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GUEST EDITORIAL

The other face of Lyell: historical biogeography in his *Principles of geology*

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ABSTRACT

Although some excellent articles about Lyell's work have been published, they do not explicitly deal with Lyell's biogeographical conceptions. The purpose of this paper is to analyse Lyell's biogeographical model in terms of its own internal structure. Lyell tried to explain the distribution of organisms by appealing to a real cause (climate). However, he was aware that environmental conditions were clearly insufficient to explain the existence of biogeographical regions. Lyell's adherence to ecological determinism generated strong tensions within his biogeographical model. He shifted from granting a secondary weight to dispersal to assigning it a major role. By doing so, Lyell was led into an evident contradiction. A permanent tension in Lyell's ideas was generated by the prevalent explanatory pattern of his time. The explanatory model based on laws did not produce satisfactory results in biology because it did not deal with historical processes. We may conclude that the knowledge of organic distribution interested Lyell as long as it could be explained by the uniformitarian principles of his geological system. The importance of the second volume of the *Principles of geology* lies in its ample and systematic argumentation about the geographical distribution of organisms. Lyell established, independently from any theory about organic change, the first version of dispersalist biogeography.

Keywords

Areas of endemism, Charles Lyell, dispersal, dispersalist biogeography, historical biogeography, history of biogeography, history of science, natural law, uniformitarianism.

INTRODUCTION

Wilkinson (2002) makes an important re-evaluation of the ecological and biogeographical ideas of the celebrated British geologist Charles Lyell (1797–1875). It is encouraging that papers with historical revisions are appearing, and that Lyell's biogeographical ideas, nowadays practically disregarded, are being reappraised. Lyell was the first naturalist to elaborate the influential dispersalist model, later on developed by Darwinian and neo-Darwinian biogeographers (Nelson & Platnick, 1981, p. 393). Although some excellent papers about Lyell's work have been published (Rudwick, 1970; Porter, 1976; Corsi, 1978; Laudan, 1982; Gould, 1987; Blundell & Scott, 1998), they do not explicitly deal with Lyell's biogeographical conceptions. As Wilkinson's paper was mostly focused on the ecological biogeography of the *Principles of geology* (Lyell, 1830–33), it now seems pertinent to study Lyell's ideas about *historical* biogeography.

The analysis presented here, like that of Wilkinson, is primarily based upon the second volume of the first edition of the *Principles*. Our purpose is to analyse the theoretical and methodological foundations of Lyell's biogeographical model in terms of its own internal coherence, and under the canons of the 'good science' then prevailing, pointing out their contradictions. We also try, according to Bowler's view, to counterbalance the marked bias of Darwinian historiography, almost always centred upon the mechanism of evolution, 'at the expense of the debates that arose over how to interpret the course of life's evolution' (Bowler, 1996, pp. 2–3). The overemphasis on Darwin has both sidelined the importance of the natural history community of Darwin's own time and distorted the understanding of Darwin's own project (Endersby, 2003, p. 386). Because Lyell's ideas about the geographical distribution of organized beings influenced the Darwin/Wallace's biogeographic approach, we hope that this analysis of Lyell's seminal presentation of the dispersalist

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model can contribute to a better understanding of evolutionary biology.

ECOLOGICAL AND HISTORICAL BIOGEOGRAPHY

Biogeography deals with the spatial and temporal distribution of organisms; its fundamental purposes are to discover general distributional patterns, both present and extinct, and to investigate the causes which have produced them (Simberloff, 1983, p. 411). Two main areas within this discipline may be distinguished: (1) *ecological biogeography*, devoted to the study of the present distribution of organisms and species, in terms of the influence that physical and biological factors exert upon geographical distribution, generally at a local scale, although it also deals with the broad-scale patterns of biodiversity (Brown & Maurer, 1989); and (2) *historical biogeography*, devoted to the study of the causes which have operated in the past to affect organic distribution, in terms of broad spatial and temporal scales and analysis of the genealogical interrelationships among groups of higher taxonomic categories.

Ecological biogeography and historical biogeography represent two traditions of research with independent developments. Historical biogeography has occupied itself mainly with recognizing, delimiting and establishing the interrelationships among different biotic areas. From Buffon's first generalization about organic distribution in the eighteenth century up to the present-day debates among the dispersalist, vicariant, panbiogeographic and phylogeographic models (Myers & Giller, 1988; Llorente & Espinosa, 1991; Espinosa & Llorente, 1993; Crisci & Morrone, 1995; Brown & Lomolino, 1998; Zunino & Zullini, 2004), two basic criteria have been used to establish interrelationships among areas: (1) *phenetic*, estimating the similarity among areas based on shared biotic elements; and (2) *genealogical*, considering the historical interrelationships among areas based on their endemic taxa.

EXPLANATIONS OF BIOGEOGRAPHIC REGIONS

Toward the second half of the eighteenth century a crucial fact was perceived: organisms from different regions, including those with similar physical conditions, are specifically different (Nelson & Platnick, 1981, p. 361; Browne, 1983, p. 24; Papavero *et al.*, 2004, pp. 148–149). In the second half of the eighteenth century a great amount of data about the spatial distribution of several groups of plants and animals had been accumulated. Moreover, stratigraphical studies had clearly shown that two important phenomena occurred in the temporal succession of animated beings: the appearance of new organic forms and the extinction of older ones. By the end of the eighteenth century two central objectives of studies of organic distribution became explicit: (1) to discover the geographical distribution of plants and animals, and (2) to explain their causes. This inquiry necessarily implied a historical dimension, so as to explain the origin of species (Kitcher, 1993, p. 32). However, British naturalists lacked a theoretical framework for their study of organic distribution (Kinch, 1980, p. 91).

One of the issues that was still being debated in natural philosophy was whether populations were originally created in the places where they are now found or whether they migrated from other areas. This debate raised the issue of the extent to which God interfered with natural phenomena (Kinch, 1980, p. 117). The belief that the biota of the biogeographic regions are autochthonous was commonly associated with the doctrine of species immutability. Louis Agassiz is an example of the theistic belief, according to which God directly intervened in nature to impose order in the spatial distribution of living beings:

> there is only one way to account for the distribution of animals as we find them, namely, to suppose that they are *autochthonoi*, that is to say, that they originated like plants, on the soil where they are found. In order to explain the particular distribution of many animals, we are even led to admit that they must have been created at several points of the same zone, as we must infer from the distribution of aquatic animals, specially that of fishes (Agassiz, 1848, in Richardson, 1981, p. 13).

According to Agassiz, disjoint distributions are explained by independent acts of creation. This hard version of theism, which implied that the same species had been created more than once in separate areas, gained little support, even among those who rejected Darwin's theory (Browne, 1983, p. 139). Eberhard Zimmermann had previously made the first detailed regionalization of the zoological kingdom, ridiculing the Linnaean idea of the dispersion of all the terrestrial biota from a single point and from a single pair. He pointed out that it was more reasonable to suppose that God had created every animal species in the area where it lives at present, with many individuals from the beginning and with all the species in a perfect mutual equilibrium (Browne, 1983, p. 26). Among those naturalists accepting this view was the British ornithologist Phillip Lutley Sclater (1829–1913). He assumed that there were several areas of creation (Kinch, 1980, p. 110). There was no necessity for species to migrate, because they had been designed to fit the areas they now live in:

> But I suppose few philosophical zoologists, who have paid attention to the general laws of the distribution of organic life, would now-a-days deny that, as a general rule, every species of animal must have been created within and over the geographic area which it now occupies…and the awkward necessity of supposing the introduction of the red man into America by Behring's Straits, and of colonizing Polynesia by stray pairs of Malays floating over the water like cocoa-nuts, and all similar hypotheses, would be avoided… (Sclater, 1858, p. 151).

On the other hand, naturalists such as James Cowles Prichard and Charles Lyell held a different point of view. They were radically opposed to the inclusion of divine interventions within the explanations of natural philosophy, and tried to explain natural phenomena by means of physical laws.

In short, during the first half of the nineteenth century, two conceptions about organic distribution were being discussed: one, preferred by theists, assumes independent creations to explain both disjoint distributions and endemisms; the other, deist, admits that the origin and introduction of species was governed by natural laws and processes (Mayr, 1982, p. 445).

EXPLANATION BY LAWS

Different patterns of explanation may be distinguished through history, each one of them representing a conceptual framework within which the relationship between the world and the cognitive capacities of those who tried to explain it is articulated (Martínez, 1997, pp. 15–16). The science of the nineteenth century developed within a long tradition which began in the Renaissance, and assumed a particular pattern of explanation. In that tradition the concept of natural law plays a central role. The new concept of natural law is closely tied to the mechanical conception of the world, which was radically opposed to the ancient notion that compared the world to an organism. According to the modern mechanistic conception, the world is not governed by an autonomous proper will, but by forces external to it, imposed by external conditions.[1] The notion that there exist natural laws governing organic distribution would be crucial in Lyell's biogeographical model. His *Principles of geology* (Lyell, 1830–33) had as its central aim to find out natural laws controlling the functioning of the Earth.

METHODOLOGY OF THE *PRINCIPLES OF GEOLOGY*: UNIFORMITARISM AND *VERA CAUSA*

The *Principles of geology* is governed, from beginning to end, by *uniformitarianism*. The term was introduced by William Whewell (Laudan, 1982, p. 215) in his works about the philosophy and history of the inductive sciences (Whewell, 1847, 1857), opposing it to the catastrophist point of view. Uniformitarianism claims that, although the past is unobservable, it must be presumed to have been governed by exactly the same forces as those we can observe in the present. The past can thus be reconstructed by comparing the results of those processes with what we now observe.

In Lyell's own words, the whole thing 'necessarily aris[es] out of the admission of such Principles, which, as you know, are neither more nor less than that no causes whatever have from the earliest time to which we can look back, to the present, ever acted, but those now acting, and that they never acted with different degrees of energy from that which they now exert' (Rudwick, 1970, p. 7).

But uniformitarianism has distinct meanings, sometimes confused, including both methodological and ontological assumptions. Rudwick (1972) differentiated four meanings of uniformitarianism in Lyell's work: (1) uniformity of laws, (2) uniformity of processes, (3) uniformity in the rhythm of change (gradualism), and (4) uniformity of state or anti-progressionism.

The first two meanings are methodological precepts, referring respectively to the principles of induction and simplicity generally employed by scientists. Methodological uniformitarianism was widely accepted during Lyell's time, even by the catastrophists. On the other hand, gradualism and anti-progressionism are ontological suppositions about the manner in which the Earth functions, and, as such, are subject to empirical proofs (Gould, 1987, pp. 117–126). One of Lyell's aims was to extend his ontological uniformitarism from the inorganic world to the animated one, as we shall see later.

Lyell's work follows the methodological ideal of the Newtonian tradition, that is, it tries to explain facts through the search for *verae causae* (true causes), rejecting *hypotheses*, understood here as mere speculations. The very title of his book, *Principles*, is a clear reference to Newtons's *Principia mathematica*.[2] Although Newton never dedicated himself to developing a methodology of natural philosophy, he proposed four methodological prescriptions, called 'Rules of Reasoning'. His aim was to obtain genuine knowledge of the world. Those rules are a kind of maxim in the style of scholastic philosophy. The first affirms that, in explaining natural things, no other causes are to be admitted but the true and sufficient ones; this is known as the principle of the *vera causa* (true cause), an inductive procedure contrary to the hypothetical method practiced by contemporaries of Newton such as Descartes. According to Newton, the point is not to invent different explanations, all of them being possible and even having explanatory power, but to find the *vera causa*. The search for true causes is contrary to the speculative hypothetical explanations. As Newton's work became the methodological ideal in science, his ideas attracted much attention. Reid (1785), Herschel (1830) and Whewell (1847, 1857) analysed in detail the 'rules' of the *Principia mathematica*.[3]

Lyell deliberately worked to build a system based upon the best canons of the scientific methodology of his time. He was familiar with the ideas of John Herschel and believed that the

[1]There is an important conceptual difference between understanding a natural law as (1) something imposed upon nature and (2) as an immanent thing in the structure of reality itself (Oakley, 1961). The concept of imposed laws implies a metaphysics in which there are no direct connections among individuals, these being autonomous. As the relationships existing among them are imposed from the outside, those laws cannot be discovered from the study of the characteristics of the individuals. On the other hand, the concept of immanent law implies that things are interdependent, and therefore that, once the nature of things is studied, one may know their relationships. This implies acceptance of the existence of order in the world, with patterns and regularities. The character of things result from their interconnections and the interconnections of things are the result of their characters.

[2]An excellent biography of Newton that includes a detailed analysis of the debate between his ideas and those of his contemporaries is in Westfall (1980).

[3]An analysis of the development of the *vera causa* methodology and their different versions (Thomas Reid, John Herschel and William Whewell) is in Laudan (1987); also in Guillaumin-Juárez (1997).

vera causa methodology was the best way to avoid both unfounded conjectures and theoretical absurdities created by too strict adherence to an inductive methodology (Laudan, 1982, p. 216). Science progressed by the judicious union of appropriate ideas and scientific facts. Ideas not based upon facts are mere scholastic philosophy, while pure facts without ideas are devoid of meaning. Thus, Lyell tried to justify his system through a methodology legitimated in his time. His aim was to establish geology as a scientific discipline, capable of explaining the geological past by means of true causes. He built his uniformitarian system appealing only to known facts, such as earthquakes, volcanism and sedimentation as the only acceptable causes within his non-hypothetical system (Guillaumin-Juárez, 1997). The *Principles of geology* was much praised by Herschel, who considered the book a brilliant example of application of the *vera causa* methodology to geology.

In general terms, the explanation elaborated by Lyell is this: in the past there were climatic changes caused by changes in the relative distribution of land and oceans, caused, in their turn, by differential upheavals and sinkings of the earth's crust. Climate is fundamental in the Lyellian system. Climate is the influence that mediates between the organic and the inorganic kingdoms (Laudan, 1982, p. 217), and is therefore a key factor in his model for explaining the spatial distribution of organic beings. By contrast, other common explanations of his time, such as the assumption that earth's surface had been sculptured by the retreat of the waters of a primitive ocean, are not valid. The reason for this is simple: there is no evidence supporting them. On the other hand, there is a lot of empirical evidence that sea level fluctuates.

CONTENTS OF THE PRINCIPLES OF GEOLOGY

The *Principles of geology* consist of three volumes, published between 1830 and 1833. The work reached 11 editions, the last one appearing in 1872.[4] The first volume begins with a history of geology. In the first five chapters, Lyell builds up a narrative of the development of that discipline from an irrational primitive stage to its status as a science based upon empirical knowledge. However, this is a distorted and oversimplified history (Ospovat, 1976), in which the catastrophists appear as irresponsible speculators opposed to the patient empiricists, who took pains to study the facts of the present.

In the first volume of the *Principles* the evidence that the northern hemisphere had a warmer climate in the past is explained (for instance, the great coal deposits). Lyell argues that the cold conditions that followed the Carboniferous epoch were due to the emergence of new land. However, the cooling was not continuous, unidirectional and irreversible, as maintained by the catastrophists. The climatic changes that had occurred on the Earth were cyclical, due to the ceaseless changes in the distribution of land and sea. The colder conditions now present will be followed up eventually by another cycle of warming. Deeply entrenched in this cyclical conception of terrestrial changes is the thesis of a 'steady-state' for the planet's overall conditions (Rudwick, 1970, p. 8). Continents rise to be eroded, and this cycle is repeated again and again. The world is essentially uniform, both in its general state and in the intensity of its processes.

The second volume is dedicated to the effect of the imperturbable physical laws upon organized beings. The entire volume considers how the ceaseless changes of the earth's surface have affected the geographical distribution of plants and animals, and how the perfect adaptation that exists between the species and their environment may determine both their extinction and origin.

In the third volume, Lyell reconstructs the past history of the Earth from its present state. According to him, the supposed mass extinctions are simply gaps in the record due to periods of non-deposition of sediments.

LYELLIAN BIOGEOGRAPHY

The discussion of the geographical distribution of organized beings begins in Chapter V of volume II, and is a subject to which Lyell grants the greatest importance. Lyell opens his discussion with a fundamental question: what are the laws regulating the geographical distribution of species? In the same tone used to discover laws regulating the physical world, he reasons that only through precise knowledge of the spatial distribution of present species, as well as by the study of the effects that changes in physical geography and the phenomenon of migration exert over such distributions, can one answer a crucial question: whether species are permanent entities or have a limited duration.

From the beginning, Lyell established what he considered to be the most important point in the study of organic distribution, an idea attributed to the French naturalist George Louis Leclerc, Comte de Buffon: 'That different regions of the globe are inhabited by entirely distinct animals and plants' (Lyell, 1832, p. 66). In fact, Buffon had noted only that among the mammals of the torrid zones of the Old and the New Worlds there were no shared species (Nelson, 1978, p. 275). The generalization of this discovery and its extension to other groups and other regions were later achieved by Alexander von Humboldt, Georges Cuvier, Augustin de Candolle, André Latreille and Robert Browne.

The work of Augustin Pyramus de Candolle was fundamental for the development of biogeography. He published an article (Candolle, 1820a), which also appeared as a booklet (Candolle, 1820b). Candolle attributed to Linnaeus the distinction between the occurrence of plants *as species* in their 'homeland' (*habitations*) from an entirely different aspect having more to do with the particular nature of those localities

[4]Lyell had at first thought to publish only two volumes, but afterwards decided to write a third one. But it happened that before the third volume was edited, the second edition of the first two volumes was already published; for this reason the complete second edition of the three volumes is also known as the 'third edition' (Rudwick, 1990, p. liv); this explains the discrepancy with other authors claiming that there were 12 editions.

where plants thrive *as individuals* (*stations*). The term 'station' is basically related to the climate of a certain locality, while that of 'habitation' is related to geographical and geological circumstances. Candolle claims that the confusion between these two concepts had retarded the advance of botanical geography, preventing it of becoming truly scientific. As a general rule, plant species are restricted to a determined area of the terrestrial surface. The discovery of the laws responsible for this restriction would constitute the study of habitations.

A common idea during the first half of the nineteenth century was that floras and faunas of each region were the product of their particular 'circumstances'. However, this did not agree with the fact that different countries were inhabited by distinct animal and vegetable species, even when they shared the same climate, the same elevation and the same latitude; in short, the same physical conditions. If plant distribution was not explained by the physical conditions alone, some other unknown primary causes must exist. The existence of habitations thus implied a search for the causes of origin. Candolle attributed the origin of habitations to geological causes no longer operating in the present, without entering into the subject any further. In this way Candolle established a clear-cut distinction between ecological and historical factors, from then on recognized by other students of organic distribution, among them Lyell, Darwin and Wallace. The study of habitations, into which the terrestrial surface could be divided, each one of them characterized by a particular and specific biotic composition, must be explained only by historical factors. In short, Candolle created the concept and established the limits of biogeographical regions or areas of endemism (Candolle, 1820a, p. 412).

Giving a temporal dimension to the study of habitations, Candolle foresaw the creation of a historical biogeography. His concepts of station and habitation established different causalities for biogeographical data: a physical–ecological approach (which he proposed to call *botanical topography*) and a historical–geological approach (to which he reserved the term *botanical geography*). However, due to the lack of theories about the subject, he was cautious enough not to proceed further into this new field. Following Humboldt, he believed that knowledge of the primary causes of the world's phenomena surpassed the capacity of the human intellect.

Lyell used Candolle's conclusions directly. The surface of the globe could be divided into clearly distinct regions. He was puzzled by the fact that such a notable thing had not been recognized before. Presumably the reason for such ignorance among ancient civilizations was the poor knowledge of plant species, limited to fourteen hundred species. Lyell himself pointed out that 'perhaps upwards of seventy thousand species' (Lyell, 1832, p. 67) had been collected all over the world.

The fundamental purpose of biogeography was to try to explain the regionalization of the terrestrial surface into areas of endemism:

> that each separate region of the globe, both of the land and water, is occupied by distinct groups of species, and that most of the exceptions to this general rule may be referred to disseminating causes now in operation, is eminently calculated to excite curiosity, and to stimulate us to seek some hypothesis respecting the first introduction of species which may be reconcilable with such phenomena (Lyell, 1832, p. 67).

At first, as Candolle had done, Lyell assigns only a subsidiary role to dispersal, as he recognized that this phenomenon did not alter the existence of regions with proper biotic identity. Dispersal could not extend the distribution-area of the species, nor produce mixtures of inhabitants of different regions. It only explained those exceptional cases where the same species existed in more than one country. He dismissed the polygenetic hypothesis, because it implied miraculous interventions. The same species could not have been independently created in two different areas: 'the original stock of each species is introduced into one spot of the earth only' (Lyell, 1832, p. 170); 'species, like an individual, cannot have two birth-places' (Lyell, 1832, p. 71).

In order to explain the exceptional cases of species present in more than one area, Lyell made a full review of the diverse means of dispersal used by organisms, the processes which allowed them to cross enormous distances and to colonize new areas. He distinguishes between inanimate agents, through which organisms are transported passively, and those intrinsic to the organisms. He compiled a series of cases registered in the literature showing the notable capacity for dispersal among different animal species. These cases, although rare, could account for the exceptions to the general rule of species confined to a single area.

Lyell employed a probabilistic reasoning, which, curiously enough, would come to be common among dispersalist biogeographers (e.g. Simpson, 1965): an isolated case of dispersal seems to be a highly improbable, occasional and fortuitous event; however, considering vast periods of time, dispersal may become a practically certain event. For Lyell, the foremost defender of the concept of *deep time* (Gould, 1987), time is not the limiting factor for the occurrence of natural processes.

The most remarkable point is that, after making an ample and exhaustive exposition of the varied means and mechanisms through which species are dispersed, what really amazed Lyell was not the great capacity for the dispersal of organisms, but that, *in spite of it, the division of the earth's surface into biogeographic provinces had still remained as a general pattern*:

> The real difficulty which must present itself to every one who contemplates the present geographical distribution of species, is the small number of exceptions to the rule of the non-intermixture of different groups of plants. Why have they not, supposing them to have been ever so distinct originally, become more blended and confounded together in the lapse of ages? (Lyell, 1832, p. 81).

In Chapter VI, Lyell continued by refuting the deeply entrenched notion of the perfect adaptation of organisms to their environmental conditions and in Chapter VII he emphasizes biotic regionalization, including marine organisms.

But a new and obscure issue is dealt with in Chapter VIII: the origin of species. Lyell asks how the original introduction of the species could have occurred, and how, from that initial state, the present distribution appeared. The common notion during Linnaeus' time was the permanence and immutability of species, but in Lyell's own time the study of the fossil record had revealed that individual species have become extinct and have been replaced by others. It was then necessary to consider the temporal dimension in biogeographic studies.

Lyell proposed a tentative explanation for the original introduction of species, both terrestrial and aquatic:

> Each species may have had its origin in a single pair, or individual, where an individual was sufficient, and species may have been created in succession at such times and in such places as to enable them to multiply and endure for an appointed period, and occupy an appointed space on the globe (Lyell, 1832, p. 124).

However, no mechanism was specified. He supposes that the process of the species creation is continuous: different species appear successively both in time and space. But even if we could spread the several species over the entire terrestrial surface in a homogeneous way, in the long run distinct botanical and zoological provinces would appear, for 'there are a great many natural barriers which oppose common obstacles to the advance of a variety of species' (Lyell, 1832, p. 125). In due time, exceptions might appear, but the exceptions would not invalidate the general rule of biotic regionalization.

The opposite idea, according to which there had been different foci or centres of creation, supposes the existence of certain particular areas in which the creative energy had acted with a higher power, originating the biotic provinces. Lyell dismissed it by pointing out that no tangible evidence whatsoever could be found of the action of such mysterious forces. Species appeared through a gradual, non-directional process, disseminated both in time and space and under appropriate ecological situations (Rudwick, 1970, p. 20). With this Lyell extended the ontological presuppositions of his geological model to the organic world.

But before directly merging into the swampy terrain of mechanisms and laws regulating the introduction of new species, he considers it convenient to analyse first which laws might limit their *duration* on the Earth. He begins by examining the theme of species extinction, essential within his system. Contrary to the old Aristotelian idea that only individuals become extinct, but that species are permanent, Lyell maintains that species have a limited existence.

Besides the physical conditions, the complex relationships among species, chiefly competition, also influence the stations. The idea of competition introduces a contingent factor affecting organic distribution, because the species which, by chance, established themselves first in a particular locality would tend to exclude others arriving later. It was not only its own resources that allowed a species to maintain and extend itself in its locality, but also the number of enemy or allied species inhabiting the same place and interacting with it.

Lyell added another idea, allowing him to further refine his uniformitarian conception of the organic world: nature remains in an equilibrium established by the beneficial and harmful relationships among species. He concludes that the mutual interrelationships between the organic and inorganic components of nature are highly complex and that the stations of the distinct vegetable and animal species depend upon numerous intermingled relations.

Lyell summarized the causes of species extinction: changes in sea level modify both the organic and inorganic circumstances, which, in their turn, affect the species, possibly even causing their extinction. Therefore, species are the subject of incessant vicissitudes. If these changes are sufficiently pronounced to alter the general state of the stations, then the species might become extinct. Based upon a principle of equilibrium, more than upon the evidence of facts, Lyell established that the addition of a new species to a determined area, or the increase in the number of individuals of another already inhabiting that area, would necessarily entail the decrease or extinction of another. Also, since there is a finite amount of resources, the numerical increase of individuals of any species, including of the new one, necessarily supposes a reduction in another.

Moreover, due to the complex interconnections existing between the inhabitants of the Earth, the increase or decrease of a species would provoke a chain of unforeseeable consequences in other species. Every change, organic or inorganic, produces a new order of things. Lyell cites as example the case of the human species. Man has been the main cause of the extinction of indigenous species through the introduction of domesticated foreign species or races. This effect will go on, 'as the colonies of highly-civilized nations spread themselves over unoccupied lands' (Lyell, 1832, p. 156).

It should not surprise us that the action of these causes, lasting for millennia, would lead to complete changes in the state of the organic creation (Lyell, 1832, p. 157), equal to the endless mutations of the inorganic world. With this idea, the equilibrium proposed for the physical world is transferred to the organic world. Lyell applied in a masterful way the *vera causa* in its gradualist, uniformitarian and actualistic principles.

In Chapter IX, he deals with the influence that inorganic causes have on the habitations of species. His argument is that the earth's surface is basically unstable, and only the great power of the dispersal of the organisms and Providence might counterbalance the enormous effect produced by terrestrial changes, thus keeping the continuity of life and preventing the extermination of the species:

> Every flood and landslip, every wave which a hurricane or earthquake throws upon the shore, every shower of volcanic dust and ashes which buries a country…these and countless other causes displace in the course of a few centuries certain plants and animals from stations which they previously occupied. If, therefore, the Author of Nature had not been prodigal of those numerous contrivances before alluded to, for spreading all classes of organic beings over the earth…it is evident

> that considerable spaces, now the most habitable on the globe, would soon be as devoid of life as are the Alpine snows, or the dark abysses of the ocean, or the moving sands of the Sahara (Lyell, 1832, p. 159).

Thus, Lyell realized that the capabilities of dispersal and migration of organisms served to repopulate the localities where populations were wiped out by the incessant changes of the terrestrial surface. The function of dispersal was not only to extend the areas of distribution of the species, but mostly to avoid local or regional extinction.

The effects that geographical changes exert over the distribution of species are mainly two: (1) to promote or delay their migration, and (2) to alter the physical condition of localities inhabited by them. However, the conclusion stressed by Lyell is that, although the operation of inorganic causes is uniform, their effects upon organic beings are very irregular, at least during relatively limited periods of time:

> A new archipelago might be formed in the Mediterranean, the Bay of Biscay, and a thousand other localities, and may produce less important events than one rock which should rise up between Australia and Java so placed that winds and currents might cause an interchange of the plants, insects, and birds, of the latter countries (Lyell, 1832, p. 165).[5]

By following the logical consequences of the incessant changes of stations and habitations it is easy to conclude that 'species cannot be immortal, but must perish one after the other, like the individuals which compose them' (Lyell, 1832, p. 169). This consequence seemed to him so necessary that it was only possible to evade it by referring to such an extravagant hypothesis as that of Lamarck, 'who imagined, as we have before seen, that species are each of them endowed with indefinite powers of modifying their organization, in conformity to the endless changes of circumstances to which they are exposed' (Lyell, 1832, p. 169).

After concluding that extinction is a natural fact, Lyell finalized his system symmetrically with a discussion about the contrary process: generation. If the species we know now must inevitably and successively disappear, because time fights against them, what processes are responsible for the origin of new species and for the reestablishment of their number? The question is whether species become gradually extinct until a point is reached where a great creative power manifests itself to re-establish their number or whether they originate in a continuous way in the measure that they become extinct.

To begin with, Lyell poses an empirical difficulty: it is easier to demonstrate the extinction of a species with numerous individuals than to demonstrate the origin of a new one, surging into existence at a unique point from a single pair of individuals. He points out that, in the course of history, more and more species have been discovered, although it is not known whether this increase is due to the fact that those species were previously unobserved, or if they had recently appeared by migration, or if they had newly formed. What kind of evidence shows that new species are coming into being? It would consist in suddenly finding a new species belonging to a very well known group, for example, a mammal or a tree, in a country that had been exhaustively surveyed, and where it could be demonstrated that the species was absent from any other region from which it could have dispersed.

The difficulty in obtaining positive evidence of the creation of new species reflects ignorance of both the rate of extinction and the rate of creation. Lyell speculated that if the rate of creation and extinction was of one species per year, and if these processes occurred randomly in any area and within any group of animals or plants, it would result that, amongst the mammals of Great Britain, for instance, some eight centuries would be required for the extinction of only one species, while another might appear.

After presenting such a hopeless panorama, Lyell concludes that the only available evidence that could shed some light upon the origin of species is the fossil record. He thus establishes the following programme: only by a temporal ordering of the fossil species and knowing their taxonomy might it be possible to answer the great question: whether species originate in a successive or simultaneous way. And he thus concluded his analysis of organic distribution.

DISCUSSION

Ecological determinism and dispersal

The importance granted by Lyell to environmental conditions becomes evident in his model of the creation and extinction of species, for both processes are completely determined by the adaptive requirements of the species (Hodge, 1990, p. 253). Extinct species are replaced by new, albeit similar ones, because they are created with the necessary characteristics for very similar circumstances. Lyell explained how environmental changes lead to extinction, but not how species appear adapted from the beginning to their area of origin. It has been pointed out that the incapacity of his uniformitarian system to give a convincing explanation for the origin of species left the way open for his theistic opponents to claim direct miraculous intervention (De Beer, 1970, p. 8). However, Lyell himself maintained that species arose providentially in areas appropriate to their way of life.

Lyell did not justify why he supposed that creation and extinction are gradual and continuous processes. Extinction is a gradual process, in opposition to the catastrophist thesis, but there is not cause now in operation that would empirically sustain his assertion. His statement that creation should be a continuous process seems more a consequence of logical, rather than empirical, symmetry. The idea of a natural balance is an extension of his uniformitarianism into the organic world: the addition of a new species or an increase in the number of its individuals might cause the extinction or the

[5]Wallace (1860) would emphasize years afterwards that neither continuity of islands nor ease of dispersal would have been capable of creating the great faunal difference between the Eastern and Western portions of the Malay Archipelago.

decrease of another, in such a way that, in the course of ages, complete changes in endless cycles can be produced, both in the inorganic and organic worlds. The steady-state of geology was thus transferred to the world of animate beings.

Two decades later, Wallace (1855) tried to clarify Lyell's vague concept of 'creation'. He found out that the geographical distribution of species is not capricious, but follows a clear and simple rule: species appeared by direct derivation from their immediate predecessors in contiguous areas. The implication is easy to grasp: species become modified with time. As there is a constant change in the physical world, in which its present state is a consequence of the past, so in a similar way species are perpetually transform by a process in which the present species arises from an immediate ancestral species.

Lyell's adherence to ecological determinism created strong tensions within his biogeographical model. Since Augustin de Candolle it was clear that the central theme of biogeographical research is to answer why there existed regions of endemism. After the appearance of the concept of biogeographical regions, the study of organic distribution abandoned the mere description of empirical data, advancing towards generalization and abstraction (Nelson, 1978, p. 283). As it became evident that the expectation of finding the same species in all the areas having the same physical conditions was not fulfilled, Linnaeus' ecological determinism was refuted. Candolle transcended the mere empirical fact pointed out by Buffon, elaborating a conceptual and perceptual system about the distribution of organisms that now had to be explained.

Lyell was well aware of this consequence. He knew that every species was restricted to a particular region, independently of the physical conditions. His initial starting point was precisely the need to explain the very existence of large areas of endemism. The answer he gave was clear-cut: biogeographical regions were the result of the existence of large natural barriers, exactly the same explanation provided by Candolle. Ecological determinism by itself could only explain species distribution at a local level. For that reason, Lyell's answer remained partial and incomplete. Although he advanced an explanation for stations, he did not try to give a consistent answer to explain the more general pattern, i.e., the parcelling of the terrestrial surface into biogeographical regions.

Ecological determinism also served for Lyell to extend his anti-progressionist model to the animated world. Against the palaeontological evidence that showed a progression, he argued that this was an illusion and proposed instead the adaptation of organisms to circumstances. Geological changes conditioned the appearance of new species in such a way that the same groups reappeared from time to time, whenever the conditions were favourable. As continents arise and erode, species are created and extinguished in a continuous, incessant and undirected process.

Lyell tried to convince his readers, without much success, that his anti-progessionist system is a necessary consequence of the uniformitarian principle. He was however forced to gradually modify this position in the successive editions of the *Principles of geology*, because of conclusive evidence of the fossiliferous strata (Gould, 1987). In fact, the steady-state model proposed by Lyell never enjoyed great support among contemporary naturalists (Bartholomew, 1976, 1979).

At first, Lyell assigned to dispersal a secondary role. But he could not admit multiple creations as an explanation for disjoint distributions. The only *vera causa* available to him, as an alternative to the hypothesis of multiple creations, was dispersal. Consequently, it was pertinent to investigate how organisms disperse, and he undertook a detailed review of the several means of dispersal, anticipating that which later appeared in the *Origin of species*.

In spite of considering dispersal as a lesser phenomenon, Lyell (somewhat inconsistently) referred to it to explain the most diverse phenomena. He avoided explaining the existence of habitations, and instead assigned an ever increasing importance to dispersal and environmental conditions. At first he used dispersal to explain only exceptional cases of cosmopolitan species; later on, he employed it also to explain cases of disjoint distributions; finally, he assigned it a restoring power. This last role seemed to solve the evident contradiction between the existence of stable, well-defined regions, on the one hand, and the prodigious capacity of dispersal of organisms, on the other. In so doing, however, Lyell entered into a still greater contradiction because dispersal tended to disrupt the general pattern of biogeographical regions, being at the same time the cause of their maintenance!

Why did Lyell shift from granting a secondary weight to dispersal to assigning it a major role? There were probably tactical reasons. By maintaining that dispersal was a minor factor, Lyell risked agreement with the multiple creation doctrine of theistic naturalists, such as Agassiz or Swainson, according to whom there is no need for species dispersal because species had been created in areas where all their necessities would be satisfied. There was, in addition, another motive of logical congruence, thanks to which it was useful for Lyell to have recourse to dispersal, as pointed out by Wilkinson (2002, p. 1110): if he supposed *a priori* that every new species originated in a small area of origin from a single pair of individuals, it would necessarily have to disperse in order to attain its modern distribution. Under this premise, the pertinence of investigating particular episodes of dispersal for each group to understand their present distribution is apparent. Thus, there appears in Lyell the dispersalist model later developed by Darwin and Wallace. Proposing this scheme, Lyell renounced the possibility of explaining convincingly the fundamental biogeographical divisions. He therefore became trapped in an evident inconsistency, as he knew well that the division of the terrestrial surface into large areas of endemism is explained neither by ecological conditions nor by dispersal.

Anti-progressionism

Why did Lyell not go deeply into the problem of the origin of species? It must be considered beforehand that he had to embody the accepted epistemological principles of his time. In the first volume of the *Principles* he had inserted a precautionary note: geology should not be confounded with cosmogony (Lyell, 1830–33, I, p. 4). Rudwick (1970, p. 9) makes it clear that the purpose of this statement was to free scientific geology from vain speculations about the origin of the Earth and to focus only on the subsequent events which have taken place. It is a well established fact that Herschel's (1830) methodological precepts had a great influence upon Lyell (Martínez, 1997, pp. 121–125). The first requisite demanded by Lyell in his methodology of real causes was to appeal to causes whose effects could always be observed. For that reason, he believed that no genuinely scientific answer could be given to the origin of a process. The epistemological goal was to investigate how natural laws operated, and not how they originated. In this way, an epistemological defect of the empiricist tradition became a methodological ideal (Martínez, 1997, p. 128). Lyell subscribed to the supposition that the sensible world has an invariable ontology. He equated scientific knowledge with the discovery of correlations. His biogeographical scheme tries to explain the distribution of organisms by climate, but his compromise with Herschel's epistemology created a conflict because the refutation of climatic determinism was the opening idea with which Lyell started his discussion of organic distribution.

Lyell's inconsistency was present not only in his biogeographical model. For instance, he also excluded the human species from his anti-progressionist position. Iguanodons would reappear and again become extinct in an endless cycle, as would all other extinct species, but the human species was unique and unrepeatable. There were also inconsistencies in his attitude to empirical evidence. He ridiculed Leopold von Buch, the influential German geologist, who had become aware that the land around the Baltic Sea was rising slowly and insensibly. Although there were exceptionally careful records about this elevation, Lyell, who so much praised factual evidence surprisingly refused to believe this particular fact. Von Buch's hypothesis was completely actualistic and gradualistic, but Lyell dismissed it because it did not agree with his own theory, which attributed such elevations to earthquakes. So, while von Buch's theory obeyed the uniformitarian, actualistic and gradualistic requisites, Lyell's hypothesis became frankly catastrophist (Rudwick, 1970, p. 16)!

The permanent tension in Lyell's ideas arose from the prevalent explanatory pattern of his time. The explanatory model by means of laws did not produce satisfactory results in biology because it did not deal with historical processes; moreover, the study of biological processes invariably suggested teleological explanations. Lyell established the concept of deep time in geology (Gould, 1987), but he avoided confrontation with the problem of the origin of species. He also avoided giving a historical explanation for the existence of biogeographical regions. This led to the paradox that, although Lyell studied historical processes such as the changes of the terrestrial surface and the distribution of organic beings, he created a markedly anti-historical system (Martínez, 1997).

Bowler (2000, p. 96) noted that Lyell's ideas were partially based on philosophical compromises and not only by hard factual evidence. We may conclude that the knowledge of organic distribution interested Lyell as far as it could be explained by the same uniformitarian principles of his geological system. The specific questions that he asked himself at first were to know whether species were entities with an unlimited duration or if they originated in a simultaneous or successive manner. However, the answers he gave were not obtained from the data of geographical distribution. His model of the animate kingdom was preconceived as an extension of his uniformitarian system. Lyell ended up giving *a priori* answers. Species appeared gradually, and not massively, all having extinction as their final destiny.

Lyell's aim was to find laws governing the adaptation, extinction and creation of species, assumed by him to be equivalent to the mechanical laws ruling the regular movement of stars (Hodge, 1990; Guillaumin-Juárez, 1997). The investigation of the origin of those immanent laws surpassed the human intellectual capacity, so to attempt this was not only useless, but immodest.

Darwin's evolutionary theory would erode this mechanicist explanatory pattern, because, although dealing with the forbidden issue of the origin of species (a clearly historical process), it became highly convincing. Lyell himself finally converted to it. He eventually accepted that at least in the organic world there is change with directionality. With Darwin, historical explanations for the organic world began to gain credibility, so it now became meaningful to consider particular episodes of dispersal as an explanation of modern patterns of geographical distribution.

The importance of the *Principles* lies in its elaboration of a coherent theoretical and methodological scheme for the entire science of geology. Paraphrasing Rudwick (1970, p. 32), Lyell's biogeographical concepts were just part of his strategy to develop his uniformitarian system. With his ample and systematic argumentation on the geographical distribution of organisms, Lyell established, independently from any theory about organic change, the first version of the dispersalist model. The explanatory scheme devised by Lyell was preserved within the more sophisticated Darwinian model developed later by Wallace. Modern organic distribution was to be understood as the result of hazardous and independent dispersals of the diverse groups, departing from well defined centres of origin.

Darwin and Wallace were but participants in a long discussion in which a plethora of talented naturalists took part. This debate was neglected for a long time by a whiggishly evolutionist historiography, which submitted biogeography to evolution. Nevertheless, from the works of George Louis Leclerc (Buffon), Eberhardt Zimmermann, Alexander von Humboldt, Augustin Pyramus de Candolle, Andew Murray, Edward Forbes, James Cowles Prichard, Hewett Cottrell Watson, Alphonse de Candolle, Joseph Dalton Hooker, Henry Walter Bates, Phillip Lutley Sclater, Charles Lyell, Charles Darwin and Alfred Russel Wallace amongst others to the panbiogeographic, vicariant and phylogeographic approaches, a recurring issue has caught the interest of biogeographers: to untangle the overwhelmingly complex history of the distribution of organic beings in space and time, of which so far we have only a vague idea.

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REFERENCES

Bartholomew, M. (1976) The non-progression of non-progression: two responses to Lyell's doctrine. *British Journal for the History of Science*, **9,** 166–174.

Bartholomew, M. (1979) The singularity of Lyell. *History of Science*, **17,** 276–293.

Blundell, D.J. & Scott, A.C. (eds) (1998) *Lyell: the past is the key to the present*. Geological Society, Special Publications 143, London.

Bowler, P. (1996) *Life's splendid drama*. The University of Chicago Press, Chicago & London.

Bowler, P. (2000) Philosophy, instinct, intuition: what motivates the scientist in search of a theory? *Biology and Philosophy*, **15,** 93–101.

Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*. Sinauer, Sunderland, MA.

Brown, J.H. & Maurer, B.A. (1989) Macroecology: the division of food and space among species on continents. *Science*, **243,** 1145–1150.

Browne, J. (1983) *The secular ark: studies in the history of biogeography*. Yale University Press, New Haven & London.

Candolle, A.P. de (1820a) Gèographie botanique. *Dictionnaire des sciences naturelles*, **18,** 359–436.

Candolle, A.P. de (1820b) *Essai élémentaire de géographie botanique*. G. Levrault, Paris & Strasbourg.

Corsi, P. (1978) The importance of French transformist ideas for the second volume of Lyell's Principles of Geology. *British Journal for the History of Science*, **11,** 221–244.

Crisci, J.V. & Morrone, J.J. (1995) Historical biogeography: introduction to methods. *Annual Review of Ecology and Systematics*, **26,** 373–401.

De Beer, G. (1970) Introduction. Biology before the Beagle. *Darwin* (ed. by D. Appleman), pp. 3–10. W. W. Norton & Company, New York.

Endersby, J. (2003) Escaping Darwin's shadow. *Journal of the History of Biology*, **36,** 385–403.

Espinosa, D. & Llorente, J. (1993) *Fundamentos de biogeografías filogenéticas*. CONABIO – Universidad Nacional Autónoma de México, México, DF.

Gould, S.J. (1987) *Time's arrow, time's cycle*. Harvard University Press, Cambridge, MA.

Guillaumin-Juárez, G. (1997) Metodología y causas verdaderas en la Filosofía Natural (1672–1859). PhD Thesis, Universidad Nacional Autónoma de México, México, DF.

Herschel, J. (1830) *A preliminary discourse on the study of natural philosophy*. Longman, London (reprinted edition by The University of Chicago Press, 1987).

Hodge, M.J.S. (1990) Darwin studies at work: a re-examination of three decisive years (1835–37). *Nature, experiments, and the sciences* (ed. by T.M. Levere and W.R. Shea), pp. 249–274. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Kinch, M.P. (1980) Geographical distribution and the origin of life: the development of early nineteenth-century British explanation. *Journal of the History of Biology*, **13,** 91–119.

Kitcher, P. (1993) *The advancement of science*. Oxford University Press, New York.

Laudan, R. (1982) The role of methodology in Lyell's science. *Studies in History and Philosophy of Science*, **13,** 215–249.

Laudan, R. (1987) *From mineralogy to geology*. The University of Chicago Press, Chicago, IL.

Llorente, J. & Espinosa, D. (1991) Una síntesis de las controversias en la biogeografía histórica contemporánea. *Ciencia*, **41,** 1–18.

Lyell, C. (1830–33) *Principles of geology, being an attempt to explain the former changes of the earth's surface, by references to causes now in operation*, 3 vols. John Murray, London (Facsimile of the first edition published by University of Chicago Press, 1990).

Lyell, C. (1832) *Principles of geology, being an attempt to explain the former changes of the earth's surface, by references to causes now in operation*, Vol. 2. John Murray, London.

Martínez, S. (1997) *De los efectos a las causas. Sobre la historia de los patrones de explicación científica*. Paidos & Universidad Nacional Autónoma de México, México, DF.

Mayr, E. (1982) *The growth of biological thought: diversity, evolution and inheritance*. Harvard University Press, Cambridge, MA.

Myers, A.A. & Giller, P.S. (1988) *Analytical biogeography*. Chapman and Hall, New York.

Nelson, G. (1978) From Candolle to Croizat: comments on the history of biogeography. *Journal of the History of Biology*, **11,** 269–305.

Nelson, G. & Platnick, N. (1981) *Systematics and biogeography, cladistics and vicariance*. Columbia University Press, New York.

Oakley, F. (1961) Christian theology and the Newtonian science: the rise of the concept of the laws of nature. *Church History*, **30,** 433–457.

Ospovat, A. (1976) The distortion of Werner in Lyell's Principles of Geology. *British Journal for the History of Science*, **9,** 190–198.

Papavero, N., Martins-Teixeira, D., Llorente-Bousquets, J. & Bueno, A. (2004) *Historia de la biogeografía. I. El período preevolutivo*. Fondo de Cultura Económica, México.

Porter, R. (1976) Charles Lyell and the principles of history of geology. *British Journal for the History of Science*, **9,** 91–103.

Reid, T. (1785) *Essays on the intellectual powers of man*. J. Bell, Edinburgh (Re-edited by Cambridge University Press, MIT, 1969, with an introduction of B. A. Brody).

Richardson, R.A. (1981) Biogeography and the genesis of Darwin's ideas on transmutation. *Journal of the History of Biology*, **14,** 1–41.

Rudwick, M.J.S. (1970) The strategy of Lyell's Principles of Geology. *Isis*, **61,** 4–33.

Rudwick, M.J.S. (1972) *The meaning of fossils*. MacDonald, London.

Rudwick, M.J.S. (1990) *Introduction*. Lyell, C. (1830–33). *Principles of geology, being an attempt to explain the former changes of the earth's surface, by references to causes now in operation*. 3 vols. John Murray, London (Facsimile of the first edition, pp. vii–lviii. University of Chicago Press).

Sclater, P.L. (1858) On the general geographical distribution of the members of class Aves. *Journal of the Linnean Society: Zoology*, **2,** 130–145.

Simberloff, D. (1983) Biogeography: the unification and maturation of a science. *Perspectives in ornithology* (eds A.H. Brush and J.H. Clark Jr), pp. 411–485. Cambridge University Press, Cambridge.

Simpson, G.G. (1965) *The geography of evolution*. Clinton, Philadelphia and New York.

Wallace, A.R. (1855) On the law which has regulated the introduction of new species. *Annals and Magazine of Natural History*, 2nd. Ser., **16,** 184–196.

Wallace, A.R. (1860) On the zoological geography of the Malay Archipelago. *Journal of the Proceedings of the Linnean Society: Zoology*, **4,** 172–184.

Westfall, R. (1980) *Never at rest*. Cambridge University Press, Cambridge.

Whewell, W. (1847) *The philosophy of the inductive sciences, founded upon their history*. Parker, London.

Whewell, W. (1857) *History of the inductive sciences from the earliest to the present times*, 3rd edn. Parker, London.

Wilkinson, D.M. (2002) Ecology before ecology: biogeography and ecology in Lyell's 'Principles'. *Journal of Biogeography*, **29,** 1109–1115.

Zunino, M. & Zullini, A. (2004) *Biogeografía. La dimensione spaziale dell'evoluzione*, Seconda Edizione. Casa Editrice Ambrosiana, Milan.

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