Malthus and Darwin - an ecological perspective

Dag O. Hessen

Introduction

There is a common misconception that Darwin got his Eureka during his visit to the Galapagos isles when he spotted the famous finches; suddenly, the evolutionary process and history was laid bare. In retrospect, most people have problems understanding why such a simple and outright logic idea never struck the numerous, brilliant brains that had made great discoveries centuries before Darwin. Compared with other major achievements in the history of the natural sciences, the theory of evolution is based on a set of very intuitive principles.

The story is, of course, not that simple. As a matter of fact, Darwin barely recognized the finches during his visit on Galapagos. A number of philosophers and naturalists, from Aristotle onwards, had noted similarities and gradual transitions in morphology among plants and animals, and claimed some sort of “relatedness” between all organisms. Around 350 B.C., Aristotle in his Historia Animalium provides a first attempt to sort animals into some system of classification, and although this was a system full of oddities, it nevertheless was a point of departure, and an important inspiration for later naturalists, among them Carolus Linnaeus (Carl von Linné) [1707 – 1778].

One of Aristoteles’ major achievements was to place man among the other creatures. For a long time, no really big achievement was made in evolution, systematics and man’s place in nature. This gradually changed towards the 17th century. The Italian anatomist Lucilio Vanini [1585-1619] compared skeletons of humans and other primates and noticed striking similarities. In 1699, the anatomist Edward Tyson compared the great apes and humans and like Vanini he noted surprising similarities, even in brain structure and size. The French naturalist Pierre Louis Moreau de Maupertuis [1698-1759] did in fact explicitly argue for a gradual transition of species and an evolution in modern terms. In the 17th century, leading naturalists such as John Ray [1627 – 1705] and Carl von Linné studied variability within species. Neither of them opposed the act of creation, while Linné’s rival, Georges Buffon [1707-1788] can be seen as a true proponent of evolution. A numbers of scientists, from Buffon and Linné onwards, doubted the
assumed time span of 6000 years from creation. The scientific arguments in favor of a gradual transition from one species to another, or a transmutation as Darwin labeled it, had to wait, however, until other discoveries in natural history, particularly geology and astronomy, had prepared the ground.

Fossils, land rise, and the slow geological processes were all strong arguments against the creationist dogma. For Darwin, the most enlightening textbook was Charles Lyells’ Principles in Geology, which was his second bible on the Beagle expedition. Lyell, although he later opposed Darwins claims about the human origin, thus prepared the ground for Darwins theory by clearly stating the tremendous time span over which the earth was formed. By studying processes of land rise, erosion and sedimentation, he argued that earth could indeed have a long history, perhaps several hundred million years. This should be sufficient time to allow for the world’s entangled bank of organisms to evolve by small, gradual steps. This is still far less than the present estimates, approaching 6 billion years, and where the origin of life probably occurred some 4.5 billion years ago.

Darwin was not the only one who combined pieces of evidence from natural history with the obvious facts that there were gradual transitions in the morphology of plants and animals. In fact, in one of the later issues of Origin, Darwin list 38 previous naturalists or philosophers who had raised, more or less explicitly, related ideas. As is widely known, his own grandfather, Erasmus Darwin [1731-1802] proposed ideas on relatedness and gradual transition between organisms, although Charles himself denied any knowledge of his grandfather’s far-fetched speculations when the issue was raised by captain Fitz-Roy, a fundamentalist Christian and boss onboard the Beagle. More familiar was the theory of Jean Baptiste Lamarck [1744-1829] who in 1809 - the birth-year of Darwin - put forward a radical theory of gradual improvement. Briefly Lamarck proposed a theory of evolution that was superficially close to Darwins, yet with a quite different mechanistic explanation for the gradual changes within a species (that eventually would lead to the formation of new species). Unfortunately for Lamarck he believed that features aquired by training or repetitions could be inherited - the famous example being the giraffe’s neck, which would gradually become elongated (increased number of vertebra) by stretching after the leaves of tall trees. This slow and gradual achievement would since pass on to the next generation, argued Lamarck. This hypothesis had a stronger appeal to many than Darwins natural selection, since Lamarcks theory implicit stated that improvement by training in all regards would be rewarded by improvements in the coming generations, while Darwins selection was merely an effect of pure chance (“good genes”). In spite of his scientific brilliance
in various areas, Lamarck will forever be remembered for his utterly wrong conclusions on the mechanisms of evolution.

**From Linné to Malthus**

For centuries, the natural sciences were constrained by metaphysical dogmas. Theological hegemony simply did not allow for a theory of evolution. Another aspect of this, of which both Ray, Linné and later William Paley were strong proponents, was the *teleological* aspect of nature. All species had their specific purposes, designed by the Creator. Hence both the species, and their ecological niches in more modern terminology, were, with one of Linné’s favorite metaphors, fixed actors in the Creator’s theatre. Thus while Linné did not hypothesize any evolutionary process (although the variability within species, and the inevitable presence of hybrids indeed bothered him), he paid attention to the interplay between organisms.

His duty as a leading naturalist was not only to name and sort species as a way of revealing the Creator’s great pattern of nature, it was also to study the interplay and dynamics in nature – the play on the scene. Linné saw himself as the greatest of all spectators of this play, and in addition to his famous taxonomy he also made a great achievement in the studies of “nature’s economy” which was later coined “ecology” by Ernst Haeckel. Linné made a number of splendid ecological observations, especially linked to the recycling of matter in nature – and to the population control in species. This also forms part of his natural teleology. The Creator had in his wisdom put a natural check on all populations, being grazers, predators, parasites or competitors to maintain the balance of population sizes and avoid massive collapses and piles of dead corpses.

While his interpretations are founded in a, in retrospect fairly naïve, teleology, his ecological observations on the various means of population control are brilliant and accurate. Perhaps the most interesting passages in Linné’s writings on these subjects are found in *Oeconomia naturae* (1750) (in fact an early textbook in ecology). He calculates the *potential* number of offspring from various species: “…pigeons should in four years give raise to fourteen-thousand, seven-hundred and sixty-two offspring if one assumes nine generations annually…” Darwin in fact refers to his example with a flowering plant producing two seeds only annually (he argues, however, in fact in an unrealistic low reproductive rate for a plant). This plant would, according to Linné’s calculations, within twenty years have resulted in one million offspring.

Linné did for natural reasons not probe for any evolutionary implications of these excess reproductive capacities. He did, however, frequently cite these observations with an implicit
reference to the Hobbsian *Bellum omnum contres omnes*. As an interesting turn, Linné also claimed that these principles were valid for humans as well: “...even man himself is subject to the same laws of nature, although I do not know by which laws nature regulates the human population within appropriate limits.” Yet he promoted some assumptions: “It is clear, nevertheless, that the most virulent diseases occur in the most densely populated areas. I do also believe that war is most common in densely populated areas. Scarcity in resources cause envy and hate, and then there is everybody’s war against everybody” (*Oeconomia naturae* 1750).

Linné had read his Hobbes, but he also gives this argument a panglossian turn. Dr. Pangloss was Voltaires caricature of Gottfried Leibniz *Candidae* [1710], and Dr. Pangloss argued that even the worst disasters had to be good (at the least for something or somebody), since God had created the best of all possible worlds. Like him, also Linné argued theleologically that even diseases and war in fact were positive attributes of human behavior helping to keep a check on populations.

Malthus did apparently not pay direct credit to Linné, and we do not know to which extent Malthus was influenced by his ideas. We see no reference to Linné from his elaborations on population development and control in Sweden in the second edition of his *Essay on the Principles of Population* (Malthus, 1803). Population control in plants and animals is barely mentioned by Malthus, and then without explicit reference to Linné. He was, however, strongly influenced by Adam Smith’s *Wealth of Nations* (1776), Marquis de Condorcets *Esquisse d’un Tableau historique des Progrès de l’esprit humain* (1795) as well as Jean Jaques Rosseaus writings, yet he partly opposed to the optimistic views of the two latter. Rosseau was a friend of Robert Malthus father, Daniel, who shared his interests in botany. Rosseau and Condorcorct were both great admirers of Linné. Smith surely read Linné although passages such as “Every species of animals naturally multiplies in proportion to the mean of their subsistence, and no species can ever multiply beyond it” (Smith, 1776), may be rooted in common knowledge and not necessarily draw on Linné. The point is, however, the close intellectual contacts, and mutual influence and exchange of concepts and ideas that existed between the early socials scientists and naturalists.

**From Malthus to Darwin**

So then, Darwin. There is no reason to believe that Darwin ever saw the glimpse of evolutionary light during most of his journey with the *Beagle*. Clearly, from his diary, the idea became manifest, however, shortly after the return of the *Beagle* expedition in 1836. During 1838, just a couple of years after his return, Darwin had his mind and his notebooks filled up
with ideas on the transmutation theory. He started realizing the full impact of the theory on humans, mind and morality as well. By March 1838 he started writing in his “C notebook” speculating on heredity. At this time he clearly realized that Lamarck was wrong in his “achievement by training”. Darwin speculated about whether mechanisms, such as isolation, could finally cause transmutation at a level where one species could split into two. During this year he also visited the orangutan Jenny in London zoo, to study similarities in behaviour between ape and man. These early studies were, probably for tactical reasons not included in The Origin of Species where man was almost totally omitted. But they found their way into the later Expression of the emotions in man and animals (1872) and to some extent also in his next major work The Descent of Man (1871).

Faced with the overwhelming implications of his theory and the challenges to the more orthodox theology, he started reading a wide range of philosophical and metaphysical text. This was a period with a burst of new ideas, and Darwin worked himself close to break-down. “Charles is become quite an altered character” his brother Erasmus remarked these days (Browne 1995, p. 384), not without satisfaction, since Charles finally seemed to share his interests in philosophical matters. In his pile of books was Essay on the Principle of Population. On September the 28. 1838, Darwin started reading this book - for amusement he claimed in his autobiography. Clearly Darwin was aware of Malthusian thoughts before reading the book. The themes that Malthus raised in his book was an integrated part of daily political debates that Darwin was not unaware of, although he never really became politically interested. Also his major inspirator, the geologist Charles Lyell frequently cited Malthus´ ideas on struggle in his main work Principles in Geology (1830-1833). The major breakthrough for Darwins’ theory of evolution thus clearly came when Darwin re-read Malthus’ Essay. Although he barely mentions Malthus in Origin, he fully states the importance of his influence in his autobiography in 1876:

"In October 1838, that is, fifteen months after I had begun my systematic inquiry, 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 favorable variations would tend to be preserved, and unfavorable ones to be destroyed. The results of this would be the formation of a new species. Here, then I had at last got a theory by which to work" (cited from Francis Darwin; The Life of Charles Darwin, 1902/1995, p.40).
In his notebooks (published 1980), Darwin elaborated on how Malthus’ works had inspired him to imagine selection of different traits in dogs, and realized how breeding and selection in domestic animals in fact just represented a more rapid and directed image of natural selection. This became a cornerstone in his later arguments for evolution, and in fact the first chapter of *On the Origin of Species* (1859) was devoted to such examples.

Part of his motivation was surely also that Darwin was interested in Malthus’ views on the “fruitfullness of marriages”, a theme that concerned him for several reasons. As he now approached the age of 30, his notebooks also filled with arguments for or against marriage. He was concerned that he should not wait too long if he wanted healthy children. On the other hand, children and family would certainly distract him from his scientific efforts. His final conclusion was: “One cannot live this solitary life, with groggy old faces, friendless and cold and childless staring one in one’s face, already beginning to wrinkle. - Never mind, trust to chance - keep a sharp look out - there is many a happy slave - marry - marry – marry”. And so he did, with his cousin Emma in 1839. Yet the work with his transmutation theory should last for another 20 years, before the publication of *On the Origin of Species*. Darwin did, however, disagree with Malthus on the social implications of overpopulation, at least theoretically. While Malthus suggested social remedies and birth control, Darwin saw this as an intervention with the principles of natural selection through competition and survival of the fittest.

Darwin finished reading the *Essay on Population* on 3. October 1838, but even before, he started realizing the major implications of Malthus’ work. The most obvious conclusion from Malthus’ hand was of course that humans, in Malthus words, “... were capable of doubling their number over an approximate twenty-five year period”, while agricultural production “could not possibly be made to increase faster than in an arithmetical ratio”. He also listed the “checks” on population size that continuously had to be active to balance a population of humans, early deaths, disease, famine, epidemics or wars, parameters that Darwin easily could apply to populations of plants and animals. These, in retrospect fairly obvious matters, did not fully come to Darwins mind before reading Malthus. To Darwin, the main question was why the world did not overrun with organisms, given their often tremendous reproduction capacities. The chapter *Geometrical Ratio of Increase* in *Origin* hinges directly on both Linné and Malthus. With reference to Linnés calculations of seeds and plants, he made his own calculations of the potential number of elephants, the slowest breeding organisms he could think of, and concluded that within 500 years, one single pair of elephants could have 15 million descendants. “A
struggle for existence inevitably follows from the high rate at which all organic beings tend to increase…. Hence as more individuals are produced than can possibly survive, there must in every case be a struggle for existence…. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdom…” (Darwin, 1859). Something had to check populations in nature, either scarcity of food (bottom up forces) or predators (top down control). “Take Europe on an average, every species must have the same number killed, year after year, by hawks, by cold etc, even one species of hawk decreasing in number must affect instantaneously all the rest”. This is close to Linné’s argument, and we see here an early glimpse of ecology and food web theory, a discipline that Darwin to some extent launched by Origin, but which in fact was elegantly outlined by Linné 100 years earlier.

There is a continuous discussion why Malthus became so influential to Darwin, and why these ideas never struck the brilliant naturalist like Linné from his countless hours of studying birth and death, growth and famine in natural populations. Yet Darwin was well aware of Linné’s studies on population control in animals, he paid in general little attention to these. After reading the 10th edition of Linnaeus Systema naturae (1758), he was not particularly inspired by these exhaustive list of species, and remarked dryly in his diary in 1841, three years before his first sketch on the transmutation theory was finished: “Looked through 1 & 2 volumes [of Linnaeus]. I do not think much to me.”

Another reasons why Darwin was inspired by Malthus, was that he drove the attention to the individual as the unit of selection, rather than focussing the species per se. The unit of selection has for long been a battlefield in evolutionary biology, sparked by ideological aspects as well. At a first glance, the main conflict may be between species (rabbits against foxes or vice versa). In fact this somewhat naïve view is not uncommon, but from a resource scarcity point of view (mating partners, territory, food), the somewhat hobbsian conclusion is that the main battle is between individuals of the same species. Although Darwin has been cited in favor of both individual selection and group selection, he clearly stated that the major conflict of interest was between individuals of the same species.

Although the final word is not yet said about the unity of selection (cf. Sober and Wilson 1998), the majority of evolutionary biologists clearly vote for individual selection as a major principle in nature. The bad news is, of course, that when extrapolated to humans, this could mean that we are destined for selfishness and a whole suite of problems arising from this. The most serious probably being over-exploitation of resources following inevitably as a “tragedy of the common” situation. Malthus indirectly touches on this issue in many regards when
discussing population control. The bottom line of the tragedy of the common argument is that organisms – including man – are selfish players that will not reduce their own goods for the benefit of the common. Any personal sacrifice will normally imply some costs that might be rather high (and thus a competitive disadvantage), while it might contribute little to improve the situation for a whole population or the whole community (“Why me, why not the others?”). Classical examples is the individual willingness (or rather lack of such) to reduce the number of cattle in their own herd to avoid overgrazing, an individuals willingness to reduce his own CO₂ emissions (by reduced driving) to save the global climate – or to produce fewer children in a crowded world. The pessimistic view is thus that people in general are unwilling to make such personal sacrifices, and this goes right to the core of todays major environmental problems as well as to the debate on individual versus group selection. Of course man is a cultural being too, but we should not pursue this discussion about human nature and nurture here. Malthus´ focus on the individual player is shared with Smith and his ideas on the invisible hand of the market and Darwins evolutionary theory as well as the descending neo-Darwinism with focus on the genes as selfish players.

Darwin did not really bother himself with the political and human implications of Malthus´ work, and personally, he was seemingly not too worried about Malthus´ warnings, since he and his Emma finally ended up with 10 children. In fact, although Darwin was essentially inspired by Malthus, he did not, as we have seen, agree that reproduction should be severely restricted. Rather a high reproductive rate would for him, ensure a real competition to the benefit of the species. From an evolutionary perspective, scarcity in resources would keep the selection pressure high – also in humans, as he discusses extensively in (The Descent of Man, 1998 [1871], pp. 44-48). “Like any other animal”, he wrote, “man has clearly achieved his present advanced position by struggle for survival following high birth rates; and if he shall gain further advance, he should still be subject to this hard struggle for survival. Thus our natural growth rate, although it inevitably causes lots of suffer, should not be reduced by any means...”. He also elaborates, with reference to Malthus, on the reproductive power in “barbarous” versus “civilized races”. As an analogue to domesticated plants and animals that increase their reproductive rates when brought into richer soils or given access to abundant and regular food “… we might expect that civilized men, who in one sense are highly domesticated, would then be more prolific than wild men”. Malthus have provided examples on the numerous checks on population size in less developed areas, yet he has, argues Darwin, missed what is probably the most important of all, namely infanticide, especially of female infants, and the habit of procuring
abortion. “These practices now prevail in many quarters of the world; and infanticide seems
formerly to have prevailed … on an extensive scale. These practices appear to have originated in
savages recognizing the difficulty, or rather the impossibility of supporting all the infants that
are born” (The Descent of Man, 1871). The matter of population control were in fact among the
controversies also in the later “social Darwinism” or eugenics. Francis Galton, Darwin’s cousin,
earned the dubious reputation as the founder of eugenics. He was strongly inspired both by his
cousins ideas on evolution and Malthus’ theories of the necessity of birth control. From this he
reached the conclusion that in order to breed the noble characters of man and improve the human
species per se, there was a need for breeding control among “lower” people, the carriers of bad
heritable characters (or bad genes in present terminology).

Malthus did also provide the key to the process of natural selection to other than Darwin, in
fact an interesting example of “convergent evolution” of ideas. In 1858, Darwin wrote to his
cousin William Fox that the final publication of Origin still was years ahead. Then one of the
famous letters in natural history arrived. On 18th June 1858, Alfred Russel Wallace [1823-1913]
submitted his theories on evolution to Darwin, who was then recognized as a leading naturalist.
Not only did Wallace present a brief sketch of evolutionary theory that was almost identical to
Darwin’s own (yet not supported with the wealth of empirical data that Darwin had), Wallace
had also read Malthus and been inspired by the mechanisms for natural selection. Wallace, in a
letter to his colleague A. Newton in 1887, described his discovery of the principles of selection
in parallel with Darwin:

“The most interesting coincidence in the matter is, I think, that I, as well as
Darwin, was led to the theory itself through Malthus - in my case it was his
elaborate account on the action of “preventive checks” in keeping down the
populations of savage races to a tolerable, but scanty number. This had
strongly impressed me, and it suddenly flashed upon me that all animals are
necessarily thus kept down - “the struggle for existence” - while variation
on which I was always thinking, must be beneficial, and would thus cause
those varieties to increase, while injurious variations diminished”.

In fact in his autobiography My life. A record of events and opinions (1908), Wallace explicitly
states that “…the most important book I read was Malthus Principles of Population…that
twenty years later gave me the key to the driving forces in the evolution of species”. The rest of
the story is well known. Darwin and Wallace presented their unified theory to the Royal Society of London the same year. Darwin speeded up the completion of his *Origin* which was published in November 1859. In retrospect this scientific cross-fertilization has clearly been one of Malthus greatest merits.

There is an interesting turn in the reciprocal influence between scientific disciplines. The greatest discovery in biology was clearly fuelled by ideas from social science. First and foremost Malthus of course, but also from William Paley, Adam Smith and Jeremy Bentham. Especially Smith’s “invisible hand”, with its predicted effects of competition and Malthus’ predictions of competition as an inevitable outcome of resource scarcity were instrumental to the understandings of the mechanisms for evolution, the natural selection. Some of their ideas may, however, have been sparked by natural sciences. Darwin’s theory on evolution and competition in nature in turn paid back to the social sciences as Herbert Spencer ideas of “survival of the fittest” (this was thus not Darwin’s original phrase). Probably far from Spencer intentions, it was used to legitimate sexism, racism and uneven social structures. The rich and mighty were simply determined for success, they were the best fit (a classic tautology). Clearly such ideas also reflected back on the natural sciences - with Francis Galton’s early theories on eugenics as a famous case in point. In spite of this unfortunate turn into social darwinism, the reciprocal influence between social sciences, psychology, philosophy, economy and biology is indeed an interesting turn in the history of science. Today we may see a similar co-evolution between biology and economy when it comes to game theory and the search for motives among selfish players, and we see new aspects of human acts and motives in light of our evolutionary history under headings like “darwinian psychology”.

*Malthus and ecology*

Finally we may ask for the relevance of Malthus in todays ecology. As we have seen, ecology in the terms of “the economy of nature”, as observed by Carl von Linné, was a fore-runner to Malthus’ classical theories on population control. When it comes to ecosystem regulation, there have traditionally been two contrasting views. Those who entertain a top-down view and observe a green world and conclude that there are sufficient resources, meaning that the food-webs are controlled from the top by predators (but who is then controlling the predators?), and those who support a bottom-up view and argue that ecosystems are controlled by primary production. Clearly there is no either-or. Both mechanisms are active, and the density of top
predators, like humans, must be regulated by food availability (the Malthusian view), unless there is density-dependent regulation by diseases, epidemics or war.

In classical population ecology, these aspects of regulation is merged into the idealized asymptotic population increase in an S-shaped (logistic) curve approaching stable population (and stable demography) at the systems carrying capacity (K). This is in its simplest way expressed in mathematical terms as \( \frac{dN}{dt} = r_{\text{max}} \times N \times \frac{(N-K)}{K} \), where the population change over time (\( \frac{dN}{dt} \)) is expressed as a differential equation to reduce time increments to infinity. \( r_{\text{max}} \) is the maximum population growth capacity, \( N \) is population size in individuals and \( K \) is the carrying capacity. Thus when \( N \) is small, growth rate \( (r) \) approaches \( r_{\text{max}} \), and when \( N = K \), there is zero population growth. This simple equation actually is the basic ecological parallel to the question of resource control (bottom-up control) in populations, and it also forms the basis for more applied ecology like advices on harvesting of populations (like in fisheries), since maximum harvest is achieved at a population size of \( K/2 \). This classical curve assumes increased effects of density dependent effects, like decreased fecundity when populations approach \( K \).

Malthus rather predicted a kind of “feast and famine”, where the human population would increase far beyond \( K \) and then collapse (at least locally). In fact, these kinds of events which may be illustrated by the fate of a yeast population on a sugar medium, are not uncommon in nature either.

To many, Malthus was the first example of a negative environmental prophet who was utterly wrong. Already Marx and Engels made jokes of the “monkey Malthus” who was unaware of the industrial capacities for logarithmic growth; later on the agricultural green revolution postponed Malthus doomsday. Nevertheless, there is no doubt that Malthus was essentially right in drawing the attention towards the limits to growth, the concept of carrying capacity, that for long has been an essential tool in population ecology. This inspired Darwin to look at competition at the right end of the logistic growth curve, he focussed the “competition push” rather than the “opportunity push”, yet we know today that they may be equally important as evolutionary forces. Malthus might also well be right when it comes to humans, although the essential problem today is distribution and redistribution of goods.

There is an extensive literature discussing the relevance of a Malthusian (or neo-Malthusian) view on population growth and related issues such as food production, global carrying capacity, ecosystem deterioration or environmental problems in general. Following the increased awareness of population increase and environmental concerns in the 60ties and 70ties, there was a boost in literature that built on Malthus. The Malthusian prophecies was also the basis for
highly influential book like Garret Hardins *The Tragedy of the Commons* (1968), Meadows, Meadows, Randers and Behren’s *Limits to growth* (1972), and a number of writings from influential environmentalists like Paul Erlich (*The Population Bomb*, 1968) and not the least Lester Browns *State of the World* that has occurred annually since 1983. These authors (and others) who have been collectively labeled neo-Malthusians, focussed on resource scarcity. We also see these perspectives in the following-up book of Meadows, Meadows and Randers from 1991 (*Beyond the Limits*). Most estimates on many of the non-renewable resources seem to suggest availability of these in sufficient quantities for decades. Even the reserves of fossil fuels may last for many decades, yet they will hopefully be replaced by less harmful energy carriers (like hydrogen), long before the remaining reserves are completely tapped. Returning to the simple yeast population metaphor, there are two possible fates for the rapidly growing population. Resources (e.g. sugar) may be depleted at the population peak, and unless the system is fuelled by more sugar, the story ends with a sudden collapse. The second alternative is that waste products (from the yeast perspective) like ethanol accumulates to critical levels and terminates the feast in a toxic inferno. For the yeast cells, their fate may be of less than academic interest, but from an ecological and Malthusian perspective these different fates illustrate the central theme of resource or waste control of populations, both of which commonly operate in nature.

For natural reasons Malthus did not predict accumulation of waste (including chemical substances, excess nutrients, solid waste and greenhouse gases like CO$_2$ and CH$_4$ -methane) as a potential regulator of the human population. Ironically, some of the substances that undermined Malthus prophecies and gave rise to “the green revolution” including fertilizers and pesticides belong to the list of harmful wastes. In fact even genetically modified crops may potentially add to this list. Perhaps the greatest irony of this story is the unforeseen effects of herbicides and insecticides that indeed have contributed to the agricultural success and rise in human population numbers. The first one to draw public attention to these aspects of human growth was Rachel Carson in her influential book *The Silent Spring* (1962). These chemicals, like DDT, have a number of derivatives that may decrease human fertility in different ways, partly by acting as “pseudo-estrogens”. As an example, and a surprise to many, the major threat to the top predator like polar bear in the high Arctic is not hunting or extended tourism, but rather the tissue accumulation of several organic toxins that aim at reducing the fertility and longevity. The future role of these compounds, and the long list of other chemical wastes, on ecosystems and human populations remains an open question.
When it comes to Malthus’ basic question, the growth in human population, there is still no final answer to this due to demographic uncertainties that also Malthus was well aware of. Yet most estimates tend to suggest a population peak around 10 billions within the next 100 years, and then possibly a slight decrease (Nature 412, 2001), but with the proviso that the statistical predictions are limited. There is an 80% chance that the world’s population (now 6.1 billion) will be between 5.6 and 12.1 billion in the year 2100. To increase the statistical probability to 95%, the interval must be strongly increased (between 4.3 and 14.4 billion). If we stick to the most reliable estimate, a stabilization near 10 billion, the critical question is whether this is near, or far above carrying capacity in the long term. The answer depends, as we all know, on the international distribution and consumption of goods and the resulting waste production. Thus Malthus might finally become right in his prophecies, yet for different reasons than he himself assumed.
Selected references


Dag O. Hessen,
Professor in Biology
University of Oslo,
Dept. of Biology,
P.O.Box 1027 Blindern
0316 Oslo, Norway
dag.hessen@bio.uio.no