

Review

Microbiology of the Anthropocene

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ABSTRACT

Human influences on the planet's atmosphere, hydrosphere and biosphere are of such magnitude as to justify naming a new geological epoch, the Anthropocene. Different starting dates and phases have been proposed for this epoch, depending on the criteria used. Recent advances in microbial genomics and ecology show that human perturbations to microbial populations correspond closely to the proposed phases of the Anthropocene: the 'paleoanthropocene' which began with the rise of agriculture; the industrial revolution, from the late 1700s; and the 'Great Acceleration' from the 1950s to the present day. As the Anthropocene unfolds, environmental instability will trigger episodes of directional natural selection in microbial populations, adding to contemporary effects that already include changes to the human microbiome; intense selection for antimicrobial resistance; alterations to microbial carbon and nitrogen cycles; accelerated dispersal of microorganisms and disease agents; and selection for altered pH and temperature tolerance. Microbial evolution is currently keeping pace with the environmental changes wrought by humanity. It remains to be seen whether organisms with longer generation times, smaller populations and larger sizes can do the same.

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Introduction

The speed and extent of human driven changes to planetary processes have led to proposals that we are entering a new epoch, the Anthropocene, or literally the 'Age of Man' (Crutzen, 2002). Human effects on planetary processes fall into recognizably distinct stages (Smith and Zeder, 2014). The first, the

'paleoanthropocene', corresponds to the widespread adoption of agriculture some 8–10 thousand years ago, when clearing of forests and the consequent release of greenhouse gases potentially started affecting earth systems (Ruddiman, 2013; Foley et al., 2014). Human use of fire and our role in the extinction of the megafauna may also have affected climate, potentially dating the 'paleoanthropocene' still earlier (Sherratt and Wilkinson, 2009; Doughty, 2013). The second phase began in the Industrial Revolution, coinciding with significantly increased carbon emissions and the environmental degradation associated with industry (Crutzen and Stoermer, 2000). The final phase occurred post World War II, and is called the "Great Acceleration", because it is

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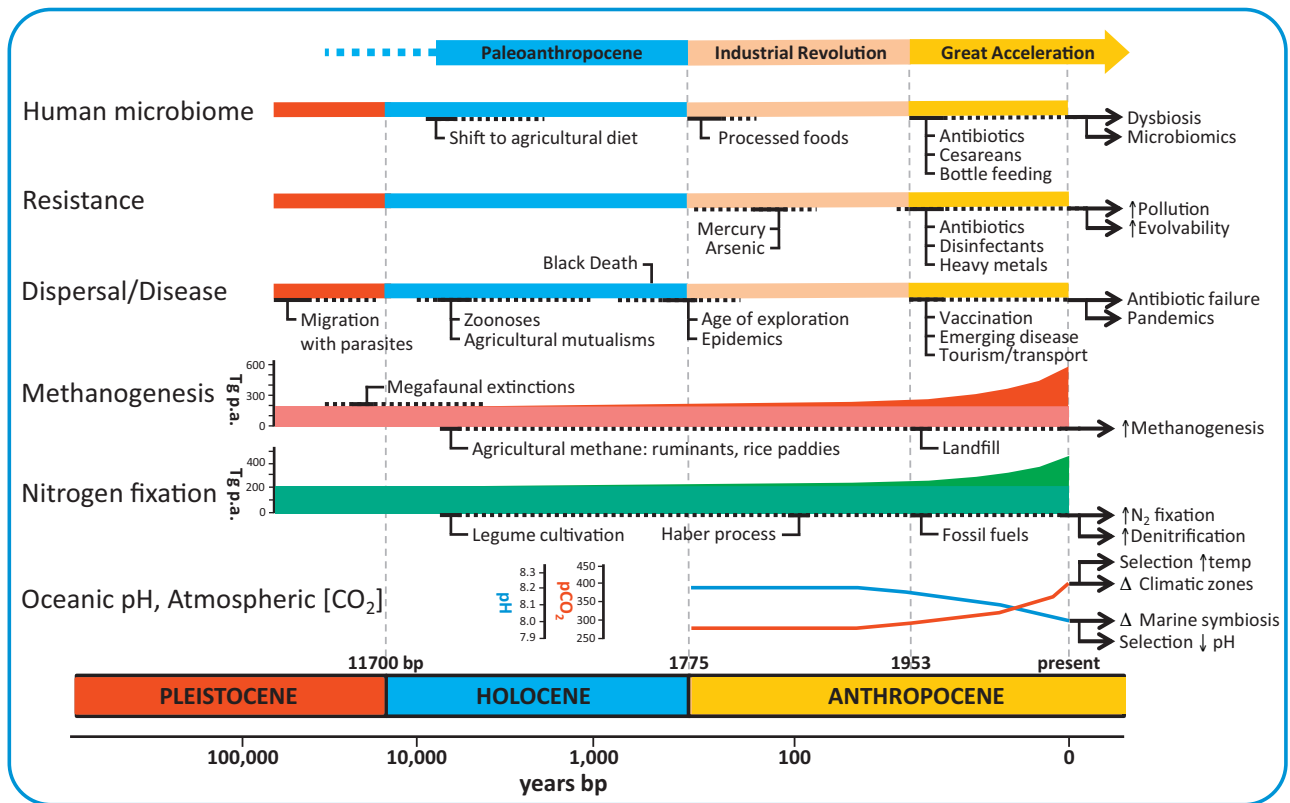


Fig. 1. Human influences on microbial ecology and evolution. A time-line for the three recent Epochs, the Pleistocene, Holocene and Anthropocene, is given at the base of the figure on an approximate log scale. Dates for the transitions between epochs are given. The suggested date of 1953 for the start of the Great Acceleration is based on the publication of DNA structure (Watson and Crick, 1953) and the increased frequency of nuclear tests during that year (see Crutzen and Stoermer, 2000). Arenas where humans have influenced the microbial world are given on the left hand side, with key developments noted along the timeline. Likely future outcomes are noted on the right hand side. Rates for methane generation and nitrogen fixation are plotted as Tg per year. Atmospheric CO₂ is plotted as ppm. Data for methane, nitrogen, oceanic pH and carbon dioxide concentrations are taken from a synthesis of the literature cited.

associated with very rapid growth in human population, resource consumption, energy use and pollution (Fig. 1) (Zalasiewicz et al., 2010; Steffen et al., 2011).

Human effects on earth system processes are now on such a scale that we are arguably the greatest evolutionary and ecological force on the planet (Palumbi, 2001). Global changes in climate, shifts in oceanic pH, altered nutrient cycles, loss of biodiversity and widespread pollution have all been identified as potential planetary tipping points (Rockstrom et al., 2009). These factors also imply biotic tipping points that will affect all living things, and where each human-induced change will result in a period of intense natural selection.

Dealing with the transition into the Anthropocene requires careful consideration of its social, economic and biotic effects (Gillings and Hagan-Lawson, 2014). Discussions on conservation of the natural world, and responses to human impacts, usually ignore microorganisms, despite the fact that they are central to ecosystems and biogeochemistry (Wilkinson, 2007; Falkowski et al., 2008). Here we explore the effects that human activities have had on microbial populations and ecology, starting with the organisms closely associated with humans, and then moving to larger and larger scales. How might conditions arising in the Anthropocene affect distributions, abundance and evolution in the microbial world?

The human microbiome

The microorganisms associated with humans are notably diverse, varying between individuals, between body sites and

over development. By adulthood, there are ten times more microbial cells in a human body than there are human cells. This diverse community of microorganisms is known as the human microbiome, and can be analyzed in a manner similar to more conventional ecosystems, by examining colonization, climax communities, and perturbations by disturbance or invasion (Costello et al., 2012). Questions can be asked about how the human microbiome might have changed over evolutionary time, how human activities might alter colonization and community development, and the role of the microbiome in health and disease.

On a very general level, the human microbiome has changed in parallel with phases of the Anthropocene (Fig. 1). Oral microbiota from fossilized dental calculus shows a marked change in bacterial diversity and composition during the transition from a hunter-gatherer lifestyle toward a greater consumption of cereals during the Neolithic (8000 years bp). A second major shift is apparent around the start of the industrial revolution, coinciding with increased availability of processed flour and sugar (Adler et al., 2013).

Analyses of gut bacteria preserved in coprolites show that ancient human microbiomes were similar to those from modern rural communities, and that diet dramatically affects microbiome composition. For instance, the increased availability of simple carbohydrates in the Neolithic selected for altered microbiome components (Walter and Ley, 2011). Such 'Neolithic' microbiomes still dominate the gut flora of communities with high fiber, polysaccharide rich diets (De Filippo et al., 2010; Yatsuneneko et al., 2012), whereas shifting to a modern, high protein and animal fat diet causes a corresponding shift in microbiome composition

(De Filippo et al., 2010, Wu et al., 2011). Dietary influences on gut microbiomes are also evident at higher taxonomic levels, since mammalian gut flora cluster according to diet, not phylogeny, and herbivore microbiomes can be clearly distinguished from those of carnivores and omnivores (Muegge et al., 2011).

Acquisition of the microbiome begins at birth, when the neonate is first exposed to both maternal and environmental bacteria. Delivery mode affects this early colonization, since C-section babies harbor different microbiomes compared to vaginal delivery (Dominguez-Bello et al., 2010). This basic shift in the initial microbial colonization of infants corresponds with the Great Acceleration (Fig. 1), since C-sections were rare before the 1950s, but now comprise up to one third of births (Lavender et al., 2012). Subsequent microbial succession in the developing infant depends on both infant diet and exposure to antibiotics (breast vs. bottle feeding; solid food) (Dethlefsen and Relman, 2011; Koenig et al., 2011; Cho and Blaser, 2012). Artificial baby feeders were used in ancient times, but it was not until the 19th century that modern feeding bottles and formula were developed (Stevens et al., 2009). Both the widespread adoption of bottle feeding and the routine availability of antibiotics are phenomena of the post-war era (Fig. 1).

Our gut microbiota interacts with gastrointestinal tissues to influence the development of our physiology and our immune system (Lee and Mazmanian, 2010; Kau et al., 2011). Perturbations to the developing microbiome brought about by birthing, dietary and medical practices may have serious health consequences (Cho and Blaser, 2012), and are now being linked to medical conditions whose frequency has increased dramatically since the Great Acceleration. These include allergies, asthma, inflammatory bowel disease, type 2 diabetes, psoriasis and obesity (Cho and Blaser, 2012; Greenblum et al., 2012). Microbiome composition is also thought to influence brain development and behavior (Bravo et al., 2011; Heijtz et al., 2011), and there are links between microbiome composition and disorders such as anxiety and depression, whose incidence has increased in the last 60 years (Foster and McVey Neufeld, 2013).

In summary, human activities affect the microbiome by altering colonization, exerting selection through shifts in diet, and by changing species composition via antimicrobial use. The various phases of these perturbations can each be assigned to distinct phases of the Anthropocene (Fig. 1). The influence we exert over our internal ecosystems is significant, and has long term consequences for human health and well-being. In the future, medical diagnostics may well identify dysbiosis using analysis of personal microbiomes, thus opening the way for targeted probiotic therapies and transplantation of microbiota from healthy donors (Table 1).

Antimicrobial resistance

The global spread of resistance to antimicrobial agents is possibly the best example of human-driven evolution in action. Antimicrobial therapy selects for bacteria that have accumulated specific mutations, or that have acquired resistance genes from other bacterial species via lateral gene transfer (Davies and Davies, 2010). Selection for resistance to antimicrobials probably began with the prophylactic use of arsenic and mercury compounds in the late 1800s, although a significant shift in abundance and identity of mercury resistance genes in lake sediments can be observed as early as 180–120 years ago, presumably tied to industrial activity (Fig. 1) (Poulain et al., 2013).

The increasing use of antibiotics post-WWII corresponds with the Great Acceleration, and resulted in an intense period of selection for antimicrobial resistance (Fig. 1). Prior to this period, mobile DNA elements such as plasmids did not carry resistance

Table 1

Key research questions about human effects on microbial evolution and ecology.

Topic	Research questions
Human microbiome	Have changes in microbiomes led to changes in human development, behavior or disease states? Can personalized microbiomes improve the targeting of probiotics?
Antibiotic resistance	What alternatives are there for controlling bacterial growth? Is pollution with antimicrobial compounds altering microbial ecology and evolution?
Biogeochemistry	Have human activities fundamentally altered microbial nitrogen and carbon cycles? Can microbial biogeochemistry be manipulated to address global change?
Dispersal and disease	Have human activities permanently altered microbial biogeography?
Global change	How can we predict and model emerging diseases? Which organisms and which genes will be affected by altered pH and temperature regimes? What processes will be altered by this natural selection, and can we factor it into earth system models?
DNA technology	What pathways, organisms and ecosystems are the best targets for synthetic biology? How can we minimize the risks of this technology?

determinants, but after this period there was a huge advantage for the initially rare cells that had sampled resistance genes via lateral transfer. Many of the resistance determinants now found in pathogens originated from environmental bacteria, whose genomes are a repository for an enormous pool of genes that can be co-opted to confer antibiotic resistance (Forsberg et al., 2012).

During the Great Acceleration, the use of diverse antimicrobial agents resulted in the acquisition of an ever-expanding number of resistance genes into a range of mobile DNA elements. Complex, mosaic DNA molecules carrying multiple genes with independent origins were assembled as a direct result of the selection pressure mediated by antibiotics, disinfectants and heavy metals (Toussaint and Chandler, 2012). These DNA molecules are xenogenetic, in the sense that they arise as a direct result of human activity (Gillings and Stokes, 2012).

Antibiotics affect non-target organisms, including both commensal and environmental bacteria. Consequently, antimicrobial therapy alters the human microbiome, and results in the accumulation of resistance genes in commensal gut flora (Hu et al., 2013). The majority of ingested antibiotic is often excreted essentially unchanged, and enters the environment via waste streams, resulting in high concentrations of antibiotics in sewage, downstream from animal production facilities, and in spread manure (Sarmah et al., 2006). Antibiotics released into the environment have unintended effects on environmental bacteria (Kristiansson et al., 2011), and should be regarded as significant pollutants, particularly in aquatic systems (Taylor et al., 2011).

Human waste streams also release antibiotic resistant bacteria. The diverse resistance genes and mobile DNA elements in these bacteria should also be regarded as pollutants (Pruden et al., 2013). However, such xenogenetic DNAs are critically different from other pollutants, because they can replicate, and they can transfer to new hosts (Gillings and Stokes, 2012). The concentration of resistance genes in soil has been increasing since the first use of antibiotics in the 1940s (Knapp et al., 2009), and resistance genes from human sources now pollute the whole planet, such that they are now found in situations far removed from direct antibiotic use, such as the Amazonas, polar regions, and in wild animals (Stokes and Gillings, 2011).

Because bacteria that contain resistance genes are released into waste streams simultaneously with antibiotics, disinfectants and heavy metals, this creates hotspots where complex interactions

and selection events can occur (Gaze et al., 2011). Wastewater treatment plants are essentially high volume reaction vessels for gene exchange and *de novo* assembly of new gene combinations (Zhang et al., 2011; Moura et al., 2012). Sub-inhibitory concentrations of antimicrobial agents in the environment affect the distribution and abundance of non-target bacteria, and promote the penetration of mobile DNA elements and diverse resistance genes into new species (Taylor et al., 2011). Such antimicrobial pollution is likely to affect the entire microbial biosphere by increasing basal rates of bacterial evolution via selection for lineages with increased rates of mutation, recombination and lateral gene transfer, and by increasing the abundance of resistance genes and their mobile DNA vectors (Gillings, 2013).

In summary, antibiotic use during the Great Acceleration has had significant effects on all bacteria, not just those of clinical concern (Martinez, 2012; Gillings, 2013). Pollution with antimicrobials and heavy metals affects both the structure and gene content of microbial communities (Wright et al., 2008; Kristiansson et al., 2011), and increases the basal rates of evolution in the microbial world (Gillings and Stokes, 2012), with long term consequences that are currently unknown (Table 1).

Microbial biogeochemistry

Much of global biogeochemistry is driven by microorganisms (Falkowski et al., 2008). Consequently, altering the abundance of microbial species has the potential to alter biogeochemistry, and vice versa. Over the last 10,000 years, humans have domesticated a variety of animals and plants, and in doing so, have inadvertently domesticated the microbial symbionts associated with these species. This has significantly altered the abundance of key organisms involved in cycling carbon and nitrogen.

Pre-agricultural emissions of methane probably stood at about 200 Tg per year. There has been a steep rise in methane emissions since the industrial revolution, such that by the end of the 20th century, this value was 600 Tg per year, raising atmospheric methane concentration to its highest level in 600,000 years (Fig. 1) (Ruddiman, 2013). Anthropogenic methane emissions mainly arise from agricultural practices, and are a consequence of the increased abundance of methane-generating microorganisms created by flooded rice cultivation, ruminant farming and associated animal waste. Together these sources generate about 250 Tg of methane per year (Dlugokencky et al., 2011). Microbially generated methane from agriculture is a significant factor in warming of the atmosphere, and needs to be factored into climate predictions (Table 1) (Lorenz et al., 2012). In the distant past, methane production by sauropod dinosaurs might have helped to maintain the high temperatures of the Mesozoic era (Wilkinson et al., 2012), demonstrating that microbial activity in the gut of large herbivores could have significant effects on climate. Extinction of the Pleistocene megafauna and increasing use of fire by early humans probably both affected atmospheric methane levels in the paleoanthropocene (Doughty, 2013).

Agricultural activities have also altered the abundance of microorganisms involved in the nitrogen cycle. Nitrogen gas is abundant in the atmosphere, but must be converted into reactive nitrogen (N_r) to become biologically available. Biological nitrogen fixation is accomplished by bacteria, and prior to the industrial revolution, this process generated 58 Tg of N_r per year (Vitousek et al., 2013). Humans cultivate a variety of legumes that house nitrogen fixing bacteria in their roots, thus increasing the abundance of nitrogen fixers. This agricultural activity now accounts for an additional 60 Tg of N_r per year (Fowler et al., 2013).

In more general terms, microorganisms are responsible for driving the global nitrogen cycle, fixing gaseous nitrogen into ammonia, converting this into nitrates (nitrification), and thence to

nitrous oxides or back to nitrogen gas (denitrification). Human inputs into the nitrogen cycle through industrial fixation (the Haber process), fossil fuel burning and legume cultivation now account for 45% of global nitrogen fixation (Fig. 1) (Vitousek et al., 2013). This may be the largest perturbation to nitrogen cycling in the last 2.7 billion years.

Increased inputs of nitrogen into ecosystems can be detected from the late 1800s, with a large increase apparent after 1950 (Holtgrieve et al., 2011). In terrestrial ecosystems, increased concentrations of available nitrogen cause decline in the biomass of mycorrhizal fungi (van Diepen et al., 2010) and consistently alter microbial community structure (Ramirez et al., 2012). Nitrogen runoff from soils causes eutrophication of water bodies, and leads to blooms of cyanobacteria, dinoflagellates and diatoms, all of which can produce toxins (Camargo and Alonso, 2006). Controlling eutrophication requires reduction of both nitrogen and phosphorus inputs to receiving waters (Lewis et al., 2011). The effects of nitrogen pollution on oceanic ecosystems are more difficult to predict, since some components of the marine nitrogen budget are still not known (Großkopf et al., 2012).

Over time, a new steady state for nitrogen cycling should arise. Intuitively this should involve a decrease in the rate of natural nitrogen fixation, together with increased rates of nitrification and denitrification (Schlesinger, 2009). Rates of marine nitrogen fixation do slow after long-term exposure to increased concentrations of nitrate and ammonia (Knapp, 2012), but this observation is complicated by the fact that ocean acidification slows both nitrogen fixation and nitrification (Beman et al., 2011; Shi et al., 2012). Denitrification rates appear to have responded to anthropogenic nitrogen fixation, because increasing nitrogen content in soils leads to an increase in efflux of nitrous oxide, especially in combination with increased temperature and precipitation (Brown et al., 2012). Between 1860 and 1960 a steady increase in atmospheric nitrous oxides was probably driven by expansion of livestock production, while the steeper rise in emissions after 1960 was due to increasing use of industrially fixed nitrogen as fertilizer (Davidson, 2009).

Thus perturbations to the microbial production of biologically available nitrogen and of methane correspond closely to the origins of agriculture, the industrial revolution and the Great Acceleration (Fig. 1).

Dispersal and disease

In the past, microorganisms were thought to be cosmopolitan, because their small size, large populations and ability to form dormant cells favored ready dispersal. It is now known that many microorganisms do exhibit strong spatial patterns, similar to those exhibited by macro-organisms (Green et al., 2004; Horner-Devine et al., 2004). Consequently there is potential for human activities to foster the dispersal of viruses, bacteria, fungi and protists into novel locations, whether these are pathogens, mutualists or organisms from the general environment (Litchman, 2010; Wilkinson, 2010).

The first transport of microorganisms occurred as humans dispersed from Africa, carrying their parasites with them (Fig. 1) (Michelet and Dauga, 2012). This movement of human-specific parasites can now be used to track the migration of early humans around the globe (Araujo et al., 2008). The next major change to human-microbial ecology occurred with the domestication of animals and the development of agriculture. Agricultural settlements allowed humans to achieve population densities where infectious diseases were self-sustaining, and did so in an environment where close contact with animals was a daily occurrence. This allowed animal pathogens to infect and adapt to human hosts. Viral diseases such as mumps, measles and smallpox, and bacterial diseases like diphtheria and pertussis

originated in this manner. Permanent settlements also created new niches for disease vectors such as rodents and arthropods (Smith and Guégan, 2010). Production of crops and the introduction of invasive plants inadvertently spread plant-associated mutualists such as mycorrhizae and rhizobia around the globe, a phenomenon that continues to the present day (Pringle et al., 2009; Rodríguez-Echeverría, 2010).

The age of exploration relied on maritime transport, and this was instrumental in the long-distance dispersal of diseases such as syphilis, smallpox, cholera, bubonic plague and anthrax (Fig. 1) (Keim and Wagner, 2009). The movement of plants, animals and soil that accompanied this exploration also spread environmental organisms around the world, beginning a trend that now sees humans as an important factor in microbial biogeography (Wilkinson, 2010). Modern ships transport microorganisms, such as vibrios and dinoflagellates, in ballast water (Davidson and Simkanin, 2012), and airplanes facilitate international travel, while incidentally ensuring the rapid transit of passengers infected with SARS or antibiotic resistant enterobacteria (Olsen et al., 2003; van der Bij and Pitout, 2012).

Changes in microbial dispersal and disease incidence broadly correspond with phases of the Anthropocene: the evolution of zoonotic diseases and inadvertent spread of soil organisms that accompanied the rise of agriculture; the transport of organisms by sea during the age of exploration, hastened by the development of mechanized transport in the industrial revolution; and culminating in the rapid mass transit systems and consequent rise in international tourism that accompanied the Great Acceleration (Fig. 1).

Global warming and ocean acidification

Anthropogenic production of carbon dioxide is warming the planet. The speed of warming has been offset by the absorption of almost a third of anthropogenic CO₂ emissions by the oceans, but this has the effect of lowering oceanic pH, a phenomenon known as ocean acidification. Both warming and acidification will have effects on the microbial biosphere, through selection of genetic variants suited to warmer, more acidic conditions, by affecting the biochemical activity of individual species, and by altering microbial community composition and dynamics (Fig. 1).

Increases in ambient CO₂ have significant effects on plant growth. This, in turn, increases secretions from roots, directly affecting the growth of soil fungi and bacteria. In general, mycorrhizae are favored over bacteria, but effects vary depending on the plant species studied and the microorganisms involved (Compant et al., 2010; Drigo et al., 2013). Warming of soil affects microbial species composition, changes the proportions of functional groups, and suppresses plant pathogens (Chakraborty et al., 2012; Deslippe et al., 2012; Pold and DeAngelis, 2013). Temperature influences the spatial distribution of key microbial species in soil (Garcia-Pichel et al., 2013), so in a warmer world microorganisms may have to migrate to higher latitudes, thus exposing themselves to the same problems of range fragmentation and ecosystem disruption faced by macro-organisms (Pickles et al., 2011). Climate change and extreme weather events will also change the distribution of disease vectors and will precipitate outbreaks of water-borne disease (Cann et al., 2013).

As climate and the oceans change, it will affect keystone species. Ocean acidification changes microbial communities in biofilms, reducing their functional diversity (Witt et al., 2011; Kroecker et al., 2013). Mutualistic associations with corals, foraminifera and crustose coralline algae are also affected by acidification, as are microbially mediated settlement cues (Webster et al., 2013). Alterations to ocean chemistry will lead to natural selection in key phytoplankton species (Lohbeck et al., 2012).

In some taxa, selection on existing genetic variation will lead to rapid adaptive responses. This, when coupled with the ability for phenotypic plasticity, will ensure that some phytoplankton groups respond quickly to ocean acidification. However, because marine phytoplankton comprise diverse groups, such as diatoms, dinoflagellates, coccolithophores and prasinophytes, each with their own niches and biochemistry, conclusions drawn for one group will not apply to all taxa (Collins et al., 2014).

Climate change and ocean acidification will affect microbial distributions and functions in similar ways to macro-organisms, affecting both community composition and abundance. In the microbial realm, this will have consequences for biogeochemistry, and these effects need to be factored into predictive models of the future earth (Table 1) (Treseder et al., 2012; Wallenstein and Hall, 2012). Since significant warming and ocean acidification are recent, their effects on microbial physiology and ecology are phenomena of the Great Acceleration (Fig. 1).

DNA technology

Technical expertise in molecular biology has advanced to the point where a rapidly growing number of microorganisms have been completely genome sequenced. This trend will continue, to eventually include representatives of all microbiota. Large volumes of microbial DNA sequence data are now stored as binary code, replicated at multiple nodes across the web, and can be used to resynthesize new DNA molecules at distant locations or in the future. These *in silico* forms of biological information can persist, and replicate, with little metabolic cost. *In silico* models have already been used to predict phenotypes not yet observed in their living counterparts (Karr et al., 2012).

Sequences stored in DNA databases can be used as a template for chemical synthesis of microbial genomes, aided by advances that make complex DNA syntheses fast, accurate and efficient. This technology allows whole bacterial genomes to be constructed (Isaacs et al., 2011). The first successful transfer and expression of a synthetic chromosome has been achieved with construction of a chemically synthesized bacterial genome (Gibson et al., 2010).

Biological information flows from DNA, to RNA, to protein, and thence to phenotype, in the process known as the Central Dogma of cell biology. This flow of information has driven all organisms since the last universal common ancestor, some 3.7 billion years ago. As a result of the technology described above, humans have now expanded the Central Dogma, to include *in silico* storage of biological information. Conversely, rapid advances in both DNA synthesis and sequencing now allow digital information to be effectively stored as DNA molecules (Goldman et al., 2013). In this case, non-biological information would be stored in a biological repository. Consequently, humans are embarking on fundamental extensions to the flow of information circumscribed by the Central Dogma (Gillings and Westoby, 2014). This is a major development in the course of evolutionary history.

We would suggest that fundamental developments in living systems should be added to the criteria for epochal transitions, and in this regard human advances in molecular technologies would qualify. Even so, the extension of the Central Dogma does have a strong chance of contributing to geological signals. Ready access to DNA sequence databases raises the possibility that extinct pathogens could be deliberately constructed and released (Suk et al., 2011), thus leaving a significant signal in the fossil record. Our abilities to manipulate DNA will progress from assembly of new biochemical pathways to the design and synthesis of novel organisms (Ellis et al., 2011). These might be tailored to address the adverse trends in C, N and P biogeochemistry that characterize the Anthropocene (Table 1). Such projects depend on continuing

molecular advances, but given our recent rapid progress, they will be feasible within decades.

Human manipulation of the Central Dogma has the potential to expand the power of gene technology to whole earth scales. DNA technology will be a powerful force in our future, and for dealing with the Anthropocene. For this reason, we suggest that the period known as the 'Great Acceleration' be assigned a formal starting date of 1953, the year that the structure of DNA was first published (Franklin and Gosling, 1953; Watson and Crick, 1953). The early 1950s also corresponds with significant deposition of radio-nuclides from atomic detonations (Zalasiewicz et al., 2010).

Conclusions

The effects of human activities on the planet's microbiota broadly conform to the three phases of the Anthropocene: the paleoanthropocene of our agricultural forbears; the industrial revolution, suggested as a starting date for the Anthropocene proper; and the Great Acceleration, from the 1950s onward (Fig. 1). The correspondence between changes in microbial ecology and each of these phases helps confirm the suggested dates and the logical division of time frames for human impacts on the planet (Foley et al., 2014; Smith and Zeder, 2014).

Many of the biotic effects that will occur during this epochal transition may not be reflected in the future fossil or stratigraphic record. Fundamental changes to C, N and P biogeochemistry will leave a distinct signal, but perhaps without direct evidence of the biology behind such transitions. There are some geological signals that coincide with microbial activity, for instance the production of oxygen in the early atmosphere, but this occurred over hundreds of millions of years (Hohmann-Marriott and Blankenship, 2011). Other signals may have been laid down in a comparatively short time period, such as evidence for elevated fungal biomass at mass extinction events (Benton and Twitchett, 2003; Vajda, 2004). However, we must conclude that many microbiological aspects of past planetary upheavals have not necessarily been recorded in the geological column. We can ask whether the general kinds of phenomena we observe today also occurred during transitions between previous geological eras. The changes wrought by the Anthropocene offer an opportunity to observe epochal transitions and their evolutionary consequences in real time.

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