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"A Great Complication of Circumstances" – Darwin and the Economy of Nature

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Abstract. In 1749, Linnaeus presided over the dissertation "*Oeconomia Naturae*," which argued that each creature plays an important and particular role in nature's economy. This phrase should be familiar to readers of Darwin, for he claims in the *Origin* that "all organic beings are striving, it may be said, to seize on each place in the economy of nature." Many scholars have discussed the influence of political economy on Darwin's ideas. In this paper, I take a different tack, showing that Darwin's idea of an economy of nature stemmed from the views of earlier naturalists like Linnaeus and Lyell. I argue, in the first section of the paper, that Linnaeus' idea of *oeconomia naturae* is derived from the idea of the animal economy, and that his idea of *politia naturae* is an extension of the idea of a *politia civitatis*. In the second part, I explore the use of the concept of *stations* in the work of De Candolle and Lyell – the precursor to Darwin's concept of *places*. I show in the third part of the paper that the idea of places in an economy of nature is employed by Darwin at many key points in his thinking: his discussion of the Galapagos birds, his reading of Malthus, etc. Finally, in the last section, I demonstrate that the idea of a place in nature's economy is essential to Darwin's account of divergence. To tell his famous story of divergence and adaptation, Darwin needed the economy of nature.

Keywords: Charles Darwin, Carl Linnaeus, Augustin Pyrame de Candolle, Charles Lyell, John Hunter, economy of nature, polity of nature, animal economy, place, niche, divergence, Galapagos Islands, *Mimus thenca*

Introduction

One hundred years before the publication of Charles Darwin's *On the Origin of Species*, Benjamin Stillingfleet translated and published a collection of dissertations presided over by Carl Linnaeus, entitled

Miscellaneous Tracts Relating to Natural History, Husbandry, and Physick. Among the dissertations was "The Oeconomy of Nature," defended by Isaac Biberg.[1] This phrase should be familiar to readers of Darwin, for he claims in the *Origin* that "all organic beings are striving, it may be said, to seize on each place in the economy of nature."[2] Whenever the word 'economy' appears in Darwin's texts, there is a tendency to look to political economy for precursors. While it is undeniable that there is a real historical connection between ideas about natural organization and ideas about social organization, as demonstrated by scholars from Robert Young to Margaret Schabas, concepts like the animal economy and the economy of nature debatably belonged to intellectual lineages that were relatively independent of their social and political context.[3] In this paper, I will investigate one such lineage, exploring the origins and role of Darwin's idea of an economy of nature. I will argue that Darwin's idea of a place in the economy of nature stems from the work of previous naturalists like Carl Linnaeus and Charles Lyell, and that it played a key role in the development of his evolutionary ideas.

Some Darwin scholars may shudder at the phrase "relatively independent of their social and political context." Since the work of John Greene and Robert Young in the 1960s and 1970s, there has been an influential approach to the history of evolutionary biology that emphasizes the connections between ideas and precisely this context.[4] Adrian Desmond and James Moore's landmark biography of Darwin, published in 1991, pursues a similar line, condemning "historians of disembodied ideas" and stressing "the cultural conditioning of knowledge."[5] This kind of approach has prompted a variety of historical and historiographical debates. For example, scholars agree that the economist Thomas Malthus had a decisive influence on Darwin, but argue over the form and extent of that influence.[6] Despite such debates, most now take for granted the impact of political economists on Darwin's ideas – a view inserted into

[1] Darwin, 1859; Stillingfleet, 1759; Linnaeus, 1749. In the eighteenth century, dissertations were typically written by the professor and defended by the student. These particular dissertations were dictated by Linnaeus in Swedish to the doctoral candidate, who then translated them into Latin and defended them (see Koerner, 1999, p. 283; Smit, 1978, p. 130, note 6).

[2] Darwin, 1859, p. 102.

[3] Young, 1985; Schabas, 1990, 2005. See also Koerner, 1999.

[4] See the essays collected in Greene, 1981 and Young, 1985. On Young, see also Bohlin, 1991.

[5] Desmond and Moore, 1991, p. xx.

[6] Desmond and Moore, 1991, pp. 264–268; Benton, 1995, 1998; Moore and Desmond, 1998. See also Hull, 2005.

popular consciousness by Stephen J. Gould's claim that Darwin's theory is "the economy of Adam Smith transferred to nature."[7] Silvan Schweber is the historian who has most clearly championed this view, arguing that "Scottish views […] of the market deeply influenced Darwin."[8] However, other historians have more recently taken issue with this position, as Darwin only read a short summary of Smith's economic ideas, and did not refer to them in his extensive notebooks.[9] In this paper, I will not discuss the ideas of political economists or the social and political context of Darwin's theory. These topics have been extensively discussed by other scholars. Instead, I will focus on the intellectual sources of Darwin's idea of a place in the economy of nature, employing both his notebooks and his published works. My investigation of the economy of nature is thus complementary to previous work on the relation between natural and social economies.

Darwin viewed divergence and adaptation as dependent on the pre-existing structure and organization of the natural world – nature's organization provides the backdrop against which evolution happens. In the first part of the paper, I will explore Linnaeus' ideas of the economy of nature (*oeconomia naturae*) and the police of nature (*politia naturae*), placing them in their intellectual context. In the second part, I will trace the origins of Darwin's concept of a *place* in nature's economy, discussing the role of stations in the work of Augustin Pyrame de Candolle and Charles Lyell. In the third part, I will show that the idea of places in the economy of nature first emerged at key junctures in Darwin's thought, e.g. his reading of Malthus and his discussions of the Galapagos Islands. Finally, in the last part of the paper, I will argue that the economy of nature is essential to Darwin's principle of divergence. To tell his famous story of divergence and adaptation, Darwin needed the economy of nature.

Linnaeus, the Animal Economy, and *Oeconomia Naturae*

Darwin read translations of Linnaeus' dissertations "*Oeconomia Naturae*" (1749) and "*Politia Naturae*" (1760) in May of 1841.[10] Although

[7] Gould, 1977, p. 12.

[8] Schweber, 1985, p. 37. See also Schweber, 1977, 1980, 1983, 1994.

[9] Darwin, 1987, pp. 545–546 [M108]. For critiques of Schweber's position, see Gordon, 1989; Schabas, 1990; Tammone, 1995; Winch, 2001; Hull, 2005. See also Paul and Beatty, 2007. All of Darwin's works, and many of his notebooks and manuscripts, are now online at http://darwin-online.org.uk.

[10] Darwin, 1985, Vol. 4, pp. 462–463; Stauffer, 1960, p. 239.

the phrase "economy of nature" appears only once in Darwin's notebooks of the late 1830s it can be found throughout his first sketches on transmutation in 1842 and 1844.[11] Given this chronology, it is likely that the idea came to play a greater role in Darwin's work because of his encounter with these Linnaean texts. Thus, before exploring the form taken by the ideas of *oeconomia* and *politia* in Darwin's own writings, it is necessary to investigate their use in the works of Linnaeus, and in the eighteenth century more generally. In this section, I will argue that Linnaeus' *oeconomia naturae* is related to the idea of an animal economy, and that his *politia naturae* is related to the idea of a *politia civitatis*.

In the seventeenth century, the word *oeconomia* still had its Aristotelian meaning: the "guiding & ordering of things pertaining to household."[12] However, this usage was also metaphorically extended to both the macrocosm and microcosm, i.e. to nature as a whole and to the human body. For instance, Walter Charleton's *Oeconomia Animalis* was published in 1659 in both English and Latin. The 'animal economy' of his title refers to the function and organization of the various systems of the human body; thus Charleton's book includes lectures on nutrition, the circulation of the blood, respiration, and muscular movement.[13] Charleton makes the macrocosm–microcosm analogy explicit, claiming that he is offering "a compleat History of the Oeconomy of Nature in an Animal."[14] By the middle of the next century, '*Œconomie animale*' had its own article in the *Encyclopédie*, where Ménuret de Chambaud defined it as "the *order*, the *mechanism*, the *ensemble* of functions and movements that maintain the life of animals, whose perfect, universal exercise […] constitutes the most flourishing state of *health*."[15] The idea was not restricted to the animal body, of course, and John Ray speculated in 1691 that "some intelligent Plastick Nature […] may understand and regulate the whole Oeconomy of the Plant."[16] Thus, in seventeenth century medicine and natural history, the animal economy,

[11] Darwin, 1987, p. 375 [D135]. Darwin, 1909. On Darwin and the economy of nature see also Pancaldi, 1977 (reviewed by Glick, 1978).

[12] Thomas, 1606.

[13] Charleton, 1659a, b. For more on Charleton and the animal economy, see Booth, 2005, pp. 81–87. For the origins and nature of the animal economy, see Balan, 1975 and Folter, 1978, pp. 184–188.

[14] Charleton, 1659b, p. 149. *Cf.* Balan, 1979, pp. 87–95.

[15] Chambaud, 1765, p. 360.

[16] Ray, 1691, p. 48.

the economy of a plant, or even the economy of a woman's body, was the ensemble of functions that maintained health and life.[17]

Like most naturalists of his time, Linnaeus was trained in medicine, and thus would have been familiar with the term '*oeconomia animalis*' as employed by Charleton, Hermann Boerhaave, and others.[18] However, Linnaeus set his sights higher – what he wanted to describe was not the animal economy, but the economy of nature as a whole. Of course, others had used the term 'economy of nature', e.g. Sir Kenelm Digby in a variety of works, but only as a brief metaphor. For example, Digby writes in 1644 that natural motion "hath its birth from the universall oeconomy of nature here among us."[19] What Linnaeus did instead was extend the physiological idea of the animal economy to nature in its entirety. In his eyes, the economy of nature deserved a description just as detailed and rational as that of the animal economy.[20]

In the dissertation "*Oeconomia Naturae*," defended by his student Isaac Biberg in 1749, Linnaeus defines his title as follows: "By the oeconomy of nature we understand the all-wise disposition of the creator in relation to natural things, by which they are fitted to produce general ends, and reciprocal uses."[21] The "reciprocal uses" are the key to the whole idea, for "the death, and destruction of one thing should always be subservient to the restitution of another;" thus mould spurs the decay of dead plants to nourish the soil, and the earth then "offers again to *plants* from its bosom, what it has received from them."[22] Linnaeus points out that natural processes always follow a certain order, with each stage dependent on the previous. A fallen tree, for instance, does not go to waste, but is colonized and eliminated by an ordered series of creatures: liverworts, mushrooms, beetles, caterpillars,

[17] Boyle, 1686, p. 316.

[18] Linnaeus, 1805, pp. 514–517; Boerhaave, 1741. Linnaeus had a high respect for Boerhaave, with whom he met and corresponded. See Boerhaave, 1962–1979, Vol. 3, pp. 186–191.

[19] Digby, 1644, p. 100. This usage of the term is explored to some extent in La Vergata, 1988.

[20] *Cf.* Egerton, 2007, p. 81. For an introduction to Linnaeus' idea of a natural economy, see Limoges, 1972. Many have discussed the relation between Linnaeus' economy of nature and his interest in economics. See Koerner, 1999, pp. 82–112; Müller-Wille, 2003; and Rausing, 2003. Lisbet Koerner = Lisbet Rausing. On the theological aspects of Linnaeus' "*Oeconomia Naturae*," see Worster, 1985, pp. 26–55.

[21] Linnaeus, 1749, p. 31. I am quoting from Stillingfleet's English translation, published in 1759. Although the dissertation was defended by Biberg, it was written by Linnaeus (see footnote 1 above).

[22] Linnaeus, 1749, pp. 32, 64. Emphasis in original.

and woodpeckers.[23] Just as the respiratory, cardiovascular, lymphatic, and digestive systems play different functional roles in the economy of the human body, different species play different functional roles in the economy of nature as a whole. For example, each kind of insect lays its eggs on a particular kind of plant:

> […] every different tribe chooses its own species of plant. Nay, there is scarce any plant, which does not afford nourishment to some insect; and still more, there is scarcely any part of a plant, which is not preferred by some of them. Thus one insect feeds upon the flower; another upon the trunk, another upon the root; and another upon the leaves.[24]

Each type of organism, therefore, according to Linnaeus, has its special function in nature's economy.

Just as the animal economy ensures the health and well-being of the animal body, the economy of nature ensures the health and well-being of the natural world. Linnaeus discusses the many creatures that help cleanse and purify nature's body, without which the "whole earth would be overwhelmed with carcases [*sic*], and stinking bodies."[25] Thus if a horse dies near a roadway, its body will "be filled with innumerable grubs of carniverous [*sic*] flies, by which he is entirely consumed, and removed out of the way, that he may not become a nuisance to passengers by his poisonous stench." Likewise, specialized aquatic predators like the thornback, the hound fish, or the conger eel, consume fish carcasses near the shore.[26] Linnaeus even suggests an experiment to prove the purifying potential of insects:

> […] knats lay their eggs in stagnant, putrid and stinking waters, and the grubs that arise from these eggs clear away all the putrefaction; and this will easily appear, if any one will make the experiment by filling two vessels with putrid water, leaving the grubs in one, and taking them all out of the other. For then he will soon find the water, that is full of grubs, pure and without any stench, while the water that has no grubs will continue stinking.[27]

Thus, for Linnaeus, even scavengers and grubs, the lowest of all species, play an essential role in the economy of nature.

[23] Linnaeus, 1749, p. 66.
[24] Linnaeus, 1749, p. 71.
[25] Linnaeus, 1749, p. 101.
[26] *Ibid.*
[27] Linnaeus, 1749, p. 102.

Linnaeus' dissertations were collected and published in Latin, beginning in 1749, in a series of volumes entitled *Amoenitates Academicae* (Academic Delights). However, they were also circulated prior to the publication of these collections, as evidenced by a letter from Nils Rosén von Rosenstein to the famous physiologist Albrecht von Haller: "Colonel Baron Posse has departed for Germany. I have placed a package in his charge, which he has promised to give you, containing […] Linnæi Dissertationes de oeconomia naturae, de Taenia, Ligno colubrino, [etc.]."[28] "*Oeconomia Naturae*" (1749) appeared in the second volume of the *Amoenitates*, published in 1751, and the related dissertation "*Politia Naturae*" (1760) appeared in the sixth volume, published in 1764. Whereas '*oeconomia*' referred to the "guiding & ordering of things pertaining to household," '*politia*' referred to the "governance and rule or pollicie of a towne or common wealth."[29] Thus, although '*oeconomia*' related to a household and '*politia*' to a town or city, both involved management and organization.

In 1841, Darwin read both of these dissertations in English translation, and seems to use the terms 'polity of nature' and 'economy of nature' interchangeably in the *Origin*. He also read the second volume of Lyell's *Principles of Geology*, which cites Linnaeus' "*Politia Naturae*" (defended by C.D. Wilcke) in the early 1830s.[30] It is thus necessary to investigate how Linnaeus arrived at the idea of a *politia naturae*, closely related to that of an *oeconomia naturae*. The term '*politia*' was often translated into both French and English as 'police'; however, this word had a quite different sense in the seventeenth and eighteenth centuries.[31] Michel Foucault, in a set of lectures only recently published, discusses this earlier concept of the police at length, offering a preliminary definition: "From the 17th century onwards, one began to define 'police' as the ensemble of means by which one could promote the growth of the forces of the State while maintaining its good order."[32] On Foucault's account, the police involved a variety of different objects: the number

[28] Rosén to Haller, Stockholm, 16 May 1749. In Rosén, 1964, p. 123. The dissertation "*Oeconomia Naturae*" was defended on March 4, 1749; its "instant success" is mentioned by Hestmark, 2000. Rosén was Linnaeus' colleague in the faculty of medicine at Uppsala (Berg, 1964, p. 104).

[29] Thomas, 1606.

[30] Stauffer, 1960, p. 239; Lyell, 1832, pp. 132–135 (cited as Wilcke rather than Linnaeus).

[31] Febvre, 1930, Sect. 2. *Cf.* also Goldstein, 1987, p. 21.

[32] Foucault, 2004, p. 321. Foucault summarized some of this material on the police in his Tanner Lectures on Human Values, delivered at Stanford University in October of 1979. See Foucault, 1981, pp. 153–160.

and activities of men, the necessities of life, the maintenance of health, and the circulation of products.[33] Foucault's claim is borne out by a treatise of 1722 by Nicolas Delamare, entitled *Traité de la Police*, which boasts an extensive table of contents ranging from economics to education.[34] In his epistle to the king, Delamare speaks of his majesty's "constant inclination […] for all that concerns the Police, that is, for that beautiful order upon which depends the happiness [*bonheur*] of States."[35] Delamare suggests, in his first chapter, that "The General Idea of the Police" is linked to an ancient Greek model. The Greeks, says Delamare, divided *politia* into three parts: "the conservation, the goodness [*bonté*], & the charms [*agrémens*] of life."[36] He goes on to say that people still subscribe to this ancient division, even though religion and morality have taken on a greater role in modern times. Thus in the eighteenth century, *politia* referred not to a negative force of control, but rather to a positive force ensuring the well-being of the state and the *bonheur* and *bonté* of life.

'*Politia*' and '*oeconomia*' are closely related: just as *oeconomia animalis* maintains the health and well-being of the animal, *politia civitatis* is "an exercise that itself contains all that which is necessary for the conservation and maintenance of the Inhabitants, & for the public good of a City."[37] Linnaeus' *politia naturae* is just an extension of the idea of *politia civitatis* to nature. There is a key difference, however. The task of the latter is taken up by particular men serving in the various administrative offices of the state, led by the magistrate of police or some equivalent. These men promote a particular set of practices designed to ensure *bonté de vie* for the inhabitants of the city.[38] Nature, on the other hand, is self-policing: each inhabitant, each type of organism, holds a particular office in the police of nature; God, the natural equivalent of the magistrate, merely assigns the offices. Thus Linnaeus writes, "The Birds, whose tribes are so numerous, have all their peculiar distinctions

[33] Foucault, 2004, pp. 330–334. For the connection between the police and the politics of health in the eighteenth century, see Foucault, 1979.

[34] Delamare, 1722. The first volume of this work was published in 1705. For its complicated publication history, see Foucault, 2004, p. 366, note 1. I am working from a microfilm of the 1722 edition.

[35] Delamare, 1722, n.p.

[36] Delamare, 1722, p. 3.

[37] Delamare, 1722, p. 2.

[38] Delamare, 1722.

and offices in the Police of Nature."[39] Some animals, like the small crab *pinnotheres*, which hides inside the *pinna* (pen shell) and warns it of approaching enemies, are "in the Police of Nature […] appointed as watchmen to warn other animals of their danger."[40] *Politia naturae* is a kind of self-regulating version of *politia civitatis*: "Thus we see Nature resemble a well regulated state in which every individual has his proper employment and subsistence, and a proper gradation of offices and officers is appointed to correct and restrain every detrimental excess."[41] In the eighteenth century, the police was not simply "the visible and heavy hand of the state," as Lisbet Rausing would have it; these apparently negative aspects were means to a positive end – the health, well-being, and flourishing of the natural world.[42]

Linnaeus extended the idea of the animal economy – that ensemble of functions that maintains the life of an animal – to nature as a whole. He also borrowed the existing idea of a *politia civitatis* – that order which ensures the well-being of the state – and applied it to nature. These concepts meld in the work of Linnaeus: at the heart of both is the idea of the organization and ordering of functional roles to ensure the continued prosperity of some system, be it the household, the state, the animal body, or nature writ large. This organization, this economy of nature, is what lies in the background of what Limoges has called Darwin's idea of a "division of ecological labour."[43] But this division of labour requires not just an economy of nature, but also places in that economy. As we will see in the next section, Darwin's places are related to what earlier naturalists, including Linnaeus, called 'stations'.[44]

De Candolle, Lyell, and Stations

Just as each creature has its office in *politia naturae*, each organism has a particular station. The tradition of recognizing stations begins with Linnaeus and extends to De Candolle, Lyell, and Darwin. A station initially referred to what we would call the habitat of an organism – e.g.

[39] Linnaeus, 1760, p. 148. I am quoting from Brand's English translation, published in 1781. Many eighteenth-century thinkers focused on this idea of ranks or offices. For one famous example, see Millar, 1771.

[40] Linnaeus, 1760, pp. 163–164. Also discussed in Linnaeus, 1749, pp. 92–94. *Cf.* Aristotle, 1984, pp. 547b15–19.

[41] Linnaeus, 1760, p. 164.

[42] Rausing, 2003, p. 186.

[43] Limoges, 1994, p. 330. *Cf.* Limoges, 1968, p. 114.

[44] Linnaeus, 1754.

the kind of soil that a plant prefers. In this section we will see how Lyell gave the term 'station' a more complex meaning, which included not just inanimate but also animate circumstances. It is this more complex, Lyellian concept of station that is the direct precursor of Darwin's idea of a place in the economy of nature.

The idea of stations is tied up with the geographical approach to the natural world that emerged in the early nineteenth century.[45] Most historians see this approach, anticipated by Linnaeus and exemplified in the botanical geography of Alexander von Humboldt and Augustin Pyrame de Candolle, as the beginning of 'ecological' thinking.[46] This new geography involved paying much closer attention to where particular organisms lived – climate zones, soil types, etc. In "*Politia Naturae*" (1760), Linnaeus points out that in "every country different species have different stations assigned them, growing in the sea, lakes, marshes, vallies, fields, hills, rocks and shaded places, and every one has its different soil, sand, clay, earth, or chalk, allotted to it."[47] Humboldt followed Linnaeus in investigating the stations of different plants, but added altitude to the mix, demonstrating that as distance above sea level increases, different kinds of plants appear: "ligneous plants disappear little by little and give way to herbaceous and alpine plants; even higher, one finds nothing but grasses [*les graminées*] and cryptogams."[48] When he presented his *Essai sur la géographie des plantes* to the scientists and mathematicians of the *Institut National* on January 7, 1805, Humboldt included a table of measurements that correlated physical data on the soil, humidity, air pressure, temperature, and animal life of the Andes and neighbouring regions with the kinds of plants existing at a given altitude. With this table, Humboldt ushered in the new science of plant geography, which at the time existed in name only.[49]

If Humboldt was the father of botanical geography, De Candolle was its first great champion. One of De Candolle's most important contributions to botanical geography was to emphasize the distinction, first presented by Linnaeus, between "*habitations*, i.e. the countries in which plants grow, and *stations*, i.e. the particular nature of the localities in

[45] For the rise of this approach, see Browne, 1983, pp. 32–57 and Nicolson, 1987.

[46] Egerton, 1968, pp. 230–232; Dajoz, 1984, pp. 10–20; Deléage, 1992, pp. 39–45; Acot (ed.), 1998, Sect. 1; Matagne, 1999, pp. 85–88. For a deeper history, see Frank Egerton's ongoing "History of the Ecological Sciences" series in the online *Bulletin of the Ecological Society of America*.

[47] Linnaeus, 1760, p. 133.

[48] Humboldt and Bonpland, 1805, p. 37.

[49] Humboldt and Bonpland, 1805, p. 13. The beautiful fold-out table is reproduced at the front of the 1973 reprint of the *Essai* by Theatrum Orbis Terrarum of Amsterdam.

which they are accustomed to develop.''[50] This distinction took Humboldt's comparisons between alpine plants in Europe and the Americas further by making possible the argument that species often occupy quite similar soil types or climates (*stations*) while living in completely different global regions (*habitations*). De Candolle, who was personally acquainted with Jean-Baptiste de Lamarck and Georges Cuvier, embarked upon a more detailed study of the circumstances and conditions of existence of plants, following up on the work of these older naturalists.[51] His concept of station followed naturally from their earlier ideas.

In 1820, De Candolle published an article entitled ''*Géographie botanique*'' in a new dictionary of the natural sciences edited by Frédéric Cuvier, brother of Georges. This essay, also published separately, was quite influential and read by both Darwin and Lyell.[52] The middle section is entitled simply ''Stations.'' It is here that De Candolle famously talks of the ''perpetual struggle'' between different plants:

> All the plants of a country, all those of a given area, are in a state of war relative to all the others. […] The first to establish themselves by chance in a given locality tend, simply because they occupy the space, to exclude other species: the larger plants smother the smaller; the long-lived [*vivaces*] replace those whose duration is short; the more fertile gradually take over the space that could be occupied by those that multiply with more difficulty.[53]

This perpetual struggle happens against the background of circumstances, i.e. external conditions of existence: ''Certain plants, given their organization, require certain conditions of existence: one cannot live without a certain amount of salt water; the other without, at a particular time of year, a certain amount of water or intensity of sunlight, etc.''[54] These necessary conditions of existence, demanded by the structure and organization of a plant, represent its station. De Candolle lists sixteen major classes of station, which consist of various soil and climate types. However, he makes clear that the situation in any given case is more complex:

[50] De Candolle, 1820, p. 359. I have left '*habitations*' and '*stations*' in the original French.

[51] *Cf*. Bradley (ed.), 1991, no. 179, p. 339.

[52] Darwin, 1987, pp. 174 [B13], 209 [B156], 236 [B280], 324 [C268]; Lyell, 1832, p. 68.

[53] De Candolle, 1820, p. 384. This is my translation, although there is also a translation of this passage in Lyell, 1832, p. 131.

[54] *Ibid*.

> We have seen, in the first part of this article, to what extent just one of the circumstances influencing vegetation introduces modifications, for the most part simultaneous: now, a station is a kind of average result produced by the varied and unequal combination of all these circumstances: thus, a swamp is different from itself, depending on whether it is nourished by fresh or salt water; whether it lies on clay or sand, in a plain or on a mountain, in a hot or cold climate, etc.[55]

Thus even though he takes one element (water, soil, etc.) as primary in his list of station types, he sees actual stations as complex sets of interconnected factors, each making "varied and unequal" contributions to the survival of the plant.[56]

Although Darwin read De Candolle's article, it also exercised an indirect influence via the second volume of Lyell's *Principles of Geology*, received by Darwin on the Beagle in October of 1832.[57] Lyell, however, used the word 'station' in a broader sense than De Candolle, insisting that the relevant conditions of existence included not just soil type and climate, but also interactions with other organisms:

> […] the possibility of the existence of a certain species in a given locality, or of its thriving more or less therein, is determined not merely by temperature, humidity, soil, elevation, and other circumstances of the like kind, but also by the existence or non-existence, the abundance or scarcity, of a particular assemblage of other plants and animals in the same region.[58]

Because Lyell includes both the animate and inanimate circumstances of an organism as part of its station, he has a much more complex picture of stations and their interaction:

> […] the stations of different plants and animals depend on a great complication of circumstances, – on an immense variety of relations in the state of the animate and inanimate worlds. Every plant requires a certain climate, soil, and other conditions, and often the

[55] De Candolle, 1820, p. 387. For the list of station classes, see *ibid.*, pp. 387–391.

[56] De Candolle, 1820, pp. 387, 391. The local causes determining the various stations of plants are expanded in the work of De Candolle's son, Alphonse Louis Pierre Pyrame de Candolle, to include "the action of animals" (De Candolle, 1855, Vol. 1, p. 450).

[57] An annotated copy of the article is held among Darwin's books at Cambridge (Darwin, 1987, p. 660). For the date of Darwin's receipt of the second volume of Lyell's *Principles*, see Darwin, 1933, p. 435, note 22. De Candolle appears in Lyell's index as Decandolle (Lyell, 1832, p. 315).

[58] Lyell, 1832, p. 141.

> aid of many animals, in order to maintain its ground. Many animals feed on certain plants, being often restricted to a small number, and sometimes to one only; other members of the animal kingdom feed on plant-eating species, and thus become dependent on the conditions of the *stations* not only of their prey, but of the plants consumed by them.[59]

Thus stations involve "a great complication of circumstances" – not just humidity, temperature, and the like, but also the presence of food and predators.

Lyell has a more dynamic picture of stations than either Linnaeus or De Candolle. Because the circumstances, both inanimate and animate, "are perpetually changing," stations are constantly created or destroyed.[60] For Linnaeus, each creature is created for a particular office, a particular station, in the economy of nature, and holds that office eternally; for Lyell, in contrast, the extinction of species follows naturally from the disappearance of particular kinds of stations. Darwin flipped this logic on its head to explain not the extinction, but the origin of species. Take, for instance, his example of the "carnivorous quadruped" in the *Origin*. Speaking of places rather than stations, Darwin argues that animals cannot continually increase in number without moving into new places in the economy of nature.

> Take the case of a carnivorous quadruped, of which the number that can be supported in any country has long ago arrived at its full average. If its natural powers of increase be allowed to act, it can succeed in increasing (the country not undergoing any change in its conditions) only by its varying descendants seizing on places at present occupied by other animals: some of them, for instance, being enabled to feed on new kinds of prey, either dead or alive; some inhabiting new stations, climbing trees, frequenting water, and some perhaps becoming less carnivorous.[61]

This passage shows that, for Darwin, "inhabiting new stations" is just one way of seizing a new place in the economy of nature. But the Lyellian concept of station, as we have seen, also includes the rest of his list: kinds of prey, water versus land, etc. Darwin is not consistent in his usage, but his 'station' (like De Candolle's) seems to refer simply to the inanimate circumstances of a particular locality, whereas his 'place'

[59] Lyell, 1832, p. 140. Emphasis in original.

[60] Lyell, 1832, p. 141.

[61] Darwin, 1859, p. 113.

refers (like Lyell's 'station') to the whole set of circumstances required or preferred by a type of organism.

The idea of stations, like that of an economy of nature, is a way to capture nature's pre-existing organization. For Linnaeus, Humboldt, and De Candolle, plants had particular stations, i.e. they required particular soil types, climates, etc. to exist. Lyell expanded this idea of stations to include interactions with other organisms, leading to the more dynamic view of nature embraced by Darwin. But if types of organisms can themselves change, as Darwin famously claimed, what is the role of places in nature's economy? In the next section, I will explore the rise of the idea of places in the economy of nature in Darwin's writings.

Hunter, Mockingbirds, and Malthusian Checks

The terms 'economy' and 'place in nature' do not appear in Darwin's diary of the Beagle voyage. However, beginning in the late 1830s, these terms played a greater and greater role in Darwin's thinking. In this section I will proceed chronologically, demonstrating that the idea of different places in nature, along with that of an economy of nature, appears at key junctures in Darwin's early writings.

As Frank Sulloway has shown, the birds of the Galapagos were initially nothing to write home about. They are not discussed at all in Darwin's diary during the relevant period (September 15 to November 13, 1835), and only a single remark in a letter to J.S. Henslow the following January hints of things to come: "I paid also much attention to the Birds [of the Galapagos], which I suspect are very curious."[62] However, he did make the following remark about the Galapagos mockingbirds in his field notebook: "This birds [*sic*] which is so closely allied to the Thenca of Chili […] is singular from existing as varieties or distinct species in the different Is^{ds}. […] Each variety is constant in its own Island."[63] In the early summer of 1836, this remark was elaborated in a set of notes accompanying the catalogue of ornithological specimens he was preparing for the English naturalists who would later describe his collections:

> In each Isld. each kind is *exclusively* found: habits of all are indistinguishable. […] When I see these Islands in sight of each

[62] Sulloway, 1982a; Darwin, 1933, pp. 333–344. Darwin to Henslow, Sydney, January 1836. In Darwin, 1985, Vol. 1, pp. 484–486. *Cf.* Browne, 1995, pp. 296–305.

[63] Darwin, 2000, p. 298 [CD P. 341].

> other, & [but *del.*] possessed of but a scanty stock of animals, tenanted by these birds, but slightly differing in structure & filling the same place in Nature, I must suspect they are only varieties. […] If there is the slightest foundation for these remarks the zoology of Archipelagoes – will be well worth examining; for such facts [would *inserted*] undermine the stability of Species.[64]

In this note, Darwin considers for the first time the possibility that his observations might call into question the stability of species. The Galapagos mockingbirds appeared quite similar to the Chilean mockingbird *Mimus thenca*, and filled "the same place in Nature" on each island. Sulloway has argued that Darwin's later discussion with John Gould in early March of 1837, which established that many of the Galapagos birds that Darwin had thought to be varieties were in fact distinct species, was "the final catalyst in his conversion to the theory of evolution."[65] The idea that these distinct species occupied similar places in the economy of nature was vital to this conversion.

Darwin opened his first transmutation notebook a few months later in July of 1837, but the idea of natural selection did not occur to him until the following year. In late September of 1838, Darwin read the sixth edition of Thomas Malthus' *An Essay on the Principle of Population*, and wrote the following famous entry in his notebook on September 28, 1838:

> One may say there is a force like a hundred thousand wedges trying force <into> every kind of adapted structure into the gaps <of> in the œconomy of Nature, or rather forming gaps by thrusting out weaker ones. ≪The final cause of all this wedgings, must be to sort out proper structure & adapt it to change. […]≫[66]

Thus the term 'economy of nature' appears in the notebook entry that first links struggle and adaptation – this entry is usually seen as containing the germ of the idea of natural selection.

Why does Darwin deploy the idea of an economy of nature at precisely this time? After all, he had already been exposed it through his reading of Lyell, who provides the following quotation from John

[64] Darwin, 1963, p. 262 (*cf.* Barlow, 1935). Emphasis in original. For the dating of these "Ornithological Notes," see Sulloway, 1982b, pp. 327–337.

[65] Sulloway, 1982b, p. 369.

[66] Darwin, 1987, pp. 375–376 [D135]. Single angled brackets indicate Darwin's deletions, and double angled brackets indicate his insertions (Darwin, 1987, p. 12). The transformations of this 'wedge' metaphor in Darwin's work are discussed in Kohn, 1996.

Playfair as the epigraph to the first volume of his *Principles of Geology*: "Amid all the revolutions of the globe, the economy of Nature has been uniform, and her laws are the only things that have resisted the general movement."[67] It even appears in an 1833 notebook entry, where Darwin comments that after reproduction, the ovule-bearing cone of the coralline alga "has performed its office in the economy of Nature."[68] But the proximate cause of Darwin's September 1838 use of the term 'economy of nature' seems to have been his reading of John Hunter. On his list of books read for 1838, Darwin includes, in addition to Malthus, Hunter's *Observations on Certain Parts of the Animal Oeconomy*, first published in 1786 but read by Darwin as the fourth volume of *The Works of John Hunter*, edited by Richard Owen.[69] Hunter, like his eighteenth century contemporary Hermann Boerhaave, subscribed to the physiological conception of the animal economy:

> I shall divide what is called the oeconomy of an animal: First, into those parts and actions which respect its internal functions, and on which life immediately depends […]. Secondly, into those parts and actions which respect external objects, and which are variously constructed, according to the kind of matter with which they are to be connected.[70]

Thus the animal economy is the physiological organization of the animal that maintains its life.

More importantly, Hunter links this economy to the idea of an animal's place in nature:

> The subjects [specimens of Australian organisms] themselves may be valuable, and may partly explain their connection with those related to them, so as in some measure to establish their place in nature, but they cannot do it entirely; they only give us the form and construction, but leave us in other respects to conjecture, many of them requiring further observation relative to their oeconomy.

[67] Lyell, 1830, p. i. Darwin received the first volume of Lyell's *Principles* before the Beagle's departure as a present from Captain Fitzroy. See Darwin, 1985, Vol. 1, p. 562 and Browne, 1995, p. 186.

[68] Keynes (ed.), 2000, p. 138 [CD P. 161]. The term also appears twice in Darwin's "Ornithological Notes," written in June and July of 1836 (Darwin, 1963, pp. 220, 239).

[69] Darwin, 1985, Vol. 4, p. 456, 1987, p. 322 [C270]. See Browne, 1995, p. 385. Hunter's book is a collection of articles previously published in the *Philosophical Transactions*.

[70] Hunter, 1837, p. 336. *Cf*. Cross, 1981, pp. 52–64. For more on the role of the animal economy in English physiology, see Brown, 1968 and Booth, 2005.

Owen added a footnote to this passage, which Darwin copied into his notebook on September 17, 1838: "the necessity of combining observation of the living habits of animals, with anatomical and zoological research, in order to establish entirely their place in nature, as well as to fully understand their oeconomy, is now universally admitted."[71] Thus less than 2 weeks before his use of the term 'economy of nature' in his notebook entry on Malthus, Darwin encountered the ideas of the animal economy and places in nature in these texts of Hunter and Owen, and copied the relevant footnote into his notebook. The idea of Malthusian competition, with species forced into gaps in the economy of nature or forcing out other species, harmonized perfectly with the idea of animals occupying particular places in nature's overall economy.

By the time Darwin published his Beagle journal in 1839, he had connected the idea of places in the economy of nature to his discoveries in the Galapagos Islands. As mentioned above, he had learned from Gould that the Galapagos mockingbirds were three distinct species. Reiterating his passage from the ornithological notes, he now adds the term 'economy': "I examined many specimens in the different islands, and in each the respective kind was *alone* present. These birds agree in general plumage, structure, and habits; so that the different species replace each other in the economy of the different islands."[72] The relevant section of the *Birds* volume of *The Zoology of the Voyage of H.M.S. Beagle*, also published in 1839, likewise points out that the Galapagos mockingbirds "evidently replace each other in the natural economy of the different islands," mentioning additionally that there is little difference "between their habits and those of *M. thenca* of Chile."[73] Thus the Galapagos mockingbirds, combined with the idea of places in the economy of nature, fit nicely within Darwin's burgeoning theory of transmutation. The economy of each island contained a place for a bird possessing a certain structure and particular habits; *Mimus thenca*, in its hypothetical spread through the Galapagos, thus gave rise to three separate but similar species of mockingbird.

Throughout the late 1830s and early 1840s, as evidenced by his extensive lists of books read, Darwin continued to absorb all those works that he thought relevant to the problem of transmutation.

[71] Hunter, 1837, p. 482; Darwin, 1987, p. 369 [D115].

[72] Darwin, 1839, p. 475. Emphasis in original.

[73] Darwin (ed.), 1838–1843, Vol. 3, p. 64. Birds of the genus *Mimus* are discussed on pp. 60–64 of the *Birds* volume, which includes colour plates of all three Galapagos species. These pages appeared in November of 1839 (Vol. 3, No. 4). See Freeman, 1977, p. 29.

In December of 1840, he read John Fleming's *Philosophy of Zoology*, which contains a chapter entitled "On the Polity of Nature." Fleming, like De Candolle and Linnaeus, used the word 'station' to refer only to inanimate conditions of existence: "animals are not only dependent on the character of their *station*, but on the presence of those vegetables on which they subsist, whether directly or indirectly."[74] In this chapter, Fleming emphasizes the interdependence of living beings, citing Linnaeus' dissertation "*Politia Naturae*." This may have been what led Darwin, on May 8, 1841, to read all but two of the twelve Linnaean dissertations translated in Brand's *Select Dissertations from the Amoenitates Academicae*, including "On the Police of Nature." A few days later, he read four of the six dissertations translated in Stillingfleet's earlier volume of Linnaeus translations, including "The Oeconomy of Nature."[75] Thus in 1841, Darwin encountered Linnaeus' idea of an economy or police of nature – the functional organization and interdependence of nature's creatures.

A year later, Darwin penned the first extended outline of his species theory. The term 'economy of nature' plays a much greater role here than in his notebooks, likely due to this Linnaean influence. He connects it directly with the idea of natural selection, arguing that

> […] when a new species has been selected and has obtained a place in the economy of nature, we may suppose it will tend to extend its range during geographical changes, and thus, becoming isolated and exposed to new conditions, will slightly alter and its structure by selection become slightly remodified.[76]

In the section on embryology, he points out that "variation in the structure of the full-grown species will *chiefly* determine the preservation of a species […] with a better place opened to it in the economy of Nature."[77] Here he hints at his later claim that varieties tend to diverge into new places in nature's economy. Moreover, adaptation is clearly seen by Darwin as adaptation to a place in the economy of nature. Thus, even in his first sketch of the operation of natural selection, the economy of nature is always in the background.

[74] Fleming, 1822, p. 52. *Cf.* Darwin, 1985, Vol. 4, p. 461 (15 December 1840). On Fleming and the economy of nature, see Rehbock, 1985.

[75] Darwin lists "Wilcke on Police of Nature" (8 May 1841) and "Biberg on œconomy of nature" (13 May 1841). See Darwin, 1985, Vol. 4, pp. 462–463; Stauffer, 1960, p. 239, note 35.

[76] Darwin, 1909, pp. 36–37. For the composition of the 1842 sketch, see Browne, 1995, pp. 436–439.

[77] Darwin, 1909, pp. 42–43. Emphasis in original.

This link between adaptation, the origin of new species, and the economy of nature is solidified in Darwin's second sketch of his species theory, completed in July of 1844:

> […] to form a new species, an old one must not only be plastic in its organization, becoming so probably from changes in the conditions of its existence, but a place in the natural economy of the district must [be made,] come to exist, for the selection of some new modification of its structure, better fitted to the surrounding conditions than are the other individuals of the same or other species.[78]

As Darwin indicates in his account of island colonization, there may be many or few such places available in the economy of any given district. When organisms first colonize a volcanic island, for example,

> […] we cannot believe that every place or office in the economy of the island would be as well filled as on a continent where the number of aboriginal species is far greater and where they consequently hold a more strictly limited place. We might therefore expect on our island that […] occasionally in the course of a century an individual might be born of which the structure or constitution in some slight degree would allow it better to fill up some office in the insular economy and to struggle against other species. If such were the case the individual and its offspring would have a better chance of surviving and of beating out its parent form; and […] there would be a chance of the new and more serviceable form being nevertheless in some slight degree preserved. The struggle for existence would go on annually selecting such individuals until a new race or species was formed.[79]

The colonization of island chains like the Galapagos, therefore, is a paradigm case of the origin of new species. But this colonization is unthinkable without a pre-existing "insular economy" boasting places not "as well filled as on a continent." Darwin's example fits the Galapagos mockingbirds perfectly. He predicts that the colonists, although they may now be greatly modified, will bear a resemblance to similar species on the nearest continent, just as the three *Mimus* species in the Galapagos resemble *M. thenca* of Chile. Moreover, he notes that if there are obstacles to communication between islands in a chain, "we should have several of the islands tenanted by representative races or species,

[78] Darwin, 1909, p. 145. The square brackets indicate an erasure (Darwin, 1909, p. xxi). For more on the 1844 sketch, see Browne, 1995, pp. 445–447.

[79] Darwin, 1909, p. 186.

as is so wonderfully the case with the different islands of the Galapagos Archipelago.''[80] Thus places in the economy of a district, and especially the insular economy of islands, play an integral role in Darwin's account of the origin of species.

The year after Darwin completed his second species sketch, he published a new edition of his *Journal of Researches*. One of the main additions to this 1845 edition of the *Journal* was the Malthusian passage that replaced his earlier thoughts on the ''Causes of Extinction.'' In 1839, he had suggested that ''such simple relations, as variation of climate and food, or introduction of enemies, or the increased numbers of other species,'' may be ''the cause of the succession of races,'' yet remained sceptical that this fully explained the disappearance of the giant mammals of South America.[81] For Darwin post-Malthus, however, these extinctions were less mysterious:

> […] some check is constantly preventing the too rapid increase of every organized being left in a state of nature. […] We are, nevertheless, seldom able with certainty to tell in any given species, at what period of life, or at what period of the year, or whether only at long intervals, the check falls; or, again, what is the precise nature of the check. Hence probably it is, that we feel so little surprise at one, of two species closely allied in habits, being rare and the other abundant in the same district; or, again, that one should be abundant in one district, and another, filling the same place in the economy of nature, should be abundant in a neighbouring district, differing very little in its conditions. If asked how this is, one immediately replies that it is determined by some slight difference in climate, food, or the number of enemies: yet how rarely, if ever, we can point out the precise cause and manner of action of the check![82]

Extinction is simply the natural result of the alteration of these checks, which determine species abundance – extinction, after all, is just the lower limit of scarcity. As in the notebooks, considerations stemming from Darwin's reading of Malthus appear together with the idea of an economy of nature. There is interplay between the structure of checks and nature's economy, for two species that appear to fill the same place in the economy of nature may each be abundant in a different district because of the uneven distribution of unknown checks. In his so-called

[80] Darwin, 1909, p. 187.
[81] Darwin, 1839, p. 211.
[82] Darwin, 1845, p. 175.

'Big Species Book', completed in 1858, Darwin explicitly cites Linnaeus' dissertations on *oeconomia naturae* and *politia naturae* in the section "*Checks to increase in animals*," making the connection even clearer: "This subject of the Police or economy of nature has been ably discussed by many authors from the time of Wilcke [Linnaeus] nearly a century ago to the present day when it has been ably handled by Sir Charles Lyell."[83]

Therefore, the idea of an economy of nature appears in the most famous episodes of Darwin's pre-*Origin* writings: the birds of the Galapagos Islands; natural selection and his reading of Malthus; and checks to increase and the struggle for existence. In the next section, we will explore the role played by the idea of places in the economy of nature in Darwin's mature writings on transmutation and the origin of species.

Darwin, Divergence, and Places in the Economy of Nature

Darwin called the principle of divergence, along with natural selection, "the keystone of my Book."[84] This principle and its origin have been extensively studied and debated by historians.[85] However, no one has explored the precise relation between the economy of nature and the action of divergence. In this section, I will argue that Darwin's conception of an economy of nature provides the essential background to his principle of divergence; the latter depends on the pre-existing organization of nature's economy.[86]

What is the principle of divergence? In Darwin's first full formulation, found in an 1857 letter to Asa Gray, he states that "the varying offspring of each species will try (only few will succeed) to seize on as many and as diverse places in the economy of nature, as possible."[87]

[83] Darwin, 1975, p. 180. Wilcke defended Linnaeus' dissertation "*Politia Naturae*" in 1760. Darwin cites Brand's book of Linnaeus translations, in which "On the Police of Nature" appears.

[84] Darwin to Hooker, Down, 8 June 1858. In Darwin, 1985, Vol. 7, p. 102. *Cf*. Kohn, 2008.

[85] On the origin of the principle of divergence, see Limoges, 1968, 1994; Browne, 1980; Schweber, 1980; Ospovat, 1981, pp. 170–190; Kohn, 1985; Beddall, 1988. *Cf*. Mayr, 1992 and Tammone, 1995.

[86] Because so much work has been done on the topic, I am bracketing the influence of political economy on Darwin's ideas. For more on this, see Schweber, 1980, pp. 257–287, 1994; Schabas, 1990.

[87] Darwin to Gray, Down, 5 September 1857. In Darwin, 1985, Vol. 6, pp. 448–449.

Extracts from this letter, including the section on divergence, were later read to the Linnaean Society on July 1, 1858 – the first public presentation of Darwin's transmutation theory.[88] However, the idea of divergence had by that time already been gestating for many years. In the early 1840s, Darwin had not yet formulated his "principle of divergence;" but as Silvan Schweber has emphasized, and as we have seen in the previous section, he viewed adaptation as adaptation to a place in the economy of nature.[89] In July of 1847, Darwin began to see divergence as a problem, stating in a note that the "action of divergence" ensures that the most variable species are members of the most diverse genera.[90] As many have argued, Darwin's new focus on divergence followed directly from his encounter with contemporary theories of classification, which became especially important during his work on barnacles.[91] Darwin's challenge was to give an account of divergence that followed naturally from his transmutationist views.

The single most important influence on Darwin's ideas of divergence was Henri Milne-Edwards, who was chair of entomology at the Musée d'Histoire Naturelle in Paris from 1841 to 1861.[92] 'Entomology' in its broad sense referred to the natural history of all the Articulata, i.e. insects, crustaceans, arachnids, myriapods, and annelids. Compared to the other groups, Milne-Edwards declared, the crustaceans had been virtually ignored; his *Histoire naturelle des crustacés* was an attempt to remedy this neglect.[93] In the opening pages of the first volume, Milne-Edwards writes that "the internal economy of [simple] animals can be compared to a workshop where each worker is employed in the execution of the same tasks." As one moves higher in the series of animals, these tasks become more and more differentiated. At the top of the series, "this division of labour is taken still further," and special systems, designed for defence, locomotion, etc., "appear in the economy." According to Milne-Edwards, one sees in the products of both nature

[88] Darwin and Wallace, 1858, pp. 52–53.

[89] Schweber, 1980, pp. 234–235.

[90] Cited in Ospovat, 1981, p. 173. This insight led to Darwin's account of "Variation under Nature" (Darwin, 1975, pp. 92–171; Darwin, 1859, pp. 44–59). *Cf.* Browne, 1980 and Parshall, 1982.

[91] Schweber, 1980, pp. 241–250; Ospovat, 1981, pp. 170–190; Kohn, 1985, p. 249.

[92] Bradley (ed.), 1991, no. 742, p. 407.

[93] Milne-Edwards, 1834, p. i. For the main groups within the Articulata (though he does not mention annelids), see *ibid.*, p. 3. '*Entomologie*' was also employed in this broad sense by Jean Victor Audouin, chair of entomology at the Musée d'Histoire Naturelle from 1833 to 1841 (Audouin, 1824, p. 178; *cf.* Bradley (ed.), 1991, no. 36, p. 241).

and man "the immense advantages that result from the division of labour."[94] In a footnote to this passage, he cites his earlier article on '*Organisation*' from the *Dictionnaire classique d'histoire naturelle*, in which the same principle is articulated:

> The diverse parts of the animal economy all work towards the same goal, but each in its own manner, and the more numerous and developed the faculties of the organism [*l'être*], the more the diversity of structure and the division of labour […] are driven further.[95]

Darwin read the *Histoire naturelle des crustacées*, and likely the earlier article as well, in the 1840s while preparing to write his book on barnacles.[96]

Thus in Milne-Edwards' work, the idea of the animal economy is linked to that of the physiological division of labour. Each part of the body has its function, and these functions are more differentiated in more developed organisms. Darwin was already familiar with the animal economy through Hunter's book (discussed above), which he read in 1838; he now encountered this same economy wedded to the idea of progressive diversification. In 1852, Darwin read Milne-Edwards' *Introduction à la zoologie générale*, where the physiological division of labour is the main theme of the third and fourth chapters. Milne-Edwards here argues, as in the earlier writings cited above, that there exists a "tendency to specialization in the functions of physiological agents."[97] As Limoges and others have suggested, it is likely that Darwin saw a parallel between this tendency of parts to take on diverse roles in the animal economy and the tendency of species to diverge into new places in the economy of nature.[98]

Just as Linnaeus' economy of nature was an extension of the animal economy, Darwin's early thoughts on divergence were an extension of the idea of a physiological division of labour. In the 1840s, Darwin read Linnaeus' dissertations on the economy and police of nature, as well as Milne-Edwards' writings on the division of labour in the animal

[94] Milne-Edwards, 1834, pp. 5–7.

[95] Milne-Edwards, 1827, pp. 340–341. Also cited in Schweber, 1980, p. 251 and in Limoges, 1994, p. 319. Although the *Dictionnaire classique d'histoire naturelle* was available to Darwin aboard the Beagle, this particular article is not annotated in his copy (Darwin, 1985, Vol. 1, p. 558; Schweber, 1980, p. 250, note 151).

[96] Darwin, 1985, Vol. 4, p. 472 (30 January 1847); Schweber, 1980, p. 252; Limoges, 1994, p. 340, note 53.

[97] Milne-Edwards, 1851, p. 59. *Cf*. Darwin, 1985, Vol. 4, p. 489 (26 November 1852).

[98] Limoges, 1968, 1994; Schweber, 1980, p. 256; Ospovat, 1981, pp. 174–175.

economy. Once he finished his extensive works on barnacles, he was ready to develop his views on divergence. By November of 1854, as Dov Ospovat discovered, Darwin had arrived at "the principle, that the most diverse forms can best succeed," and will thus "be selected to fill some new office." A few years later, in September of 1856, Darwin was arguing that the "advantage in each group becoming as different as possible, may be compared to the fact that by division of land labour most people can be supported in each country."[99] Finally, in his 'Big Species Book', written between 1856 and 1858, Darwin connects his principle of divergence – "the greatest number of organic beings (or more strictly the greatest amount of life) can be supported on any area, by the greatest amount of their diversification" – directly to the "doctrine […] of 'the division of labour', so admirably propounded by Milne Edwards."[100]

Because Milne-Edwards' physiological division of labour divided the functions of the animal economy, it makes sense that Darwin's principle of divergence would divide the different places in the economy or polity of nature. As he put it in 1858,

> […] in any country, a far greater number of individuals descended from the same parents can be supported, when greatly modified in different ways, in habits constitution & structure, so as to fill as many places, as possible, in the polity of nature, than when not at all or only slightly modified.[101]

The most diverse and variable organisms and groups are the most successful in the eyes of natural selection: "the number of modified descendants from a common parent, will in chief part depend on the amount of diversification which they have undergone, so as best to fill as many & as widely different places as possible in the great scheme of nature."[102] If a group is invariable in its structure or habits, Malthusian checks will keep its number at a constant maximum; but if it can alter its habits, constitution, or structure, and thus move into a new place in nature's economy, its numbers will increase.

Before a species can move into a new place in the economy of nature, however, this place must exist. Darwin claims that the number of available places depends fundamentally on geography. In the sketch of

[99] Cited in Ospovat, 1981, pp. 176, 181. Kohn, 1985 also sees November 1854 as a key turning point.

[100] Darwin, 1975, p. 233. *Cf.* Darwin, 1859, pp. 115–116.

[101] Darwin, 1975, p. 228.

[102] Darwin, 1975, p. 234.

1844, as we have seen, he exclaims "we cannot believe that every place or office in the economy of the island would be as well filled as on a continent." This suggestion is affirmed in the *Origin*, where he states that "in the case of an island, or of a country surrounded by barriers," most "places in the economy of nature" are filled by modified variants of the original inhabitants rather than by immigrants.[103] Darwin views isolation as playing an important role:

> […] isolation probably acts more efficiently in checking the immigration of better adapted organisms, after any physical change, such as of climate or elevation of the land, &c.; and thus new places in the natural economy of the country are left open for the old inhabitants to struggle for, and become adapted to, through modifications in their structure and constitution.[104]

This passage also makes clear that "new places" are often created by "physical change, such as of climate or elevation of the land;" hence, geography and climate are primary determiners of the structure of the economy of nature.

However, biological forces also work to shape this economy. Later in the fourth chapter of the *Origin*, Darwin discusses how divergence occurs in an area that is not isolated:

> Throughout a great and open area, […] the conditions of life are infinitely complex from the large number of already existing species; and if some of these many species become modified and improved, others will have to be improved in a corresponding degree or they will be exterminated. Each new form, also, as soon as it has been much improved, will be able to spread over the open and continuous area, and will thus come into competition with many others. Hence more new places will be formed, and the competition to fill them will be more severe on a large than on a small and isolated area.[105]

As Darwin indicates "more new places will be formed" in the face of increased or new competition.[106] It is because "the conditions of life are infinitely complex" that there always exist newly available places in the

[103] Darwin, 1909, p. 186, 1859, p. 81.

[104] Darwin, 1859, pp. 104–105.

[105] Darwin, 1859, pp. 105–106.

[106] Thus Donald Worster is incorrect to claim that divergence occurs without competition (Worster, 1985, p. 161).

economy of nature – they are the result of Lyell's "great complication of circumstances" and Darwin's "ever-increasing circles of complexity."[107] Just as Lyell believed that changing physical and biological circumstances could affect the stations of animals, Darwin believed that these same changes could create new places in the economy of nature. At the very least, according to Darwin, such changes create situations in which places could be "better filled up," i.e., are "not so perfectly occupied as might be."[108] Thus for Darwin, as for Lyell, the economy of nature is dynamic and subject to infinitely complex interactions – a stark contrast with Linnaeus' theologically planned economy.

Although new places are continuously being created and old ones are constantly disappearing, the possibilities for divergence at any given time are dependent on the state of the economy of nature at that time. This dependence is most obvious in the case of island colonization. If one species, e.g. a finch, colonizes a remote and isolated archipelago, e.g. the Galapagos Islands, divergence into the many available places in the economy of the islands is a natural result: "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends."[109] In this example, the extensive modification of the parent species, producing a diverse group of descendents, is dependent on the pre-existing economy of nature, which boasts many unoccupied places. This applies also at the level of continents. According to Darwin, the mammal fauna of Australia is less diverse than that of Europe; the places in Australia's natural economy are thus incompletely filled, and susceptible to invasion by the more diverse European mammals. Even in cases of clear separation by zone or district, changes in climate that alter the economy of the region often allow invasion by new species, which seize upon the newly created places.[110] Thus divergence is dependent on the economy of nature, even though that economy is itself continually modified by divergence.

The question of whether the economy of nature or divergence is primary is ill posed, for they are co-determining: the economy of nature is an external constraint on divergence, in that it constrains the possible paths that the latter can take, but divergence also alters the economy of nature. The smallest physical or biological change can have ramifying consequences because "plants and animals, most remote in the scale of

[107] Lyell, 1832, p. 140; Darwin, 1859, p. 73.
[108] Darwin, 1859, pp. 81, 102.
[109] Darwin, 1845, p. 380.
[110] Darwin, 1859, pp. 377–378.

nature, are bound together by a web of complex relations."[111] For instance, if the temperature of a region increases, the region's economy changes, which in turn alters the constraints on divergence; divergence and natural selection continue apace, and the (constrained) modifications lead to more changes in the economy of the region. This process is complex and never-ending, but is always constrained by a pre-existing economy:

> When we look at the plants and bushes clothing an entangled bank, we are tempted to attribute their proportional numbers and kinds to what we call chance. But how false a view is this! Every one has heard that when an American forest is cut down, a very different vegetation springs up; but it has been observed that the trees now growing on the ancient Indian mounds, in the Southern United States, display the same beautiful diversity and proportion of kinds as in the surrounding virgin forests.[112]

The role of chance in divergence is limited by the pre-existing organization of the natural world – this is what explains the regular ecological succession described by Darwin. Thus the economy of nature, although it is dynamic and variable, always limits the paths of divergence.

Because the idea of an economy of nature has played a central role in the history of ecology, it may be useful to briefly explore the connection between *places* in the economy of nature and ecological *niches*.[113] Limoges, along these lines, has suggested that divergence leads to a "division of ecological labour."[114] This phrase is no mere anachronism: Ernst Haeckel, who coined the term '*Oecologie*' in 1866, linked it directly to places in nature's economy:

> We understand by *ecology* the collective *science of the relations of organisms to the surrounding external world*, within which we include in a broad sense all '*conditions of existence*'. These are partly organic, partly inorganic in nature […]. Physiology, […] has to a large extent neglected the relations of the organism to the external world, the place that each organism takes up in the natural economy, in the economy of nature as a whole [*die Stellung, welche jeder*

[111] Darwin, 1859, p. 73.

[112] Darwin, 1859, p. 74.

[113] Worster, 1985. Historians often treat Darwin's *places* and ecology's *niches* as synonymous. See Browne, 1980, pp. 75–76; Schweber, 1980, *passim*; Worster, 1985, pp. 156–157.

[114] Limoges, 1968, p. 114, 1970, p. 136, 1994, p. 330. *Cf*. Kohn, 1985, p. 245 and Tammone, 1995, pp. 126–127.

Organismus im Naturhaushalte, in der Oeconomie des Natur-Ganzen einnimmt].''[115]

Although Pascal Acot has argued that ''the *place* in the economy of nature *is not the ecological niche*,'' his evidence for this claim is faulty: first, *contra* Acot, Darwin does speak of species (and not only individuals) occupying places in the economy of nature; and second, Acot nowhere discusses the views of Joseph Grinnell, who introduced the term 'niche' into ecology.[116]

Grinnell had quite similar ideas to Darwin on the role of the economy of nature, arguing that divergence and evolution are dependent on available niches: ''New occupants of ecologic niches, new associations, new subfaunas, and new faunas have been molded out of the various biotic materials which happen to be available. New types of living things, to fit into all the new niches, have been evolved, not abruptly but through long lapse of time.''[117] Divergence, according to Grinnell, is prompted by a change in nature's economy: ''if a new ecological niche arises, or if a niche is vacated, nature hastens to supply an occupant, from whatever material may be available.''[118] Grinnell agrees with Darwin that geographical change or variability begets divergence, which in turn begets more variability: ''If the topography and vegetation be varied, there are many of these niches; if more uniform, there are few of them.''[119] And like Darwin, Grinnell views invasive species as demonstrating that there are always places available in the economy of nature, especially if the invader is flexible. An invasive species like the English sparrow can succeed even in Death Valley, California: ''by reason of its marvellous powers of accommodation, and finding no competitor in exactly its own ecologic niche, it has gradually advanced its frontiers and overleaped all the faunal boundaries which hem in the habitats of our native bird races.''[120] Darwin's idea of places in an economy of

[115] Haeckel, 1866, vol. 2, pp. 286–287. Emphasis in original. For a complete translation of this passage, see Stauffer, 1957, pp. 140–141 (I have modified Stauffer's translation). Stauffer points out that *Naturhaushalt* is used to translate both 'economy of nature' and 'polity of nature' in the German version of the *Origin of Species*.

[116] Acot, 1983, p. 39. Emphasis in original. *Cf.* Acot, 1988, p. 49, note 12, pp. 252–253. Ernst Mayr suggests that Darwin fluctuates between a geographic and ecological conception of place (Mayr, 1992, pp. 351–352). For species occupying places, see (e.g.) Darwin, 1859, pp. 157–158, 173. On the history of the term 'niche' in ecology, see Cox, 1980 and Griesemer, 1992.

[117] Grinnell, 1924, pp. 227–228.

[118] Grinnell, 1924, p. 227.

[119] Grinnell, 1922, p. 673.

[120] Grinnell, 1919, p. 471.

nature is therefore consonant with the later idea of ecological niches. Like divergence and the economy of nature, evolution and ecology are mutually determining.

Conclusion

In the seventeenth and eighteenth centuries, the term 'animal economy' was often used in medical literature to refer to the functional organization of the animal body – "the *ensemble* of functions and movements that maintain the life of animals," as the *Encyclopédie* put it. Linnaeus, in his dissertation "*Oeconomia Naturae*," extended this physiological idea to the whole of nature, emphasizing the reciprocal dependence of different organisms. He also borrowed the idea of *politia civitatis*, i.e. the order that ensures the well-being of a city's inhabitants, and spoke of a *politia naturae* in which each organism holds a certain office. De Candolle and Lyell, both influenced by these works, popularized Linnaeus' term 'station', which initially referred to the physical circumstances required for the survival of a particular organism. In Lyell's hands, this idea became more complex and dynamic, including both organic and inorganic circumstances and preparing the way for Darwin's idea of place.

Darwin's idea of a place in the economy or polity of nature, used so frequently in the *Origin of Species*, appears at key junctures in his work. Moreover, Darwin's famous principle of divergence depends on the idea of an economy of nature, for the paths of divergence are constrained by that economy. Divergence is always thought of as divergence into newly available places in the economy of nature – this availability is constantly fluctuating, and is a function of both physical and biological circumstances.

In 1904, the German biologist Oscar Drude divided the history of ecology into several periods, the first and second represented by Linnaeus and Humboldt respectively. Although Drude does not associate any one figure with his fourth period, it was a key turning point: until then, no one had "made clear the mutual dependence of the animal and plant kingdoms in their household economy."[121] It was Lyell, with changing circumstances causing the disappearance of stations, and Darwin, with new opportunities for divergence arising from minute changes in the economy of nature, who ushered in this new, more dynamic picture of nature's economy.

[121] Drude, 1906, p. 182. He associates August Grisebach with the third period, and Eugenius Warming with the fifth.

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Appendix: 'Economy' and 'Place in Nature' in Darwin's Work

1836: Galapagos mocking-birds occupy same "place in Nature."
1838: Reads Hunter/Owen on "oeconomy" and "place in nature" (September 17).
1838: Writes Malthus note on "gaps in the oeconomy of Nature" (September 28).
1839: Galapagos birds "replace each other in the economy of the different islands."
1841: Reads Linnaeus' "Oeconomy of Nature" and "On the Police of Nature."
1842: Adaptation is adaptation to a place in the economy of nature.
1844: Places and "the economy of the island" – island colonization.
1845: Interplay between the structure of checks and the economy of nature.
1858: Divergence fills places in the economy or polity of nature.

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