

IJEE SOAPBOX:
DARWIN, MALTHUS, AND MOVEMENT:
A HIDDEN ASSUMPTION IN THE
DEMOGRAPHIC FOUNDATIONS
OF EVOLUTION



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We all have our heroes. For myself and, I suspect, many ecologists and evolutionary biologists, Charles Darwin is very high up in the pantheon of truly admirable thinkers and human beings. Few other 19th-century scientists produced books that bear close reading and even re-reading today—yet *On the Origin of Species* and Darwin's other volumes certainly do. In honor of this Year of Darwin, and to complement the other fine pieces in this special feature of IJEE reflecting on the future of ecology and evolution, in this essay I instead look at the past, returning to a familiar episode in the early history of evolutionary biology. This episode has to do with how the theory of evolution by natural selection first formulated by Darwin and Wallace was—and still is—based on an understanding of the basic principles of demography. In so doing, I will try to bring out a subtle but vital assumption not evident on the surface in accounts of the demographic basis for evolution—an assumption that, as we will see, is even evoked in the celebrated, poetic ending to *On the Origin of Species*.

Darwin in his *Autobiography* (1892; reprinted 1958) recounts a crucial juncture in his life when he reflected on the fruits of his voyage around the world (pp. 41–42):

From September 1854 onwards I devoted my whole time to arranging my huge pile of notes, to observing, and experimenting, in relation to the transmutation of species. During the voyage of the *Beagle* I had been deeply impressed by discovering in the Pampean formation great fossil animals covered with armour like that on the existing armadillos; secondly, by the manner in which closely allied animals replace one another in proceeding southwards over the Continent; and thirdly, by the South American character of most of the productions of the Galapagos archipelago, and more especially by the manner in which they differ slightly on each island of the group; none of these islands appearing to be very ancient in a geological sense....

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The IJEE Soapbox provides an informal forum for leading ecologists and evolutionary biologists to expound on issues that they find particularly exciting, thought provoking, and novel.

Robert D. Holt is our first invited *IJEE Soapbox* essayist. Bob is Professor of Biology and Arthur R. Marshall, Jr., Chair in Ecology at the University of Florida, and is one of the foremost theoreticians in ecology and evolutionary biology. His research focuses on theoretical and conceptual issues at the population and community levels of ecological organization and on linking ecology with evolutionary biology. Bob is best known for his pioneering work on apparent competition, multispecies interactions in food webs (community modules) in time and space, and the evolution of niche conservatism.

It was evident that such facts as these, as well as many others, could be explained on the supposition that species gradually become modified; and the subject haunted me.

So here we have a crisp description of Darwin's growing conviction as to the genealogical relationship of all living organisms. He goes on to say (p. 42):

But it was equally evident that neither the action of the surrounding conditions, nor the will of the organisms (especially in the case of plants), could account for the innumerable cases in which organisms of every kind are beautifully adapted to their habits of life,—for instance, a woodpecker or tree-frog to climb trees, or a seed for dispersal by hooks or plumes. I had always been much struck by such adaptations, and until these could be explained it seemed to me almost useless to endeavour to prove by indirect evidence that species have been modified.

Darwin thus viewed elucidating the mechanism generating the pattern to be even more important, and troubling, than recognizing the fact of the pattern itself. He continues (p. 42):

I soon perceived that selection was the keystone of man's success in making useful races of animals and plants. But how selection could be applied to organisms living in a state of nature remained for some time a mystery to me.

The key to this “mystery” was found by pondering the ecology of populations, and in particular the imperative dynamics of population growth (pp. 42–43):

In October 1838, that is, fifteen months after I had begun my systematic enquiry, I happened to read for amusement Malthus on *Population*, and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result of this would be the formation of new species.

The basic argument of Malthus was that human populations can increase exponentially and so could outstrip any conceivable increase in the food supply supporting those populations. In *On the Origin of Species* (1859, reprinted 1964) Darwin notes (p. 63) that

A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase....Every being...must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the *principle of geometrical increase*, its numbers would quickly become so inordinately great that no country could support the [species]. [emphasis added]

In a fascinating example of convergent intellectual evolution, Alfred Russel Wallace likewise was prompted towards the theory of natural selection in part by his reading of Malthus. As he recounts in his autobiography (cited on p. 32 in Browne, 2002), while he lay in a Malayan fever:

One day something brought to my recollection Malthus's *Principles of Populations*, which I had read about twelve years before. I thought of “the positive checks to increase”—dis-

ease, accidents, war, and famine—which keep down the population....It then suddenly flashed upon me that this self-acting process would necessarily improve the race....that is, the fittest would survive.

Thus demography, and Malthusian exponential growth in particular, in a certain sense is historically foundational in the discipline of evolutionary biology. It is often viewed as having that role in contemporary treatments of the fundamental logic of evolutionary theory. For instance, Martin Nowak in his elegant recent book *Evolutionary Dynamics* (Nowak, 2006) at the very beginning (p. 9) defines the “fundamental and defining principles of biological systems” as “replication, selection, and mutation”. He then immediately moves on to the familiar ground of examining geometric growth from a single bacterial cell, where a unit of time is required for a cell to divide, leading to a geometric growth model $N(t + 1) = 2N(t)$. In an unchanging environment, iterating this expression leads to

$$N(t) = N(0)2^t.$$

More generally, if an individual leaves R offspring behind each generation, then we have a mathematical expression of the *principle of geometric increase* noted above by Darwin:

$$N(t) = N(0)R^t.$$

With continuously overlapping generations, we of course have $N(t) = N(0)e^{rt}$, where r is the intrinsic rate of increase.

Given mutation, bacteria may heritably differ in their survival rates or probabilities of division per unit time, leading to the opportunity for selection to emerge from differences in the traits of individual bacteria, as expressed in their per capita Malthusian growth rates r —a measure of fitness. Crow and Kimura (1970), in their magisterial text on population genetic theory, start with an exponentially growing population, and then (with a thanks to Egbert Leigh) use exponential growth to derive a simple model for natural selection between two clones with different Malthusian parameters. The basic notion of exponential growth would thus seem to provide a foundation for Darwinian evolution, not just in terms of the historical contingencies of how Darwin and Wallace came to conceive of natural selection, but in terms of the conceptual foundations of the discipline today.

So I will take as a proposition worth considering that the principle of geometric or exponential growth is also part of the bedrock upon which evolutionary dynamics stands. Ginzburg and Colyvan (2004) indeed state that “the whole body of the spectacularly successful evolutionary theory has Malthusian growth in its foundations”.

In the last few years, several population ecologists have argued that one of the few candidate “laws” of ecology is the Malthusian principle of geometric or exponential population growth (Ginzburg, 1986; Murray, 2000; Turchin, 2001; Berryman, 2003; Colyvan and Ginzburg, 2003). Ginzburg and Colyvan (2004), for instance, propose that this law has a conceptual role in ecology comparable to the inertial law of motion in

Newtonian physics, and state:

A statement that will serve as a foundational principle must be precise and informative. We know of only one such unanimously agreed upon principle in ecology: the Malthusian law of exponential growth, a simple statement stressing the multiplicative character of reproduction.

Lockwood (2008), by sharp contrast, argues that exponential growth is not a scientific law at all—if by “law” one means (among other desiderata) a statement that is factually true and universal across space and time. Most populations do not in fact show exponential growth, and even when they do it is for short periods of time in restricted spatial domains. My own take on this philosophical issue is that the statement “all organisms arise by replication from other organisms” is to a reasonable approximation a scientific law (the statement appears to be universally true on our globe today, presumably has held for a very long time, and had to be discovered empirically, so it does not follow simply from how we define the term “life”). By contrast, geometric or exponential growth of populations described by the above equations should not be called a “law” but rather provides an example of what the philosopher W.V.O. Quine called a “limit myth” (Quine, 1960), along the lines of the concept of an idealized perfect pendulum in classical mechanics (see Ginzburg et al., 2007). Essentially no populations exhibit exponential growth (just as no pendula in nature really fit the assumptions of a frictionless simple pendulum), but no ecologist can pretend to understand how populations behave unless he or she grasps exponential growth as a conceptual hook on which to hang our understanding of more complex dynamics.

Leaving aside this philosophical issue about whether or not the Malthusian principle of geometric growth should be deemed a scientific “law”, given that exponential growth is in some sense conceptually foundational in evolutionary theory, it is important to be clear about the assumptions that underlie it. There are two assumptions that are not usually mentioned in discussions of exponential growth, but which are worth making explicit, even if they are rather obvious, once stated.

The first unstated assumption is that we are assuming that there is no spontaneous generation; in other words, in a living population one cannot get “something for nothing”. A very important exception is prebiotic evolution, where at least once (and maybe often), life arose from non-life. There may have been a phase of chemical evolution where the appropriate dynamical equations would have had substantial non-replicative inputs into populations of replicating chemicals.

The second unstated assumption can be identified by reflecting on the fact that replication and survival are both physical processes, and so must be subject to all the laws of physics and chemistry. Life is metabolism, not merely replication. All organisms require fresh supplies of energy and materials merely to survive, and even more so to replenish their substance, and to reproduce, and just like all material objects, each organism occupies a finite bit of space. An alternative (albeit minority) tradition in population dynamics to the Malthusian tradition starts not with the vital rates of demography and replication per se, as in the above equations for geometric and exponential growth, but

with these material transformations (Getz, 1984; Kooijman, 1993; Ginzburg, 1998; Owen-Smith, 2005). Owen-Smith (2005) points out that

From a biomass perspective, population growth is not the result of a difference between births and deaths (despite the appearance of this statement in most textbooks), but rather of the difference between rates of uptake and conversion of resources into biomass, and losses of biomass to metabolism and mortality....The biological law of regeneration...underlies exponential population growth.

Now we all know this. But just as exponential growth has the assumption that one cannot get “something for nothing” (i.e., no spontaneous generation), the same is true for life and population growth when viewed as a set of material transformations. The principles of conservation of mass and energy, and the 2nd law of thermodynamics, apply across all spatial scales and to all organisms. From this fact, we can bring out a hidden assumption in exponential growth.

To do so, I will carry out a thought experiment. The ancestor of all organisms on the Earth today was doubtless something like a bacterium, and a substantial fraction of the Earth’s biomass, possibly up to half, currently consists of bacterial biomass (Meinesz, 2006). Bacteria nearly always reproduce by simple division. The smallest spatial scale that is meaningful to bacterial population dynamics is the unit that defines a single individual cell, and its immediate surrounding environment. The doubling of bacterial replication requires extraction of resources from that environment, and then the placement of each daughter bacterium into a different cell (which might overlap, but cannot be coincident).

When I was a schoolboy I read with pleasure and delight the 19th century intellectual fantasy *Flatland* (1884, and frequently reprinted) by Edwin Abbott. As a device for helping those of us who live in three spatial dimensions to conceive of a fourth and even higher dimensions, Abbott created an imaginary world where all life occurred on a plane of two dimensions. The first part of the book, “This World”, laid out different aspects of life in a two-dimensional world. The second part, “Other Worlds”, related this world to other worlds, in particular Spaceland (with three dimensions). But Abbott also briefly discusses Lineland, where all life is restricted to a line. So what I want to do is craft the appropriate model for bacterial population growth (and hence the foundation for natural selection), were we to live in Lineland.

Imagine that the world is an infinitely long cylinder with a diameter exactly equal to that of one bacterial cell. Initially, material resources are uniformly distributed along the cylinder of Lineland, with no material flow along its length, and energy comes in from the otherwise impermeable walls (think of an optical fiber sustaining an interior linear population of photosynthetic bacteria). We subdivide space into units, each one cell in length. These bacterial cells are not ghosts, so cannot pass through each other, or occupy the same place at the same time, and do not have special mechanisms for motility, other than their own growth. How would we describe bacterial population growth in Lineland?

We start with a single cell at a single location. It has used all the material resource at

its location in its construction, and so to replicate, it has to draw down resources at an adjacent site. It divides, and one daughter cell remains at the site of the parent cell, and the other is found at an adjacent location. These in turn divide, and the same rules of conservation apply. So our numerical progression is 1, 2, 4. So far, this looks like geometric growth. But as growth continues, the next population size is 6 (only individuals on the edge of the population double; those in the interior merely replace themselves). As we continue, the law of population growth in Lineland is

$$N(t + 1) = N(t) + 2, \text{ or } N(t) = N(0) - 1 + 2t.$$

So rather than geometric growth, in Lineland the basic law of population dynamics is clearly *arithmetic* growth.

Back in Flatland, similarly, if only one individual can be found in one location (and if we define "location" finely enough, this must be the case), and movement is required to be to adjacent cells, then the basic law of growth would emerge from the fact that populations can only grow at their periphery (think of a lichen growing on a tree trunk, or a crustose algae growing on an intertidal boulder), which again does not lead to geometric growth. Back in Spaceland, if again space is divided up into contiguous cells, and individuals can only move to adjacent cells after division and utilize finite static resources during growth, replenished only by death, all growth will be on a surface. So the overall population will again not grow geometrically.

So how do we get back to a population which grows in an approximately exponential fashion, even in 3-dimensional space? Because of conservation of mass at all spatial scales, what is clearly required is that there is movement in space of either resources (replenishing the local resource supply), or organisms (so they are foraging in fresh pastures, as it were), or both. Moreover, because organisms occupy finite bits of space, as population growth occurs individuals have to be found in different places. This is difficult in Lineland (because one direction of potential movement will always be blocked at the moment of replication), and fairly hard in Flatland (for individuals in the middle of the population, who are surrounded by neighbors), but easier in Spaceland, simply because it is easier during movement to go around (or over, or under) any given anchored individual.

In discussions of exponential growth, everyone recognizes the assumption that resources are not limiting, but what is usually left unstated is that because of conservation of mass and energy, movement at the level of individuals, or their offspring, and their material constituents, is absolutely *required* for organisms and their descendants to not be resource-limited over even a single generation. A hidden assumption in the exponential growth "law" is thus that organisms must become spatially dispersed as they grow, reproduce, and die, relative to the resource base that they require if they are to construct and maintain their bodies as well as reproduce daughter bodies. Considering processes in space is not a complicating "add-on" to evolutionary theory, because demography must be grounded in space, and movement is a ceaseless and inescapable dimension of the ferment of life.

Darwin himself recognized the fundamental importance of movement at several points in *On the Origin of Species*. In Chapter 3 (Struggle for Existence), for instance, he crisply argued that adaptations for movement such as the lovely plumes on dandelion seeds exist precisely because of the need to avoid competition. In several later chapters, he discussed many of the larger-scale biogeographic consequences of long-distance dispersal, and how an understanding of dispersal could help interpret biogeographic patterns such as those noted in the above quote from his *Autobiography*.

Yet my point goes beyond simply repeating that dispersal is important. Because of the physical nature of life, organismal growth and reproduction themselves have an implicit dependence on movement, and hence a concern with movement is—or should be—relevant in ecology and evolution even if there are no specific adaptations for movement. The scale of the spatial dispersion that defines the potential for demography to play out is of course not determined just by what organisms do, but is also influenced by the diffusion and transport of materials in the environment (Reiners and Driese, 2004). Some resource fluxes occur even in the absence of life, and some fluxes arise precisely because organisms alter the local concentrations of nitrogen, phosphates, and other nutrients and thus set up gradients which evoke diffusion. There is no life without movement.

Introducing space and movement leads to a wide range of fascinating themes in contemporary ecology and evolutionary biology, and it is useful in ending to touch on a few of them here. Nathan (2008) introduced a special issue of PNAS devoted to movement by arguing that “movement ecology” provides a unifying paradigm, because movement of organisms is “one of the most fundamental features of life on Earth”. I could not agree more. The point I am making is consistent with this quote—the physical nature of life, together with basic conservation laws of physics, mandates movement at some spatial and temporal scale. Movement is therefore a necessary (if usually implicit) ingredient for reproduction and survival, and thus Malthusian growth, in the first place.

Movement of course has costs, and so a lot of movement is expected to be small in scale—no more than necessary. Close analyses of movements (e.g., Fryxell et al., 2008) usually reveal that species have a complex blend of different movement strategies, depending on both internal organismal states and the reticulate detail of resource availability and renewal rates in the environment. Much of the diversity of life may reflect how constrained movement transforms the experience organisms have of spatiotemporal variation in the environment, and spatially structured interactions may often provide an almost necessary ingredient for the origination and maintenance of evolutionary novelties. For instance, a long-standing debate in evolution has to do with whether spatial separation of populations is necessary for speciation to occur. The conventional wisdom is that allopatric and parapatric speciation can account for nearly all speciation, but some authors robustly argue for the importance of sympatric speciation, driven for instance by competition (e.g., Dieckmann et al., 2004, bemoan “the allopatric dogma” in speciation research). But both theoretical and empirical studies suggest that regardless of the precise details of speciation, the scope for diversification is greatly enhanced if dispersal occurs but is somewhat limited, permitting the honing of adaptations to specialized local environments, rather than just widescale, average conditions (as in the microcosm

experiments of Rainey and Travisano, 1998).

Having some movement (but not too much) can also lead to selection operating across various levels of organization (Okasha, 2009). This theme is believed to account for major transitions in what counts as “individuals” in evolutionary processes (Maynard Smith and Szathmary, 1998). Spatial structure and dispersal may even be a precondition for life itself. A key step in prebiotic evolution was the origin of self-replication in molecules, a necessary precursor for the evolution of life. The basic problem with simple models of the evolution of such replication is that errors in replication limit the length of single molecules that can be replicated with any accuracy. Eigen and Schuster (1979) proposed that this length limit could be surmounted if different molecular species catalytically facilitate replication in each other (the hypercycle theory). Maynard Smith (1979) pointed out that this model implicitly involves molecular altruism, and thus these systems should be vulnerable to invasion by parasitic molecules which enjoy the catalytic boost, but do not pay any costs of providing catalysis. Space provides a way out of this logjam on the road to life (Hogeweg and Takeuchi, 2003). Boerlijst and Hogeweg (1995), for instance, demonstrate that molecular parasitism in hypercycles can be prevented if facilitative interactions are spatially localized, particularly if the interactions occur along a spatial gradient.

To me, one of the really fundamental questions in our discipline today is gauging the importance of selection simultaneously operating across multiple levels of organization. This is relevant to a wide range of fascinating topics, from the evolution of life itself, to the evolution of altruism and the emergence of individuals (e.g., eukaryotic cells, multicellular organisms) as cooperative units, to the potential role of species selection and spatial self-structuring in determining community organization and stability (Johnson and Boerlijst, 2002). All of this wealth of biological possibilities would not be feasible, were there either no movement, or too much.

To conclude this meditation on hidden assumptions about the role of spatial dynamics at the foundation of population ecology and evolutionary theory, let us return to the justly famed concluding paragraph of the *Origin*: “It is interesting to contemplate an entangled bank... with various insects *flitting* about, and with worms *crawling* through the damp earth...” [emphasis added]. Darwin goes on to refer to the basic laws that generate organic diversity, the most basic of which is “Growth with Reproduction”, i.e., Malthusian dynamics. What I have suggested here is that growth with reproduction is not even possible without spatial fluxes of organisms and their resources. Life likely would not exist at all without a modicum of flitting, crawling, or at least (for the passive among us) diffusing and floating. The perpetual spatial churning of organisms at all spatial scales as they seek resources, find mates, avoid competition, and escape predators, parasites, and hostile environmental conditions lies at the very core of the conditions that make life possible, and moreover opens up dimensions of interactions within and among species that almost surely lie at the base of a good deal of organic diversity—the explanation for which was the aim of *On the Origin of Species*, and the ongoing task of ecology and evolution today.

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