

Chapter 4

Some Conceptions of Time in Ecology

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Abstract Whether one is dealing with variations in the size of populations, changes in landscapes, or modifications in the composition of species, all these phenomena are characterized by their temporal structures. Although, like geology, ecology is a historical science, it is also a science of processes like physiology. It is in the combination of these two aspects, and by using both of these paradigms, that the present paper looks for the conceptions of time specific to ecology. Thus, overall representations of ecological phenomena have brought several conceptions of time into play, which can be distinguished in terms of the timescale, its rhythm and its structure. Schematically, descriptions of ecological processes have been founded successively on the idea of a cycle, then on the idea of organic growth, before coming around to unpredictability and chaos. At a more detailed level, this succession of paradigms goes hand in hand with the continued use of concepts that were characteristic of a previous paradigm. The success of some classical concepts can thus be measured by their ability to be inscribed into a new theoretical framework.

There was a time when time moved backwards. The motion of the universe was the reverse of what it is today. Men emerged out of the earth, began their life with old age and became younger from adulthood to childhood before disappearing into nothingness. This is the myth proposed by Plato in *The Statesman*, which features many other elements besides this reversal of temporality (Plato 1925, 268d–274e). Plato imagines that during this epoch the general course of the world was under the control of the Deity, while lower deities ruled over each region and took care of each species, including humans, who at that time did not need any political

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constitution. But this time has passed, and the statesman must not be seen as a divine shepherd. It is this conclusion that serves to place this myth in the argumentation of the dialogue. Nevertheless, it is significant that Plato explains that in this world where “all the fruits of the earth sprang up of their own accord for men,” the creatures did not “eat one another” (*Ibid.* 271d–271e). Using fiction, Plato emphasizes the link between the temporal processes involving living beings and the complexity of the interactions between them.

Thus Plato offers us a myth that epitomizes the important role of time in ecology. Whether one is dealing with variations in the size of populations, changes in landscapes, or modifications in the composition of species, all these phenomena are characterized by their temporal structures. The present contribution is intended to relate some of these characteristic structures and the conceptions of time that have been used when studying them across the history of ecology (see Egerton 2000; Acot 1988; Deléage 1991; Drouin 1991). The French phrase “figures du temps” serves well as an umbrella term covering all these conceptions, and it has been used as the title of a comprehensive book, edited by Lambros Couloubaritsis and Jean-Jacques Wunenburger and published in 1997. It was also employed in the title of Ivar Ekeland’s 1984 essay, “Computing and the unpredictable. Conceptions of time from Kepler to Thom” (*Le Calcul, l'imprévu. Les figures du temps de Kepler à Thom*). The French word “figure” emphasizes the structure – linear or circular, predictable or unpredictable – rather than the nature – objective or subjective – of our conceptions of time.

4.1 Scales of Time

The most striking feature of the different conceptions of time is their different scales, as has been rightly stressed in a collective work from 2000 edited by Monique Barrué-Pastor and Georges Bertrand, *Les temps de l'environnement*. Indeed, Jean-Marie Legay states the issue in his introductory chapter: “When we think of the environment, we spontaneously situate the present in a window of a few decades in the past and a few years in the future. It will require a great effort of reflection and sophistication to escape from this window, and a great deal of persuasion to lead the general public out of it” (Legay 2000, 26 – *my translation*). In another contribution to the same book, Claude and Georges Bertrand remark that one commonly speaks of resources as renewable or non-renewable, but without specifying the period for the renewal (Bertrand and Bertrand 2000, 71). This same issue arises in many debates concerning the evaluation of the impact of human activity on other living species, with the contrasting optimistic and pessimistic views being underpinned by different perceptions of temporal scales. A notion such as the reduction of biodiversity has a meaning only if a particular period of time has been specified. In the controversy concerning endangered species one can easily argue that the extinction of species is inevitable and inherent to the evolutionary process, but this argument can be countered by recalling that what is frightening

about today's extinctions is the acceleration in the pace of the process and the increasing number of species affected. Thus, one cannot discuss the problem of extinction without determining the rate at which the process is occurring, which means in turn determining a timescale for considering the problem.

Such problems of timescale are only too well-known to historians. In one of his writings on historiography, his masterwork on the Mediterranean, Fernand Braudel suggests "to divide historical time into geographical time, social time and individual time" (Braudel 1996, 21 [1949]). Individual time is the time associated with the history of events, a short history full of dangers and illusions. Social time is the time of social groups and covers their evolution over the middle term, while geographical time is a timescale that reveals "a history whose passage is almost imperceptible, that of man in his relationship to the environment" (*Ibid.* 20). Scholars do not, however, all agree with the image of an essentially invariant relationship between societies and their environment that is often presented. Those who study the environments of lakes, for example, very often deal with physical entities that formed at the end of the last Ice Age, and so are more recent than the presence of *Homo sapiens* in certain regions (Bertola et al. 1999). What remains pertinent in Braudel's point of view, however, is the way he situates the events of human history on the surface of a slower and deeper history, which in turn is inscribed onto the background of a long-term history. This principle is at the heart of the process of periodization.

4.2 The Chronological Issue

A similar approach can also be found in geology. The history of science stresses how the dismissal of a short chronology of the Earth based on a literal interpretation of the Bible was tied to the development of geology. Regardless of whether contemporary authors resisted this revolution in the conception of time or enthusiastically embraced it, they did perceive its importance. Thus, for instance, in 1844 Ralph Waldo Emerson wrote in his diary that, "The use of geology has been to wont the mind to a new chronology," and he added that geology provides us with a clock even if it is "a coarse kitchen clock" compared to the clocks provided by astronomy (Emerson 2003, 102–103). The witticism of the American philosopher vividly reminds us that early geologists were able to establish only an order of succession among events, the dates of which remained unknown, thereby enabling them to compile only a relative chronology. Nowadays, the methods of isotope-dating allow geologists to establish absolute chronologies. This progress does not, however, render obsolete the division of time into era, periods, epochs, and stages. At a given level, the succession of categories, for instance the periods, depends on a structure, which is named a partition by the logicians. In a paper published in 2004 in the journal *Géodiversitas*, René Zaragüeta-Bagils, Hervé Lelièvre and Pascal Tassy suggest replacing the partition by a hierarchical classification in which each new period would be included in the preceding one, which in turn would itself be

included in the one that precedes it. For instance the Cretaceous would be included in the Jurassic, the Jurassic would be included in the Triassic, and so on. According to Bagils, Lelièvre and Tassy, this suggestion – despite its paradoxical appearance – has the advantage of presenting the temporal data in a logical structure comparable to that of phylogenetic trees (for a discussion of the conception of time underpinning such a proposition, see Zaragüeta-Bagils and Bourbon 2005). While the decision concerning whether to adopt or reject this innovation belongs to the palaeontologists and the systematicists, one can nevertheless raise the issue of whether such a formal representation of time could be used in ecology. Its adoption in this context seems unlikely, however, since ecological phenomena are not framed in a unique chronology that would at the same time be unique and specific to ecology. Although a historical science like geology, ecology is also a science of processes like physiology. It is in the combination of these two aspects, and by using both of these different paradigms, that the present paper looks for the conceptions of time specific to ecology (see Drouin 1991, 1994).

4.3 Crop Rotation

Using “paradigm” in the sense given to this term by Thomas Kuhn (1962), one can define the paradigms of scientific ecology as the successive and competing frameworks in which observations have been interpreted and theoretical constructions have been built up. First, we can note that for a long time these paradigms were characterized by their conceptions of time. These can be sorted into two groups: one based on the idea of a cycle and the other on the idea of growth.

Even before the word “ecology” was coined by Ernst Haeckel in 1866, nineteenth-century botanical geography had deployed a cyclical conception of time for the description of phenomena. This conception can be retrospectively considered as ecological, although no such term appears in the founding texts of botanical geography (Drouin 2008, 174–178). Linnaeus devoted some of his academic essays to the idea of the balance of nature (see Linné 1972; for a thorough history of the concept of the balance of nature see Egerton 1973). In these texts, he portrays a providentially organized world, which has no history other than that of the regular increase of habitable land and the preservation of an initial order through the struggle of all against all. Less than half a century later, Alexander von Humboldt, in a lecture to the Institut National on plant geography, incited botanists to study the distribution of plants on the surface of the globe and to recount their migrations (Humboldt 1807, reprinted in Acot 1998, 19–50). For this, Humboldt believed that it was necessary not only to study fossils but also to investigate human history. Humboldt proposed three timescales for this plant geography: first, the short-term timescale of physiological processes on which the physical factors of the environment could act; second, the timescale of human activity; and third, the long-term timescale of geological periods with their catastrophes and their imperceptible changes.

When we look for a conception of a timescale specific to ecology – in the sense of a dynamic inherent to ecological phenomena – we can find it in the works of Dureau de La Malle, a French man of letters. Author of erudite studies of Roman antiquity, Dureau de La Malle devoted several dissertations to the history of domesticated animals and cultivated plants. A landowner in Perche (in the department of the Orne in Normandy), he drew on botanical observations made on his lands to prepare a paper that he read at the Academy of Science on 1 September 1824, which was published in the *Annales des sciences naturelles* in 1825 under a long title that can be translated: “Dissertation on alternation, or on the problem of whether the alternate succession in the reproduction of plant species living in societies is a general law of nature?” (De La Malle 1825, 353–381, partly reprinted in Acot 1998, 117–131). Dureau de La Malle mentions the beneficial effect of the rotation of crops before going on to describe the topography and the nature of the soil on his estate. He then reports the phenomenon of spontaneous succession of species that he has observed in the woods as well as in the meadows. Thus, for instance, as soon as one clears an area in an oak forest featuring a few other trees, the soil is immediately covered with scrub, foxgloves, whortleberries, heathers, birches, and aspens. After a second mowing of the area, the birches and aspens return to the area. Then, after the third clearing of the area, some 90 years later, the oaks and the beeches reconquer the field and remain its absolute masters from then on. Dureau de La Malle reports other cases such as the alternation of whortleberries and heathers in a clearing and the alternation of grasses (Graminae) and white clover (*Trifolium repens* L.) on a lawn in Paris. In conclusion, Dureau de La Malle states that the theory of alternation, which is the “foundation of any good agriculture,” can be extended to every plant and can be considered as “a fundamental law imposed on vegetation by the author of all that exists” (1825, 381; 1998, 131 – *my translation*).

A similar idea is expressed in the works of Henri Lecoq, who makes the same link between botany and agriculture (see Drouin and Fox 1999; Pénicaut 2002). This pharmacist, who taught natural history in Clermont-Ferrand, was well known in his time for his studies on botanical geography. He was also the author of several practical books, including one on plant hybridization, which was referred to by Mendel, and a treatise on fodder plants published in 1844 under the French title of *Traité des plantes fourragères*. He devoted several pages of this book (545–549) to the question of alternation that had exercised Dureau de La Malle. Though Lecoq’s object was the natural rotation observed in permanent meadows, he nevertheless invoked an example taken from the botany of a forest. Comparing “the successive development of all these vegetables” to a “succession of crops conceived by a skilled agronomist,” he concluded that “alternation is so present in Nature that it soon led farmers to the rotation of crops” (Lecoq 1844, 545–549 – *my translation*). And to demonstrate that the Romans already knew this “great law of nature,” Lecoq quotes a verse from Virgil: “thus also, with changes of crop, the land finds rest” (Virgil 1999, *Georgics*, I, 82, 104–105).¹ Independently of Dureau de La Malle and Lecoq, the American philosopher and naturalist Henry David Thoreau, in 1860, in a paper entitled, “The succession of forest trees,” evokes, albeit implicitly, crop rotation when he writes: “if the wood was old, the sprouts will be feeble or entirely fail; to say nothing about the soil being, in a measure, exhausted for this kind of crop” (see Worster 1985, 70 and following pages; Egerton and Walls 1997).

While in retrospect one can see this first conception of the ecological succession of species as being derived from the rotation of crops, for the authors who formulated this, it was the other way around: they considered the natural phenomenon to be a model for the agricultural practice. Be that as it may, the cycles that are under consideration in this case do not imply an authentic return to the original state of affairs. When the leaves grow again, the tree is one year older, and when the oak comes back, the forest is a century older. The circularity of time in this conception is only approximate, and a helical form might well provide a more appropriate description. Nevertheless, we can consider it to be a circular conception of time if we think initially only of the repeating temporal sequence of change, and then, by extension, apply this pattern to the vision of time itself. Moreover, alternating succession is the principal conception of a dynamic inherent to vegetation, and, unlike many other temporal processes, this dynamic does not imply any irreversibility. The cycle can reproduce itself indefinitely without any degradation of the system. Evidence for this is provided by the way in which Dureau de La Malle thinks of the extension of the pattern that he described to the vegetation of tropical countries where “the extreme variety of species gathered and mixed by nature in the same field is a form of permanent alternation” (Dureau de La Malle 1825, 353, reprinted in Acot 1998, 117 – *my translation*). If the “extreme variety” is similar to a “permanent alternation,” alternate succession can conversely be reduced to a form of diversity stretched out in time. Here, the incipient domain of plant ecology tacitly makes use of the conception of time formulated by Leibniz a century earlier, when he defined Space as “the order of coexistences” and Time as “the order of successive existences” (letter from Leibniz to Conti, 6 December 1715, quoted in Robinet 1957, 42). The shortcomings of this parallel between time and space are obvious: while one can freely travel around space in any direction, and every movement can be cancelled out by a reverse movement, time is characterized by its irreversibility. At the end of the nineteenth century, the founders of the field of thermodynamics sought to take this irreversibility into account. This integration of the principle of irreversibility was first realized within the physical sciences, but its effects were also felt in the biological sciences. In contrast to the natural tendency to lose energy as formalized in thermodynamics, the phenomena of growth and evolution appeared to be so many sources of organization and novelty, the opposite of the increase in entropy that characterized other physical processes. Henri Bergson built up a philosophy based on this principle, considering life to be “an effort to re-mount the incline that matter descends” (Bergson 1911, 245 [1907]). Ecology did not escape this movement, as can be seen from the theoretical development of the concept of succession (Lepart and Escarre 1983).

4.4 Succession and Equilibrium

The pioneer in this field was Henry Chandler Cowles. In a study on the dunes of Lake Michigan published in 1899, Cowles described how over the course of a few decades the beach is changed into a moving dune and how in turn this wandering

dune is changed into a static dune and how, finally, the beach can pass from this static dune into a forest stage (Cowles 1899). Cowles termed this stage the normal “climax” of the region. Although it constituted a novelty in this context, the term “climax” was not a neologism. Originally a Greek word, climax had been integrated into English in order to name the peak of a progressive process.

During this same period, another American naturalist, Frederick Edward Clements, made this concept of climax the key to his theory of vegetation. This theory likens the plant community to an organism, and the phenomenon of ecological succession to a process of growth. Clements expresses this idea dramatically: “As an organism the formation arises, grows, matures and dies.” Extending the analogy, he writes: “Succession is the process of the reproduction of a formation,” and he adds, “this reproductive process can no more fail to terminate in the adult form of vegetation than it can in the case of the individual plants” (Clements 1916, 124–125; see Egerton 1973, 344). Several ecologists supported this vision of ecological change, which was widely discussed. Nevertheless, this discussion did give rise to competing theories, reinterpretations, and opposing conceptions.

Among the competing theories was one proposed by William Skinner Cooper in 1926. Cooper’s theory explicitly rests on a different conception of change and therefore a different conception of time. Cooper states that “a sound conception of the fundamentals of dynamic ecology must be based upon the premise of the universality of change.” In this view the vegetation is “presented as a flowing braided stream” that disappears and reappears, with more or less separate and definite elements, branches, interweavings, and anastomoses (Cooper 1926, 397–398). This valuable analogy allows a new interpretation of the concept of climax.

For Cooper, the climax is one of the large slowly-moving currents of the braided stream, formed by the merging of many streamlets. It occurs when all change-inducing factors are acting with extreme slowness. It comes into being insensibly. In a given spot, however, it usually terminates abruptly through the agency of some sudden acting factor, the result of which event will be the forking of the large stream, illustrated by the initiation of one or more “secondary successions” (*Ibid.* 409).

The British botanist Arthur George Tansley proposed another reinterpretation of Clements’s theory in a paper published in 1935 and entitled, “The use and abuse of vegetational concepts and terms.” This paper is often cited, as it is the place where the term “ecosystem” was originally coined. Tansley stresses that the ecosystem includes a complex not only of organisms but also of inorganic factors, and he describes it as a “particular category among the physical systems that make up the universe.” The climax can be considered as a “relatively stable dynamic equilibrium” and as an instance “of the universal processes tending towards the creation of such equilibrated systems” (Tansley 1935, 306). Tansley also states that: “There is in fact a kind of natural selection of incipient systems, and those which can attain the most stable equilibrium survive the longest,” and he adds two explicit philosophical references: “A corresponding idea was fully worked out by Hume and even stated by Lucretius” (Tansley 1935, 300. See Lucretius 1982, book V, 418–508, 411–417; Hume 1991, part VIII, 143–147).

Nearly 10 years before the publication of Tansley's paper, an American botanist called Henry Allan Gleason launched another criticism of Clements's theory. Rejecting the analogy of the plant community as a super-organism, Gleason proposed the fundamental principle that "every species is a law unto itself." It grows where it has been disseminated by chance and where it can grow. It "grows in company with any other species of similar environmental requirements." From this perspective, the succession of plants is nothing other than the change of vegetation that one can observe when there is a change in one of the primary factors responsible for the introduction or elimination of species, migration, or environmental selection. As for the climax, it represents "a stage at which effective changes have ceased, although their resumption at any future time may again initiate a new series of succession" (Gleason 1926, 25–26).

Despite the great differences between them, the views of Clements and Gleason on temporal change can nevertheless be analyzed using the same mathematical model, as was demonstrated by Michael B. Usher in a paper published in 1981 in the journal *Vegetatio*. In this paper, Usher characterizes Clements's position as being "deterministic" and Gleason's as being "stochastic." He stresses how Markovian models adopt Clements's view, "relying on the fact that if succession is an orderly process then probabilities from one state to another can be estimated," and he stresses too how the same models fit with Gleason's view. Thus, in so far as each individual plant is "an entity in its own right," it is possible "to estimate a series of probabilities which define all of the possible outcomes for the fate of one individual" (Usher 1981, 12. Concerning Markovian models in ecology, see also Usher 1979). Here, ecology comes close to the ideas expressed by Ilya Prigogine and Isabelle Stengers in a book whose title can be translated *Between Time and Eternity*: what one calls "Markov chains" do not result from a purely random process nor from a deterministic algorithm. In the first case, the knowledge of the start of the sequence leaves the continuation completely indeterminate. In the second case, knowledge of initial conditions could allow one to predict the continuation. In the case of the Markov chain, every term that can follow a given term or a given sequence of terms is characterized by a probability (Prigogine and Stengers 1992, 89).

Asking the question "can we imagine a natural mechanism producing such a chain?" the authors answer in the affirmative, and propose as an example a mechanism of chemical reactions. Ecology could have provided another example to support their view.

4.5 Irreversibility and Unpredictability

The application of mathematical models to ecological processes is nothing new, however, as they have been used for a long time in the study of population dynamics. In the decade between 1925 and 1935, Alfred James Lotka in the United States and Vito Volterra in Italy built up a mathematical description of the variation of size in animal populations, although quite independently of one another (on the

history of population dynamics, see Kingsland 1985; Israel and Gasca 2002). It was in this context that they formulated the equations that still bear their names. These equations describe two related cyclical fluctuations, one for the number of prey, and the other for the number of predators. Thus, to model the growth of a population in an environment with a limited capacity to sustain this population, Lotka as well as Volterra developed a now well-known formula, which, when the size of the population is plotted on the y-axis, and time along the x-axis, generates a characteristic S-shaped curve. Thus, one can now see two classical images of temporal change, the repeating cycle and the one-time growth curve, two contrasting and complementary images, which both promise to be able to predict the future state of a system (on unpredictability in ecology and what it implies concerning the place of man in nature, see Blandin and Bergandi 2000; Bergandi 2007).

This idealized model requires putting the temporal characteristics of the individuals in question to one side, at least temporarily. Thus, in 1935, when Volterra and Umberto d'Ancona ask the reader to suppose that the individuals of each species are identical, it is because they intend neither to deal with any differences in age, size, sex, and so on, nor to take into account the periodicity arising out of births and deaths (Volterra and d'Ancona 1935, 14). Recognizing this form of abstraction makes it easy to understand the interest of the work of Patrick Leslie in this area (Leslie 1945; for an explanation, see Lacroix 1987; Begon and Mortimer 1986, 54–60; on the history of their discovery, see Caswell 1989, 24–26). The population matrix named after him, the “Leslie matrix”, factors the numbers of individuals in different age-groups, the fecundities associated with different ages, and the age-specific survival rates into the computation of the changing size of a population. Proposed in 1945, this method took advantage of the development of computing power after the war and is still widely used. Thus, the Leslie matrix provides a model that allows a finer-grained analysis than the simple S-shaped curve model, but which similarly offers the hope of providing predictability. But this promise of predictability associated with the ideals of the classical physical sciences has come to see itself threatened by the extension of chaos theory to ecology (concerning the history of the theory of chaos, see Ekeland 1984; Gleick 1987; Boutot 1993; Dahan 2000; Aubin and Dahan 2002).

In 1974, Robert M. May, an Australian-born scholar, trained in physics and working in the department of biology at Princeton University, published a paper in *Science* entitled “Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos.” In the first lines of the paper, May distinguishes between two kinds of biological populations: those where growth in the population is a “continuous process” (e.g. the human being) and those where this growth “takes place at discrete intervals of time” (e.g. some species of insects). In the former type of populations, generations “overlap,” while in the latter, they do not. In the case of nonoverlapping generations, the number N_{t+1} of the population at a time $t + 1$ is obtained by using the formula $N_{t+1} = N_t [1 + r (1 - N_t/K)]$, with r being “the usual growth rate” and K the “carrying capacity” of the environment. Robert May stresses that if this simple model predicts a stable equilibrium for $0 < r < 2$, it gives rise to “essentially arbitrary dynamical behaviour” “once r becomes large

enough” ($r > 2.570$). Referring to Edward Lorenz’s seminal works, May writes: “Such behavior has previously been noted in a meteorological context, and doubtless has other application elsewhere. For population biology in general, and for temperate zone insects in particular, the implication is that even if the natural world were 100% predictable, the dynamics of population could nonetheless in some circumstances be indistinguishable from chaos, if the intrinsic growth rate r were large enough” (May 1974, 645).

The fact that the size of a population becomes stable for some values of the growth rate while becoming chaotic for other values that lie very near the first set of values makes this a good example for introducing students to chaos theory. Indeed, at the end of another paper, May himself emphasizes that the “most important applications” of this model “may be pedagogical” (May 1976, 467). He is convinced that even “in the everyday world of politics and economics, we would be better off if more people realised that simple nonlinear systems do not necessarily possess simple dynamical properties” (*Ibid.*).

Thus, one can apply what Prigogine and Stengers have written on chaotic systems in general to the ecological model studied by May: they free unpredictability from the contingency of ignorance and give it an intrinsic meaning (Prigogine and Stengers 1992, 81). Furthermore, it is in such chaotic dynamics that Prigogine and Stengers see the possibility of building this bridge which Boltzmann did not succeed in building between dynamics and the world of irreversible processes (Prigogine and Stengers 1992, 107).

This view expressed by the authors of *Between Time and Eternity* concerning the statistical interpretation of entropy – which they link to the name of Ludwig Boltzmann – converges with the analysis made, half a century earlier, by Lotka in his 1925 book, *Elements of Physical Biology*:

The failure of the differential equations of dynamics to discriminate between t and $-t$ raises the question as to the physical significance and origin of our subjective conviction of a fundamental difference between the forward and the backward direction in time – a conviction that is intimately bound up with the concept of evolution, for, whatever may ultimately be found to be the law of evolution, it is plain that no trend of any kind can be defined or even described without reference to a favored direction in time (Lotka 1925, 37–38).

As Lotka himself summarized his position a decade later in his French publication *Théorie analytique des associations biologiques*, it is difficult to speak of progressive changes, not only because there is no objective definition of progress, but also because we do not have any objective criterion for establishing the direction of time. Thus, we are obliged to content ourselves with our subjective judgment of the dissymmetry in the course of a time (Lotka 1934, 30–31). Lotka’s reflections on time did not receive any great echo in their own epoch. Lotka’s lack of recognition was resented by the biologist and mathematician Vladimir Kostitzin, who wrote in a letter to Volterra from 31 December 1935 that Lotka’s thoughts on the absence of any contradiction between the existence of living matter and the law of entropy have not been sufficiently appreciated by biologists and philosophers of nature (Israel and Gasca 2002, 233).

4.6 Persistence and Anticipation

Thus, overall, the representations of ecological phenomena have brought several conceptions of time into play, which can be distinguished in terms of the timescale, its rhythm, and its structure. As these theoretical constructions have their own history, they must be inscribed in a temporality that brings out the innovation and radical novelty of many scientific theories as well as the persistence of certain themes. Schematically, the descriptions of ecological processes have been founded successively on the idea of cycle, then on the idea of organic growth, before coming around to unpredictability and chaos. At a more detailed level, this succession of paradigms goes hand in hand with the continued use of concepts that were characteristic of a previous paradigm. Thus, the success of some classical concepts can be measured by their ability to be inscribed into a new theoretical framework.

Perhaps most surprising of all, however, is the presence of themes in ancient texts that look like anticipations of analogous modern themes. We can, for example, cite the verses of the *Georgics* where Virgil compares the repeated selection of seeds by the peasant to the action of an oarsman fighting against the stream. This can be read as a representation – originating in agronomy – of the man’s active resistance against the increase in disorder in the universe (see Virgil 1999, *Georgics*, I, 197–203, 112–113).² It is perhaps ironic, then, that reflecting on the notion of time in ecology can lead to the propagation of anachronisms, albeit in moderation.

Notes

1. “sic quoque mutatis requiescunt fetibus arva” (Virgil, *Georgics*, I, 82, 104–105).

2. “Vidi lecta diu et multo spectata labore
degenerare tamen, ni vis humana quotannis
maxima quaeque manu legeret. Sic omnia fatis
in peius ruere ac retro sublapsa referri,
non aliter quam qui adverso vix flumine lembum
remigiis subigit, si bracchia forte remisit
atque illum in praeceps prono rapit alveus amni.”

“I have seen seeds, though picked long and tested with much pains, yet degenerate, if human toil, year after year, culled not the largest by hand. Thus by law of fate all things speed towards the worse and slipping away fall back; even as if one, whose oars can scarce force his skiff against the stream, should by chance slacken his arms, and lo! headlong down the current the channel sweeps it away” (Virgil, *Georgics*, I, 197–203, 112–113).

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References

- Acot, P. 1988. *Histoire de l'écologie*. Paris: Presses Universitaires de France.
- Acot, P. (ed.). 1998. *The European origins of scientific ecology*, 2 vols. Amsterdam: Overseas Publishers Association/Gordon and Breach Publishers/Editions des Archives Contemporaines.
- Aubin, D., and A. Dahan Dalmedico. 2002. Writing the history of dynamical systems and chaos: *Longue durée* and revolution, disciplines and cultures. *Historia Mathematica* 29: 273–339.
- Barrué-Pastor, M., and G. Bertrand (eds.). 2000. *Les temps de l'environnement*. Toulouse: Presses Universitaires du Mirail.
- Begon, M., and M. Mortimer. 1986. *Population ecology. A unified study of animals and plants*. Oxford: Blackwell Scientific Publications.
- Bergandi, D. 2007. Niveaux d'organisation: Evolution, écologie et transaction. In *Le tout et les parties dans les systèmes naturels*, ed. T. Martin, 47–55. Paris: Vuibert.
- Bergson, H. 1907/1911. *Creative evolution*. Trans. A. Mitchell. New York: Henry Holt and Company. 1st French ed., published by Les Presses universitaires de France, Paris.
- Bertola, C., C. Goumand, and J.-F. Rubin (eds.). 1999. *Découvrir le Léman, 100 ans après François-Alphonse Forel*. Geneva: Slatkine, Musée du Léman.
- Bertrand, C., and G. Bertrand. 2000. Le géosystème: un espace-temps anthropisé. Esquisse d'une temporalité environnementale. In *Les temps de l'environnement*, eds. M. Barrué-Pastor and G. Bertrand, 65–76. Toulouse: Presses Universitaires du Mirail.
- Blandin, P., and D. Bergandi. 2000. L'homme et la nature: les sciences changent de rôle. In *Nature vive*, ed. C. Larrère, 88–99. Paris: Muséum National d'Histoire Naturelle, Nathan.
- Boutot, A. 1993. *L'invention des formes. Chaos, catastrophes, fractales, attracteurs étranges et structures dissipatives*. Paris: Odile Jacob.
- Braudel, F. 1949/1996. *The Mediterranean and the Mediterranean world in the age of Philip II*. Trans. S. Reynolds, 2 vols. Berkeley: University of California Press. 1st French ed., published by A. Colin, Paris.
- Caswell, H. 1989. *Matrix population models: Construction, analysis and interpretation*. Sunderland: Sinauer Associates.
- Clements, F.E. 1916. *Plant succession: An analysis of the development of vegetation*. Washington, DC: Carnegie Institution of Washington.
- Cooper, W.S. 1926. The fundamentals of vegetational change. *Ecology* 7: 391–413.
- Couloubaritsis, L., and J.-J. Wunenburger (eds.). 1997. *Les figures du temps*. Strasbourg: Presses Universitaires de Strasbourg.
- Cowles, H.C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette* 27: 95–117, 167–202, 281–308.
- Dahan Dalmedico, A. 2000. L'image 'fin de siècle' des sciences. La théorie du chaos a-t-elle engendré une révolution scientifique ? *La Recherche* 327: 58–61.
- Deléage, J.-P. 1991. *Une histoire de l'écologie*. Paris: Editions du Seuil.
- Drouin, J.-M. 1991/1993. *Réinventer la nature. L'écologie et son histoire*. Paris: Desclée de Brouwer. Repr., *L'écologie et son histoire. Réinventer la nature*. Paris: Flammarion.
- Drouin, J.-M. 1994. Histoire et écologie végétale: les origines du concept de succession. *Ecologie* 25: 147–155.
- Drouin, J.-M. 2008. *L'herbier des philosophes*. Paris: Editions du Seuil.
- Drouin, J.-M., and R. Fox. 1999. Corolles et crinolines: le mélange des genres dans l'œuvre d'Henri Lecoq. *Revue de Synthèse* 4: 581–599.
- Dureau de La Malle, A. 1825. Mémoire sur l'alternance ou sur ce problème: la succession alternative dans la reproduction des espèces végétales vivant en société, est-elle une loi générale de la nature? *Annales des sciences naturelles* 5: 353–381.
- Egerton, F.N. 1973. Changing concepts of the balance of nature. *The Quarterly Review of Biology* 48: 322–350.
- Egerton, F.N. 2000. Ecology. In *Reader's guide to the history of science*, ed. A. Hessenbruch, 190–192. London/Chicago: Fitzroy Dearborn Publishers.

- Egerton, F.N., and L.D. Walls. 1997. Rethinking Thoreau and the history of American Ecology. *The Concord Saunterer* 5(new series):5–20
- Ekeland, I. 1984. *Le calcul, l'imprévu. Les figures du temps de Kepler à Thom.* Paris: Editions du Seuil.
- Emerson, R.W. 2003. *Selected writings.* With an introduction by C. Johnson. New York: Signet Classic, Penguin.
- Gleason, H.A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53(1): 7–26.
- Gleick, J. 1987. *Chaos.* New York: Viking.
- Hume, D. 1991. In *Dialogues concerning natural religion*, ed. S. Tweyman. London: Routledge.
- Israel, G., and A.M. Gasca. 2002. *The biology of numbers. The correspondence of Vito Volterra on mathematical biology.* Basel: Birkhäuser Verlag.
- Kingsland, S.E. 1985. *Modelling nature. Episodes in the history of population ecology.* Chicago: University of Chicago Press.
- Kuhn, T. 1962. *The structure of scientific revolutions.* Chicago: Chicago University Press.
- Lacroix, H.J. 1987. Tables de survie et matrices de Leslie. In *Une approche mathématique de la biologie*, ed. R.V. Jean, 39–70. Chicoutimi: Gaëtan Morin.
- Lecoq, H. 1844. *Traité des plantes fourragères ou Flore des prairies naturelles et artificielles de la France.* Paris: H. Cousin Libraire-Éditeur.
- Legay, J.-M. 2000. Les temps de l'environnement. In *Les temps de l'environnement*, eds. M. Barrué-Pastor and G. Bertrand, 19–32. Toulouse: Presses Universitaires du Mirail.
- Lepart, J., and J. Escarre. 1983. La succession végétale, mécanismes et modèles: analyse bibliographique. *Bulletin d'Ecologie* 14(3): 133–178.
- Leslie, P.H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33: 183–212.
- Linné, C. 1972. *L'équilibre de la nature.* With an introduction by C. Limoges and trans. by B. Jasmin. Paris: J. Vrin.
- Lotka, A.J. 1925/1956. *Elements of physical biology.* Baltimore: Williams & Wilkins. Repr., *Elements of mathematical biology.* New York: Dover.
- Lotka, A.J. 1934. *Théorie analytique des associations biologiques. Première partie. Principes.* Paris: Hermann.
- Lucretius. 1982. *De rerum natura.* Trans. W.H.D. Rouse, rev. M.F. Smith. Cambridge, MA: Harvard University Press.
- May, R.M. 1974. Biological populations with non-overlapping generations: Stable points, stable cycles, and chaos. *Science* 186: 645–647.
- May, R.M. 1976. Simple mathematical models with very complicated dynamics. *Nature* 261: 459–467.
- Pénicaud, P. 2002. *Henri Lecoq. Les fortunes d'un naturaliste à Clermont-Ferrand.* Clermont-Ferrand: Mémoires de l'Académie des sciences, belles lettres et arts de Clermont-Ferrand.
- Plato. 1925. *The Statesman. Philebus. Ion.* Trans. H.N. Fowler and W.R.M. Lamb. Cambridge, MA: Harvard University Press.
- Prigogine, I., and I. Stengers. 1992. *Entre le temps et l'éternité.* Paris: Flammarion.
- Robinet, A. 1957. In *Correspondance Leibniz-Clarke*, ed. A. Robinet. Paris: Presses Universitaires de France.
- Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16(3): 284–307.
- Thoreau, H.D. 1860/1906. The succession of forest trees. In *The writings of Henry David Thoreau*, vol. V, 184–204. Boston: Houghton, Mifflin. An address read to the Middlesex Agricultural Society in Concord, Sept. 1860.
- Usher, M.B. 1979. Markovian approaches to ecological succession. *Journal of Animal Ecology* 48: 413–426.
- Usher, M.B. 1981. Modelling ecological succession, with particular reference to Markovian models. *Vegetatio* 46: 11–18.

- Virgil. 1916/1999. *Eclogues, Georgics, Æneid I-VI*. Trans. H.R. Fairclough, rev. G.P. Goold. Cambridge, MA: Harvard University Press.
- Volterra, V., and U. D'Ancona. 1935. *Les associations biologiques au point de vue mathématique*. Paris: Hermann.
- von Humboldt, A. 1807. *Essai sur la géographie des plantes*. Paris: Levrault.
- Worster, D. 1985. *Nature's economy: A history of ecological ideas*. Cambridge/New York: Cambridge University Press.
- Zaragüeta-Bagils, R., and E. Bourdon. 2005. Pithecanthropus erectus. *Sciences et Avenir* 142(hors-série): 58–63.
- Zaragüeta-Bagils, R., H. Lelièvre, and P. Tassy. 2004. Temporal paralogy, cladograms and the quality of the fossil record. *Geodiversitas* 26(3): 381–389.