deduced from the general law of animal fertility" (Spencer 1852) that was actually a review of six books, five on biology and one on human population; it was a British convention at the time to publish book reviews in general magazines anonymously, but there was no mystery as to who wrote it. Spencer's discussion of population shows the influence of his belief in evolution, but he did not explicitly integrate the two subjects before 1860. Naturalists and biologists read Spencer's writings, just as they read Malthus' *Essay on the Principle of Population* (La Vergata 1990*b*:124–172).

Spencer thought a law of population should account for two sets of forces, those preserving and those destroying the race (species). He devoted little discussion to the destructive forces, and his discussion of the preservative forces certainly reads like the discourse of a philosopher (1852:476)

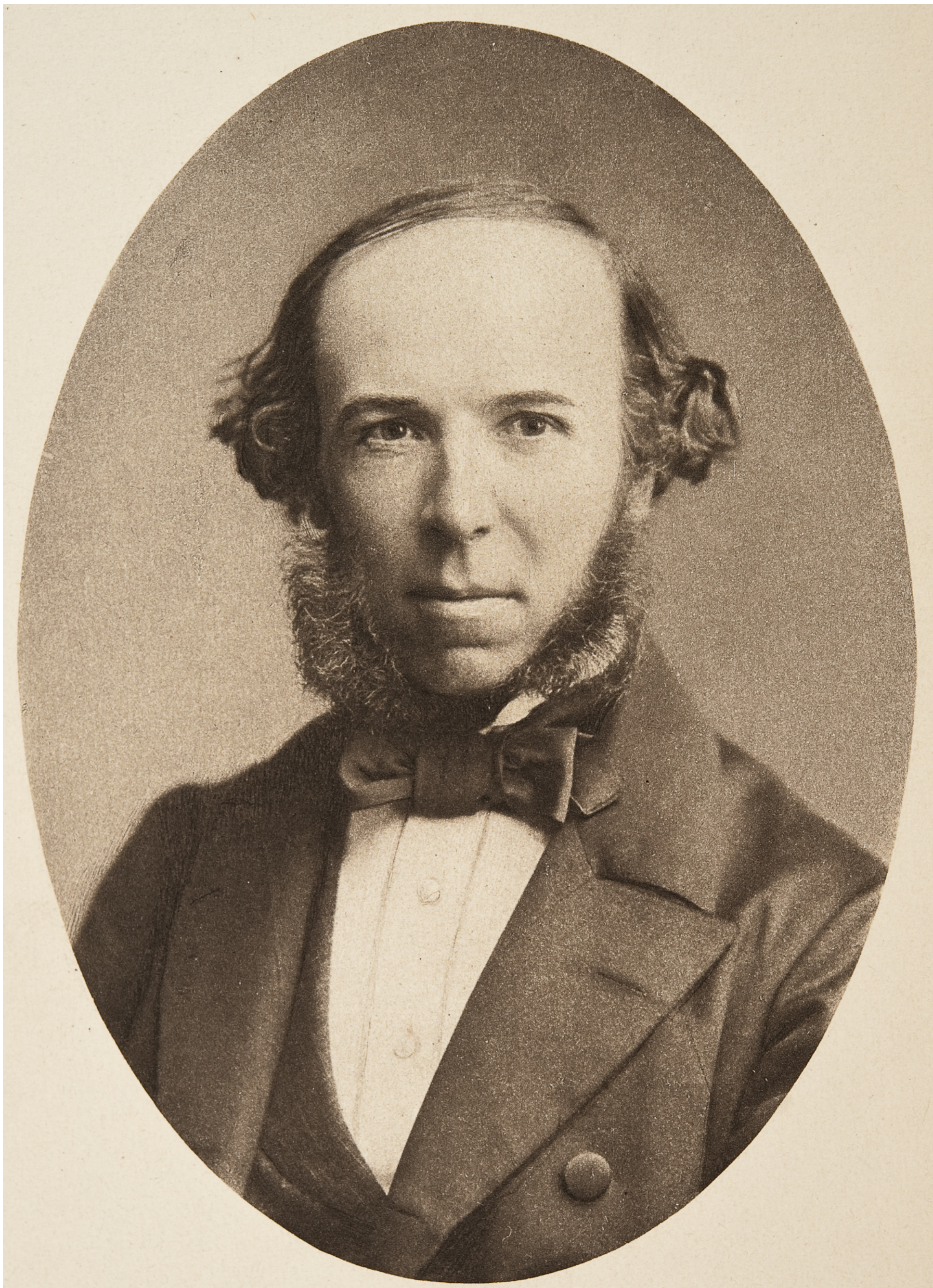

Fig. 8. Herbert Spencer, age 38. Spencer 1904:I, frontispiece.

> *Now the forces preservative of race are two—ability in each member of the race to preserve itself, and ability to produce other members…These must vary inversely. When, from lowness of organization, the ability to contend with external dangers is small, there must be great fertility to compensate for the consequent mortality; otherwise the race must die out. When, on the contrary, high endowments give much capacity of self-preservation, there needs a correspondingly low degree of fertility.*

The correlation he noticed between ability to cope with external dangers and number of offspring is generally valid, but what regulates it? In 1859, Darwin would say natural selection, but in 1852 Spencer reasoned that "the maintenance of the individual and the propagation of the race, being respectively aggregative and separative, *necessarily* vary inversely" (Spencer 1852:478). By this, he apparently meant that the integrative activities in the more intelligent species tended somehow to inhibit the reproductive tendency. He thought that the ratio of brain to body size and reproductive capacity might indicate this. When he turned to humanity, he thought population pressure stimulated the evolution of intelligence, and that this must lead to a reduction in reproductive capacity (Spencer 1852:497). This conclusion is consistent with his previous reasoning, and he thought it was supported by the progressive increase in cranial volumes of human races, going from Australian to African, Malayan, and English, though he did not offer any data on reproductive capacity among these races—harder to measure than cranial volumes. Spencer was attracted to some of the same problems that Darwin was, but he lacked enough data to reason his way to a theoretical breakthrough (Egerton 1967:297–300).

Naturalists in the first half of the 1800s transformed Linnaeus' rather static economy of nature concept into a dynamic one. The second volume of a treatise on geology is not where one would expect to find Lyell's ecological synthesis, but Charles Darwin found it. Whether Darwin also was influenced by Spencer's writings is less obvious.

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