

The Anthropocene biosphere

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Abstract

The geological record preserves evidence for two fundamental stages in the evolution of Earth's biosphere, a microbial stage from ~3.5 to 0.65 Ga, and a metazoan stage evident by c. 650 Ma. We suggest that the modern biosphere differs significantly from these previous stages and shows early signs of a new, third stage of biosphere evolution characterised by: (1) global homogenisation of flora and fauna; (2) a single species (*Homo sapiens*) commandeering 25–40% of net primary production and also mining fossil net primary production (fossil fuels) to break through the photosynthetic energy barrier; (3) human-directed evolution of other species; and (4) increasing interaction of the biosphere with the technosphere (the global emergent system that includes humans, technological artefacts, and associated social and technological networks). These unique features of today's biosphere may herald a new era in the planet's history that could persist over geological timescales.

Keywords

biosphere, evolution, global ecosystem, neobiotic species, planetary state, production and consumption, technosphere

Introduction

Humans transport organisms around the globe (McNeely, 2001 and references therein), construct unique agricultural and urban 'anthromes' for organisms to live in (e.g. Ellis, 2013; Ellis et al., 2012, 2013a, 2013b), and have concentrated biomass into a particular set of plants and animals (e.g. Smil, 2011). Ecosystem fragmentation, intensive farming, climate change and pollution threaten the biodiversity of many organism groups with a greatly increased risk of

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species extinction (Barnosky et al., 2011; Pimm et al., 2014). Though the biosphere is a resilient component of the Earth System even where biodiversity loss is significant (see arguments in Brook et al., 2012, and an interrogation of the fossil record), human influence may nonetheless threaten its current stability (Barnosky et al., 2012; Röckstrom et al., 2009; Steffen et al., 2011). Processes of anthropogenic ecological succession can enable effective ways of managing ecosystems (Ellis, 2013 and references therein), and increased biodiversity can be observed locally (though not at the global scale) as a result of the introduction of neobiotic species (Ellis et al., 2012). Nevertheless, the sum of human-induced changes to the Earth's biosphere is considerable and is expressed in the recent fossil and sedimentological record (Kidwell, 2015). Only one-quarter of the Earth's ice-free surface now represents natural wilderness (Ellis, 2010), and by measures such as climate change and distribution of pollutants, there is no place on Earth that has not been altered by humans

From a geological perspective, these changes may represent more than just being the latest in a succession of environmental perturbations that have affected this planet. We can place them within the context of the Earth's biosphere (Suess, 1875; Vernadsky, 1998), a complex system that has proven extremely resilient and has existed for some 3.5 billion years (e.g. see Altermann and Kazmierczak, 2003), a chain of evolution stretching back to the earliest simple organisms.

Palaeontologists distinguish two fundamental stages in the evolution of the biosphere, a microbial stage of unicellular and sometimes colonial organisms that persisted from c. 3.5 Ga (3500 million years ago) to 0.65 Ga, and the development of a metazoan stage of complex multicellular organisms that began to be widespread by 0.58 Ga (Butterfield, 2011; Erwin et al., 2011; see Figure 1). The transition between the microbial stage and a metazoan stage took place over more than 100 million years and is associated with a number of biotic innovations during the late Precambrian (Figure 1; see Butterfield, 2007, 2011; Erwin et al., 2011) that is expressed in the Cambrian adaptive radiation (the 'Cambrian Explosion'). The development of bilaterally symmetrical animal bodies (those with a recognisable anterior and posterior end), and of multi-tiered complex ecosystems characterised the Phanerozoic metazoan stage of the biosphere over the past 541 million years and this biosphere spread from the sea onto the land, and was associated with the evolution of complex terrestrial plants from 0.46 Ga onwards (Wellman and Gray, 2000). Since the initial colonisation of the land, the biosphere has suffered five mass extinctions with an estimated 75% or more loss of species diversity in taxa known for the respective time, these being at the end of the Ordovician Period (from 444 to 440 Ma), in the late Devonian (between 375 and 360 Ma), and at the end of the Permian (252 Ma), Triassic (200 Ma), and Cretaceous (66 Ma) periods (see Barnosky et al., 2011 for a comprehensive review). In all cases the biosphere recovered its complexity after several million years (Hart, 1996 and references therein). A number of extinction events with a lower impact on species diversity permeate the Phanerozoic record of the biosphere (Bambach, 2006), for example several events within the 50 million year duration of the Cambrian Period (Shu et al., 2006). Nevertheless, the overall resilience of the biosphere is reflected in that the metazoan phyla on Earth today were present in Cambrian faunas, despite the environmental vicissitudes of the Phanerozoic Eon.

Here, we assess the degree of human-induced biosphere change relative to past major evolutionary changes to the biosphere through Earth history, and ask the question, has the Earth evolved a new 'Anthropocene biosphere'?

The geological record of Earth's biosphere

The Earth is some 4.54 Ga old (Dalrymple, 2001) and the fossil record of life extends back for three-quarters of that time. In this section we outline the principal characteristics of the microbial and metazoan stages of the biosphere as identified above.



Figure I. Major events in the evolution of life and the planet: circled numbers 1 (microbial), 2 (metazoan), and 3 (Anthropocene) represent the three stages in the evolution of the biosphere discussed here. The origin of plate tectonics is a controversial subject and may have begun much earlier than 3.2 Ga (see for example Arndt and Nisbet, 2012).

The microbial stage of the biosphere

For 3 billion years Earth's biosphere was characterised by microscopic organisms, either as discrete entities, or grouping to form macroscopic colonies – microbial mats – such as stromatolites (e.g. Allwood et al., 2009). A microbial biosphere of prokaryotic organisms had likely emerged by 3.5 Ga, as inferred from fossil data (e.g. Altermann and Kazmierczak, 2003; Wacey et al., 2011), whilst geochemical data suggest this may extend back to 3.8 Ga (Grassineau et al., 2006; Mojzsis et al., 1996). Though it is impossible to gauge the species diversity of the prokaryotic microbial biosphere in deep time, the modern prokaryotic component of the biosphere runs into the millions of species (Curtis et al., 2002). A relative measure of species diversity and disparity can be gauged from an analysis of eukaryotic fossil cells called acritarchs that are preserved in the Precambrian record (Knoll et al., 2006): these suggest that diversity and disparity (the latter a means of quantifying the morphological differences between different organisms) remained low during the Precambrian, whilst species longevity may have been high (Butterfield, 2007, 2011).

Notwithstanding that the fossil record for the Precambrian is sparse, microbial biosphere ecosystems show little evidence for mass extinction. The microbial biosphere was innovative, and early on developed chemotrophic, phototrophic and heterotrophic pathways to energy supply. Evolution of the microbial biosphere witnessed the development of oxygenic photosynthesis by c. 2.4 Ga that resulted in the Great Oxygenation Event (GOE; see Pufahl and Hiatt, 2012), dramatically changing the course of biotic and atmospheric evolution. Free oxygen was released to the atmosphere and oceans, effectively poisoning those environments occupied by anaerobic microbes (Figure 1). Step changes in the complexity of the microbial biosphere were reached through the evolution of eukaryotic microbes at c. 1.8 Ga (Knoll et al., 2006), and by the development of sex and the appearance of multicellular organisms by c. 1.2 Ga (Butterfield, 2000). These changes were important precursors that facilitated the construction of the first metazoan animals, possibly as early as 0.7 Ga (Erwin et al., 2011), and shortly (from a geological perspective) before the Precambrian–Cambrian boundary at 0.541 Ga (see Figure 1).

The metazoan stage of the biosphere

Perhaps fundamental to a definition of the metazoan stage of the biosphere is that 'gut-based feeding yields a uniquely metazoan dynamic' (Butterfield, 2011). The evolution of guts resulted in the development of a whole series of associated anatomical innovations to detect, capture and process food prior to its digestion (Butterfield, 2011). From its inception, the evolution of metazoans had a profound impact on microbial organisms, accelerating, for example, the diversification of acritarchs possibly as a response to increased predation (Butterfield, 2011; Knoll et al., 2006). The metazoan stage of the biosphere is characterised by complex ecological interactions, with a size change at trophic levels between the tiny primary producers, the larger primary and secondary consumers, and the large tertiary consumers (Butterfield, 2007, 2011). Thus, in aerobic eukaryotes (including plants and animals), there are some 20 orders of magnitude in size change between the smallest and the largest organisms (Brown et al., 2004 and references therein). The metazoan stage of the biosphere is characterised by a major adaptive radiation of structurally complex metazoan organisms into marine ecological niches, a diversification of life that was particularly rapid from the Cambrian Explosion through the Great Ordovician Biodiversification Event (see Droser and Finnegan, 2003 for a review). Though it is difficult to assess species richness of the modern metazoan component of the biosphere – most species are as yet undescribed – recent estimates suggest as many as 8.7 million eukaryotic species are living (Mora et al., 2011; this figure includes both metazoan and unicellular eukaryotes). Unlike for the microbial stage of the biosphere, metazoan evolution shows clear geological evidence for rare mass extinctions (the classic work evaluating this being Raup and Sepkoski, 1982) that eliminate a broad spectrum of life with little regard for life history strategy (Jablonski, 2001, 2008). But metazoans are also resilient, with an ability to eventually (over a few million years) recover from extinction events – though into a different pattern of taxon composition (Hart, 1996 and references therein).

The transition from the microbial to the metazoan stages of the biosphere

The metazoan stage of the biosphere developed through a series of biological innovations over more than 100 million years (Erwin et al., 2011). It evolved to co-exist and interact with microbes. The transition from the microbial to the metazoan stages of the biosphere occurred between c. 0.7 Ga and 0.541 Ga (Erwin et al., 2011). Fossil and geochemical data indicate the presence of poriferans (sponges) by 0.65 Ga (Love, 2009, and possibly earlier – see Erwin et al., 2011). Poriferans represent a fundamental change in the structure of organisms. They define 3D spaces, and thus are able to modify their local environment, for example by controlling the flow of water over certain areas of the body. They also provide a mechanism for concentrating biomass (de Goeij et al., 2013) and are a food source for animals at higher trophic levels in the marine ecosystem. The evolution of the other major animal phyla involved the development of tissues differentiated to form organs, most notably for the internal processing of food, which are possessed by animals both with radial (e.g. jellyfish and corals) and bilateral symmetry (e.g. worms, arthropods and humans).

Some 70 million years after early evidence for sponges, the rock record contains fossils of an enigmatic group of organisms called the Ediacarans, known from more than 30 localities world-wide (Droser et al., 2005). These span an interval of time from 0.58 Ga to 0.541 Ga and are divided into three temporally successive marine assemblages that suggest increasing species diversity and ecological complexity (Erwin et al., 2011). Ediacaran fossils have been interpreted to include animals with both radial and bilateral symmetry, but divergent interpretations indicate the difficulty of interpreting the fossil record of Precambrian soft-bodied organisms with limited preserved characters (see for example, Retallack, 2012). Coincident with the second and third temporal assemblages of Ediacarans are trace fossils (Erwin et al., 2011) that likely indicate the seabed activity of animals with bilateral symmetry. Mostly, these traces are simple tracks and horizontal burrows formed in ancient seabed sediment, with some meandering grazing structures. The organisms responsible for these traces are generally attributed to the activities of mobile 'worms' with hydrostatic skeletons and guts. They indicate the invention of directionality in the locomotion of metazoans that were actively seeking out sources of food.

Ediacaran organisms were essentially limited to the surface of the Precambrian seabed and were unable to utilise the supply of organic material or nutrients buried beneath the surface, or to use this sediment as a domicile, habitat or repose from predators. Sedimentary rocks 541 million years ago, at the Precambrian–Cambrian boundary show a marked increase in animal activity at the seabed that marks the base of the Phanerozoic Eonothem (Figure 1) and reveals evidence for widespread bilaterally symmetrical animals. This was followed by the evolution of animal skeletons independently across several animal groups (Porter, 2008) by 0.53 Ga, and both of these processes (burrowing and skeletonisation) are seen as a response to the increased predation pressure that began in the late Precambrian (Butterfield, 2011) and that characterises the Phanerozoic.

The development of an Anthropocene biosphere?

In this section we argue that the Anthropocene biosphere is developing into something fundamentally different from its microbial and metazoan stages. The Anthropocene biosphere is unique in possessing four key parameters: (1) the widespread (near-global) resetting of ecosystem composition and structure, partly as a result of cross-global species invasions; (2) a major change in the energy budget that all species rely upon, brought on by the expropriation of primary productivity, with one species (*Homo sapiens*) consuming some 25% to 40% of net primary production, and by the production of vast amounts of energy by *Homo sapiens* primarily through burning fossil fuels, essentially fossil net primary productivity; (3) the human-directed evolution of plants and animals; and (4) the increasing coupling of the biosphere with an ever more rapidly evolving technosphere (Haff, 2014a, 2014b). We deal with each of these components in the subsections following, but note that they are all interlinked (see Table 1). Importantly, we also recognise that there are alternative ways of conceptualising the causes of the rise of humans as a global force transforming the biosphere beyond the emergence of technology and a technosphere, that focus equally on the emergence of human ultrasociality (Hill et al., 2009) and the upscaling of human societies through sociocultural niche construction (Ellis, 2015).

We recognise that biodiversity loss, which today is at least tens of times above background levels (Barnosky et al., 2011), is a significant process of the Anthropocene. Some estimations suggest extinction rates are now at 1000× background levels (Pimm et al., 2014); while such high rates of loss may be active in culling populations, if they were active at the species level it would imply that we should be witnessing the loss of many more than 1000 species each year, whereas the observed numbers are about 1000 species extinctions over the past 500 years. Nevertheless, the extremely high rate of population extinction has resulted in some 41% of amphibian species, 33%

Table I. Some chara the Anthropocene tha start of the Anthropoo and animals beginning back to 3.8 Ga (Mojzsi diversity' the term 'tec there being over 3.6 b 'morphological dispari of taxa).	cteristics of the microbial, met t are unique and assigns them ene biosphere is suggested to at c. 14 Ka (see Figure 3); also s et al., 1996). For 'number of thno-morphologies' refers to a dillion phones in circulation as c y' refers to the range of differ	azoan and Anthropocene stages of bios to the four main defining parameters of develop from early stone tool use at c in this category the beginning of the m species' the estimate of eukaryotic div species' the estimate of eukaryotic div fl human-produced Arructures such as r of September 2014), which can also be ent organism designs (building plans) ar	sphere evolution: the final column inde f this biosphere defined in the text. In . 2.6 Ma, and to accelerate from the d icrobial biosphere is dated to 3.5 Ga, 1 ersity is from Mora et al. (2011). For c mobile phones (now increasing in num preserved as technofossils (Zalasiewic: nd differs from taxonomic diversity (w	ntifies those features of category 'duration', the omestication of plants chough it may extend ategory 'Technological bers extremely rapidly, z et al., 2014a). The term nich is based on number
Biosphere characteristic	Microbial	Metazoan	Anthropocene	Anthropocene parameter unique
Duration	3500 million years	650 million years	Emerging since c. 2.6 million years accelerating from 14,000 years	Overlapping
Number of species	Difficult to quantify, but likely millions	Possibly tens of millions	 c. 9 million eukaryotes, but diversity declining globally and in many regions 	°Z
Morphological disparity Marine component	Microbial body plans Bacterial, fungal and 'protistan'	Animal and plant body plans Animal	Techno-morphologies Human modified and depleted	Yes, parameter 4 Yes, parameter 3
Terrestrial component	Negligible?	Animal, fungal and plant (developing post 460 Ma)	Pervasive human influence resulting in 'Anthromes'	Yes, parameters I and 3
Terrestrial biomass	Negligible?	Billions of tonnes (developing post 460 Ma)	Billions of tonnes focused on domesticated organisms and humans resulting in increased megafaunal biomass	Yes, parameter 3
Size range of organisms	Small (generally microscopic)	20 orders of magnitude	20 orders of magnitude	No
Trophic structure	Simple (primary producers and consumers)	Multi-tiered (to apex predators)	Multi-tiered and re-organised according to human needs	Yes, parameter 3
Stability	Apparently stable over long intervals	Mass extinction events	Potential mass extinction unfolding	No
Energy flow	Photo-/chemosynthetic, heterotrophic, saprophytic	Heterotrophic consumption by animals	Dependent on input from fossil fuels and other energy production through technology	Yes, parameter 2

Table I. (Continued)				
Biosphere characteristic	Microbial	Metazoan	Anthropocene	Anthropocene parameter unique
Biological–technological interaction	None	Negligible	High dependence on technology	Yes, parameter 4
Technological diversity	None	Negligible	High (millions of techno- morphologies)	Yes, parameter 4
Mode of evolution	Darwinian	Darwinian	Darwinian and human-directed	Yes, parameter 3
Ability to modify Earth environment	High, including atmosphere and hydrosphere	High, including sediment burrowing and penetration	High, with one species having global influence	Yes, parameters I to 4
Biogeographic distribution	Largely unquantified	Provincial	Global neobiota	Yes, parameter
Tissues/structures	Organic (C,H,N,O)	Calcium carbonate, apatite, silica	Prosthetics/implants of plastics, metals, glass	Yes, parameter 4
Tissue/structure complexity	Cells, nuclei and organelles	Organs, muscle, skeletons	Plastics, metals, glass, concrete etc.	Yes, parameter 4
Organism motility	Largely unquantified	Moderately high, but physical barriers (ocean currents, continents, mountain ranges) limit dispersal and result in endemism	High, humans distribute many organisms globally irrespective of physical barriers	Yes, parameter I
Social structure	Colonial (stromatolite, bacteria)	Sociality (birds) and eusociality (mostly insects)	Profusion of chordate eusociality (mostly human)	Yes, parameter I
Role of purpose	None	Medium (the cat chases the bird for the purpose of)	High, sense of history, social decision-making, forward planning, supply and demand	Yes, parameters to 4
Information systems	Molecular and genetic	Neuronal	Oral, written, printed, electronic and digital	Yes, parameter 4
Consciousness	None	Emergent	Strong force	Yes, parameters I to 4

of reef-building corals, 34% of conifers, 25% of mammals and 13% of bird species recognised as 'threatened' with extinction (IUCN, 2014), and even the lower estimates of rate of species loss observed over the last 100 years would result in loss of three out of four familiar species within as little as three centuries (Barnosky et al., 2011). Such rapid extinction is rare in Earth history, but has occurred five times in the Phanerozoic history of life, and the Anthropocene event as currently unfolding is following the pattern of these past mass extinctions (Barnosky et al., 2011), though is unique in being ultimately driven by the actions of one species. However, societal actions still have the potential to stem the currently too-high extinction rates, so mass extinction and accompanying biodiversity loss has not (yet) attained the status of a defining signal of an Anthropocene biosphere (although it well could in the future if appropriate conservation actions are not instituted). Therefore, in the sections following we focus on other indications that the transition to a new biosphere stage already has occurred.

Parameter 1: A global signal of neobiota

Here we use the term 'neobiota' (sensu Kowarik, 2010) to refer to those species that have changed their spatial ranges and moved into new territories as a result of human intervention (either deliberate or accidental). A species is considered neobiotic only in its new range (not in its prehistoric range, that is, the range it occupied before human-influenced range alterations). We use neobiota as a more neutral term to that of 'invasive species' or 'exotic species' (e.g. Olson, 2006; Pimental et al., 2004), which have also been used to denote such fauna and flora, but which involve discussion of taxa which are often detrimental to other species in the ecosystems they invade (e.g. the now globally distributed Argentine ant; Sanders et al., 2004). The Anthropocene signal of neobiota is different from that recorded in the geological record. It is a global signal that has arisen extremely rapidly (within a few millennia, and especially over the last seven decades), including continents, landmasses and coastal marine areas that are geographically isolated. This rapid homogenisation of world biota is perhaps unique in Earth history (Didham et al., 2005; Rosenzweig, 2001), and reverses the direction of the comparatively gradual evolution of biogeographically distinct fauna and flora that has been proceeding since the break-up of the Pangaea palaeocontinent some 200 million years ago. Hence incoming species today cannot be used, as previously in Earth's history, as proxies for changing palaeogeography (cf. Cocks and Fortey, 1982).

In the geological past, movement of continents via plate tectonic motion isolated geographical regions, such as Australasia. Open oceans prevent the inward or outward migration of terrestrial fauna or flora, and of marine benthic fauna without pelagic larvae, and in such contexts species assemblages become strongly endemic. Prior to recent human influence, these patterns of isolation broke down only when continents approached and collided, which takes place over the millionsof-years timescale, the classic example being the conjoining of North and South America by about 3 million years ago, which accelerated the Great American Biotic Interchange (GABI; see for example Cody et al., 2010; Lessa and Fariña, 1996). Older examples of fundamental changes in the distribution of species and their assemblages are also known from the geological record. For example, the collision of ancient England and Wales with Scotland, about 430 million years ago, produced a cosmopolitan assemblage of marine species where hitherto discrete assemblages had dominated (the classic work documenting this change is McKerrow and Cocks, 1976). The response of organisms to changing continental configurations is often complex, and the large-scale migration of terrestrial species between North and South America during GABI was countered in the marine realm by the Great American Schism between those faunas on the western and eastern tropical seas of the Americas (Lessios, 2008). Patterns of faunal and floral interactions between indigenous species and neobiota are also complex, and show different rates of speciation and

extinction between the two groups, as in South America during GABI (Lessa and Fariña, 1996). Past major migrations of fauna are clearly represented in the fossil record, for example the influx of South American species during GABI into the Miocene and Pliocene fossil assemblages of Florida (Morgan, 2005).

Homo sapiens is itself a neobiotic species par excellence, and its members have left their remains and also produced a set of characteristic (and potentially fossilisable) anthropogenic structures that extend from ancient Mesolithic campsites, through the ancient cities of Mesopotamia, to the modern research bases of Antarctica. In tandem, human migration has both deliberately and inadvertently transported a whole range of species across the globe, from microbes to large flora and fauna (McNeely, 2001 and references therein). Some of these organisms have been transplanted between continents as cultivated species, such as potatoes, maize and the rubber plant, or as deliberately transported natural species ranging from rabbits, lizards and snakes, to deer, horses and elephants. Thousands of other species have been transported unwittingly.

The impact of the neobiota is now considerable. Thus, in the European Union an initiative called DAISIE (Delivering Alien Invasive Species Inventories for Europe) now registers 6658 species of terrestrial plants, 2740 terrestrial invertebrate species, and 796 species of terrestrial fungi (Vilà et al., 2004) as neobiota. In Berlin alone, there are some 839 native species of plants and 593 alien species (Kowarik, 1990), while alien woody plants in Berlin's flora have grown from 16% in the 18th century to 67% today (Kowarik et al., 2013). In the USA, 4300 out of 50,000 neobiotic species are classified as invasive, i.e. doing harm to indigenous life forms (Corn et al., 1999). Beyond simple species proportions, individual neobiotic taxa have adopted very widespread distribution patterns both on land (e.g. Lowe et al., 2000) and in the sea (Bax et al., 2003). Many neobiotic species have become numerically dominant in particular environments, not least those that have been adapted by humans. *Quercus garryana* meadows in SW Canada and the NW USA provide a good illustration of this interaction. Only between 1% and 5% of the original habitat remains, whilst some 80–90% of the plant biomass comprises neobiota: invasion impacts correlate with the human impact on the ecosystem (Didham et al., 2005).

Some neobiota have large-scale negative effects for other species. Domestic cats (*Felis silves-tris catus*) have spread across the planet with the help of European settlers, as have brown rats (*Rattus norvegicus*). Many of Earth's 179,000 islands now possess one or both of these highly invasive species, and the subsequent toll on native species is heavy (Medina, 2011). In the USA alone, cats now kill between 1.4 billion and 3.7 billion birds, and 6.9 billion and 20.7 billion mammals annually (Loss et al., 2013), having largely replaced native mesopredators in urban environments. Another neobiotic species that restructures its arrival habitat is the Brown Tree Snake (*Boiga irregularis*). It arrived on the Pacific Island of Guam after the Second World War, decimated local bird populations and disrupted the propagation of local tree species that rely on birds for seed dispersal (Rodda et al., 1999).

By contrast with the regional geological record of earlier species invasion events, the humaninduced Anthropocene fossil record of neobiota already is global, comprising a geologically nearsynchronous patchwork of different transplanted taxa that is unrelated to native habitat. The bones of animals transported from Europe to Australasia, for example, will leave a record in landfill sites and elsewhere. Many neobiota have yet greater preservation potential, especially those occurring in marine sites with active sedimentary deposition, like the marine gastropod the 'New Zealand screw-shell', *Maoricolpus roseus*, which has invaded the shallow coastal waters of Australia (Bax et al., 2003).

Neobiotic species have already reset the path of evolution in many if not most ecosystems. Successful neobiotic taxa will be ancestral to future biotas in a unique resetting of global biosphere history.

Parameter 2: Humans dominating marine and terrestrial net primary production

The calculated trophic position of humans, using an index of 1 to 5 from primary producers to apex predators (such as polar bears) places humans at a mid-level (calculated at 2.12), equivalent to that of anchovy and pigs (Bonhommeau et al., 2013). This calculation reflects the range of foodstuffs consumed by humans, with the level being higher in wealthier countries where more meat is consumed (up to 2.57). This method of assessment does not recognise that former top predators, such as sharks and tuna in the oceans, or bears and tigers on land, have largely had their positions appropriated by humans (in this context, see Roopnarine, 2014). Whilst humans may not always, from a strictly trophic analysis, sit at the top of the food chain, a unique feature of the Anthropocene stage of biosphere evolution is that Homo sapiens nevertheless expropriates some 25-40% of the net primary production on planet Earth (Barnosky et al., 2012; Bonhommeau et al., 2013; Vitousek et al., 1986). This change has increased since the human species originated, starting with Homo sapiens' integration into African ecosystems during the Pleistocene, and extending through the global ecosystem during the Holocene. Human consumption now outstrips production in many ecosystems (Rockström et al., 2009; Steffen et al., 2011). Humans have fundamentally modified the terrestrial landscape and marine environment in which ecosystems develop, with some 50% of the land surface being modified for agricultural (about 36%), urban, and other human-dominated purposes (Barnosky et al., 2012 and references therein; Foley et al., 2011, Hooke et al., 2012), whilst approximately three-quarters of the continental shelf seabed has been trawled (Zalasiewicz et al., 2011).

Human farming methods have concentrated biomass into a few domesticated and substantially modified species of animals and plants (Smil, 2011). Through the use of synthetic fertilisers and mechanised equipment these methods have also increased the sum total of large-bodied vertebrate biomass (largely now comprising humans and domesticated animals) nearly an order of magnitude above what the energy made available by photosynthesis alone was able to support prior to humans producing energy from fossil fuels (Barnosky, 2008). Biomass harvested (and wasted) by humans in producing food, livestock feed, natural fibres, and biofuels represents an energy flux of about 300 exajoules (1 exajoule = 10^{18} joules) annually, whereas photosynthesis across the entire land surface generates a total of only about 1100 exajoules in aboveground biomass (Haberl et al., 2013). In addition to the approximately one-third of net primary productivity that humans directly appropriate, we also have to produce an additional ~550 exajoules annually to support the high human population densities found in inhospitable areas (such as deserts and areas with cold winters) and the mechanised agriculture and 'hyper-fertilising' of large parts of the land area, needed to grow enough food to support 7-billion-plus humans and their large-animal commensals (Barnosky, 2014). As a result of hyper-fertilisation, the amount of reactive nitrogen at the Earth's surface has been approximately doubled by means of the Haber-Bosch process, a perturbation of the nitrogen cycle that may be the greatest since Proterozoic times (Canfield et al., 2010) with similar massive transfer of phosphates from rock strata to surface soil (Steffen et al., 2015a).

Parameter 3: Human-directed evolution of plants and animals

Widespread biodiversity loss has resulted from the extension of human-generated 'farmed' ecosystems over wide areas of land (e.g. Haupt et al., 2009; MEA, 2005; Riecken et al., 2006; Stoate et al., 2001), and the development of simpler trophic structures in marine ecosystems (Jackson, 2008; Pauly et al., 1998, 2002). In fisheries, human activities are happening on an industrial scale (McCauley et al., 2015), with 90 million tonnes of wild fish being removed from the oceans legally on an annual basis, whilst 11–26 millions of tonnes are fished illegally (Agnew et al., 2009; FAO (Food and Agriculture Organisation), 2014a). The modern biosphere is unique in that much of the animal and plant variation, and ecosystem structure, is shaped by one species. The earliest characteristics of the transformative nature of humans on ecosystems may be the extinction of the megafauna, beginning in the Late Pleistocene (Burney and Flannery, 2005). Events that contribute to changes in the structure of the biosphere from the Late Pleistocene onwards include the domestication of animals (dogs, pigs, sheep and cattle) and the development of settled farming (see summary in Weisdorf, 2005), whilst in the marine environment the pressure of industrialised fishing has had a major effect on ecosystems (Auster and Langton, 1999 for a review; Pauly et al., 1998, 2002).

The concentration of biomass into a few animals and crops that began during the agrarian revolution has intensified during the 20th century (Smil, 2011), and continues to intensify as population grows from 7 billion towards 9 (or even 11) billion by the mid 21st century (United Nations, 2004, 2013; see also Bradshaw et al., 2014). The change in 21st century population may require a 70% increase in overall food production (relative to 2005/2007) by 2050 (Bruinsma, 2009). This equates to an annual increase of cereal production of 1 billion tonnes, and of meat production by 200 million tonnes (Bruinsma, 2009). Such increase in production could be attained by a combination of closing the yield gap through environmentally sound efficiency increases in agricultural lands currently under production, eating less meat, and wasting less food (Foley et al., 2011). But, these changes are not presently taking place fast enough to accomplish the needed gains in food production (Ray et al., 2013). Without such substantial changes to land use practices, the only solution would be to increase the agricultural footprint, which will even further diminish remaining natural habitats (Sanderson et al., 2002).

Such changes now clearly evident in the Anthropocene biosphere suggest, in magnitude and process, those that took place in the microbial biosphere at the Great Oxygenation Event c. 2.4 Ga (see Figure 1): during that event anaerobic microbes were pushed to environments where oxygen was absent or in low quantities, whilst aerobic organisms became the dominant forms at the Earth's surface. This is echoed in the marginalisation of 'natural biomes' (e.g. those little impacted by humans) by human-dominated biomes, and can be quantified by mapping the 'least (human) influenced' parts of natural biomes. Thus, for the palearctic subtropical and tropical broadleaf forest biome, just 0.3% is still wild (Sanderson et al., 2002). On a global scale, an analysis of satellite imagery has shown that only one-quarter of the Earth's ice-free land surface is still wilderness (Ellis, 2010), although even that is impacted by such global phenomena as increased CO_2 , nitrogen and various pollutants. The remaining areas consist of agricultural, residential and industrial zones and other 'anthromes', that is, areas dominated by human modifications.

This suggests that the world is no longer characterised by 'natural' ecosystems (e.g. lacking significant anthropogenic influence) with humans disturbing them, but rather is characterised by a combination of human engineered and used ecosystems and more or less modified novel ecosystems (Ellis and Ramankutty, 2008; Ellis et al., 2013b; Halpern et al., 2013; Perring and Ellis, 2013). It is important to note, however, that not all anthromes are necessarily as biologically impoverished as large-scale monocultures. Landscapes strongly influenced by humans can be managed in a way that preserves or even expands biological diversity compared with a Holocene baseline, at least regionally (Ellis, 2013; Vos and Meekes, 1999).

Plant and animal breeding constitutes a more conscious change to the biosphere. Humans add to the biosphere many agricultural and horticultural cultivars and animal crossbreeds through techniques such as crossing, preferential selection and, more recently, through Marker-assisted selection (MAS) and genetic technologies (Tester and Langridge, 2010). The Leibniz Institute of Plant

Genetics and Crop Plant Research (IPK) in Gatersleben, Germany harbours some 151,379 genotypes from 3220 species (Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung, 2014). It is estimated that worldwide, 7.4 million such anthropogenic genotypes (plant genotypes modified by humans) exist in collections (Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung, 2014). Human-directed evolution has already greatly changed the relative distribution of genes worldwide, given that an area the size of South America is under direct agricultural use (FAO, 2014b). Currently, only a small proportion of cultivars are actually reproduced out in the field, and agricultural plants and animals tend not to propagate, or survive, beyond the boundaries of fields and farms. However, current attempts to add, via genetic engineering, the more efficient photosynthetic capabilities of some cyanobacteria into higher plants are likely, if successful, to produce new plant forms that can out-compete wild forms (Lin et al., 2014; see discussion in Le Page, 2014); this would mark an enduring change to the Earth's biology, comparable with the evolution of C4 from C3 plants along multiple lineages in the Neogene (see Osborne and Sack, 2012). And, genetic engineering of crop plants to withstand higher levels of herbicides has already stimulated evolutionary changes in the targeted weeds (Gilbert, 2013).

In the animal realm, most megafauna biomass now consists of domesticated cows, sheep, horses, pigs and other animals used by humans, and humans themselves account for the second-largest constituent of megafauna biomass. As a whole, humans and their domesticated stock elevate megafauna biomass an order of magnitude above 'natural' carrying capacity for the planet (made possible by augmenting photosynthetic energy primarily by fossil fuels, as noted above, and see Barnosky, 2008).

Synthetic biology provides another dimension to the Anthropocene biosphere (e.g. Gibson et al., 2008a, 2008b). Although of little ecological significance so far (as specimens are kept isolated in research buildings), the biochemical synthesis of complete genomes according to humanmade plans and the planned creation of whole cells through biochemical synthesis are wholly new developments in Earth history. Equally important are advances in stem cell cultivation and manipulation, giving humans control over basic properties of organism growth (e.g. Doulatov and Daley, 2013). With advances in synthetic biology, biomimicry and robotics, there is the theoretical possibility of living or life-like technological artefacts being released into the environment. The widespread infusion of biology into technology, and vice versa, would represent another unique characteristic of the Anthropocene biosphere.

Parameter 4: The technosphere and the Anthropocene biosphere

Through most of their history humans (*Homo sapiens*) and their immediate hominid ancestors possessed limited capacity to influence the environment around them. This began to change gradually during the Palaeolithic as technology amplified and extended human biological capabilities, first at the individual level, for example in the increased force levels that could be applied using a stone tool and the greater range and lethality attainable via a pointed projectile. And then, over time, at larger scales, for example with the development of agriculture during the Neolithic, and the first road networks about 3000 BC, which, respectively, increased supplies of food and mobility. Technology enabled strong positive feedback loops that changed the relation of technology to its inventors. Thus, technology became an increasingly critical element in a system of artefactual and human components, leading to an increase in the probability of human survival and providing a basis for population growth, which in turn became a factor in the discovery of new technologies (Vasey, 1992). This coupled system could survive only on the basis of the mutual interaction and support of its human and technological parts. For example, roads, mobile (animal) power sources, agriculture and the subsequent concentration of habitation and specialisation of knowledge and practice that technology made possible led to expanded human populations that could not sustain themselves on the basis of individual or clan-size aggregation of people alone. Technology helped people survive and reproduce, and humans increasingly invested their efforts in inventing, fabricating and protecting as possessions their technological implements. Humans and technology became interdependent. Eventually, technology allowed regional populations to grow beyond the individual survival capabilities of their members, and as global population growth accelerated local networks became connected to form a complex system of planetary scale. This system can be conceived as one in which the huge population of humans is embedded within an intricate and increasingly necessary network of supporting technological parts that has been termed the technosphere (Haff, 2014a, 2014b). Alternate views posit that the technologies are embedded within human societies (Basalla, 1988).

For a number of reasons, including the global reach of its networks, its mode of evolution (see below), its correspondingly great separation in scale and complexity from the gene – the unit of biological selection – and its dependence on non-biological processes (e.g. radio waves) and materials (e.g. aluminium and steel), the technosphere can be treated as a novel Earth phenomenon in its own right, i.e. with its own emergent dynamics that is coupled to, but distinct from, the biosphere (Haff, 2014a). In this view, humans and domesticated animals and plants, while biological, are intimately linked into as well as producing the technosphere, within which they can exist in large numbers and outside of which they cannot. Alternatively, noting the critical role of humans and other organisms in the function of technological systems, the technosphere might be taken as an extension of the modern biosphere or perhaps as a parasite on it, given that it consumes quantities of biological products to help sustain its own metabolism. Conversely though, it provides the means to sustain larger numbers of organisms (up to some point) and rapidly transform ecological structure (species richness, evenness, biomass, etc.). In developing the present perspective we treat the technosphere as inextricably linked into the biosphere – in effect parasitising it, but with the potential to become commensal. We return to the relation of technosphere and biosphere below in discussing possible future trajectories of the Earth System.

The emergence of an Anthropocene biosphere is unique in that it arose from the intervention of a single species of hominid (although other, earlier, hominin species possessed technical skills in cruder form (e.g. Semaw, 2000)). It has developed over many millennia as a consequence of the increasingly close coupling between humans and technology, and at an accelerating speed over the past couple of centuries, to become a truly global system. Its acceleration is measured in the rate of increase of matter and energy that it uses, and in the evolution of both hardware (all our material constructions, from which the technofossils of the future are being shed) and software (social and communication systems) that support it (Haff, 2010, 2014a; Zalasiewicz et al., 2014a). Figure 2 suggests the scale of energy that now flows through the technosphere, in comparison with the scales of some important natural energy flows. The speed of the technosphere's evolution, as expressed in technofossil change, is now several orders of magnitude more rapid than that of biological change (even during the 'Cambrian Explosion'), and is accelerating (Zalasiewicz et al., 2014a). And, the extraordinary diversification and increase in disparity of technofossils too, marks a further step change from the unmodified biosphere (see Table 1).

The speed of evolution reflects the fundamentally different nature of evolution of technology and culture with respect to biological evolution. Whereas biological evolution requires mutation and selection at the genetic level across individual generations to produce long-term phenotypic change, technological and cultural traits can be transmitted, alter phenotypes, undergo selection, recombine to create new phenotypes and evolve at speeds up to near real time (e.g. Basala, 1988;



Figure 2. Estimates of power levels in TW (1 terawatt = 10^{12} W) for the technosphere (world energy usage (IEA, 2014)), and several natural systems: the world's rivers (gravitational potential energy loss), lithosphere (planetary-wide geothermal flux (Smil, 2008)), and biosphere (NPP (Haberl et al., 2013 Vitousek et al, 1986)).

Henrich et al., 2008; Ziman, 2000); that is, the existing parts of technological systems, or newly invented parts, i.e. phenotypic information, are manufactured and used directly to construct the next generation of technology. Some material constructions (and software systems) are able to outcompete others to spread around the world: for example, the spread of ballpoint pens, mobile phones, nitrogen-based fertilisers, surveillance systems and the factory production line. The success of the technosphere has enabled a geologically unprecedentedly high population of a single terrestrial vertebrate species – its human component – and of its preferred prey captive species (cows, pigs, sheep). The effects of this evolution have created a globally distributed layer of disturbed or worked soil, the archaeosphere (Edgeworth et al., 2015), and are being imprinted into strata now forming as the signature effects of the Anthropocene. The combination of resulting stratigraphic signals (see Waters et al., 2014 and references therein; Williams et al., 2011; Zalasiewicz et al., 2008) is unlike anything else in the geological record, and signals a major shift in Earth process.

When did the Anthropocene biosphere develop?

Crutzen and Stoermer (2000) proposed the term Anthropocene to designate a geological epoch characterised by the global impact of humans on ecology and geology. The timing of detonation of the world's first atomic bomb at Alamogordo, New Mexico on 16 July 1945 has been suggested as a possible start point for a proposed Anthropocene Epoch (Zalasiewicz et al., 2015). The Alamogordo bomb detonation was followed by more than 30 years of atmospheric nuclear detonations and tests that accumulated a global signature of radiogenic isotope fallout. This, together with the disruption of the land surface and near surface via detonations (e.g. see Zalasiewicz et al., 2014b and references therein), may serve as a proxy of biospheric change. However, the exact placement of any chronostratigraphic boundary is decided as much for the pragmatic recognition of stratal units, as for the planetary significance of any particular instant of time. In contrast, identifying a definitive temporal boundary when the evolution of the Anthropocene biosphere occurred



Figure 3. Major events in the development of the Anthropocene biosphere and the chronology of its four unique components identified here: (1) human transported neobiotic species (beginning with *Homo erectus* at c. 1.8 Ma); (2) human expropriation of net primary production (accelerating since the 1950s to reach levels of between 25 and 40% of NPP); (3) human-directed evolution of plants and animals (commencing with the extinction of the megafauna from c. 50 Kyr); (4) Technosphere (beginning with stone tool technology at c. 2.6 Ma). Also plotted are major 'evolutionary' steps in human abilities to influence the biosphere: the origins of language are hotly debated (but see, for example, Nichols, 1998).

is less essential. As with the development of metazoans between 700 and 541 million years ago (e.g. Erwin et al., 2011), steps leading to an Anthropocene biosphere stage have unfolded over a long period of time (several million years), and their record is diachronous between continents, originating first in Africa, and then extending through Asia, Europe, Australasia, the Americas, Oceania and finally Antarctica: this last phase began just over a century ago with the exploratory expeditions of the late 19th and 20th centuries (e.g. Mawson, 1998, reprinted from 1914). The origin of the global signal of neobiota begins with the spread of early human species out of Africa more than 1 million years ago (Figure 3). The origin of the technosphere and of significant hominid modification of the landscape lies with the origin and development of tool use in Africa, a technology whose origins is shared with great ape cousins including chimpanzees and gorillas, and which extends back at least 2.6 million years (Semaw, 2000). The development of 'anthromes' and of the concentration of biomass into selected plants and animals has a history extending back to the early Holocene (Ruddiman, 2003).

In identifying the most important development in the evolution of a metazoan stage for the biosphere, one could look to the Precambrian–Cambrian boundary 541 million years ago, defined at the appearance of a particular trace fossil *Treptichnus pedum*, that marks a fundamental change in animal behaviour exhibited by worms with bilateral symmetry moving through sediment (Landing et al., 2013 and references therein). With the development of an Anthropocene biosphere one might look to the development of metro systems beneath mega-cities – giant human trace fossils, beginning with the Metropolitan Line in London in 1861, and a possible signal of a major change in animal behaviour (in this case the mass transit of humans and human ideas, associated with industrialisation: see Williams et al., 2014). More generally, the 'Great Acceleration' of a number of environmental parameters starting more or less in the mid 20th century (Steffen et al., 2007, 2015a) may be regarded as a wider reflection of the change in Earth state we discuss here. No matter where a boundary might ultimately be placed, we contend that the anthropogenic modifications to the planet already are on par with the changes leading up to the Cambrian Explosion (cf. Wolff, 2014), and that future developments (technological and social) may be yet more substantial.

The future of the Anthropocene biosphere

The further evolution of the biosphere depends critically on both social behaviour and interactions of humans on multiple scales (individuals, families, villages, cities, online communities and social networks, companies, states and supranational institutions) and on the development of technology. The technosphere is a non-anthropocentric framework which specifies physical constraints on the dynamics of a global system of humans plus technology, but it is mute on the mechanisms of how that system evolves. The theory of anthroecology, however, can address exactly the question of how such systems evolve (Ellis, 2015). In anthroecology theory, the global force of human societies (sociocultural systems) that is transforming the Earth System and the biosphere is conceived of as a 'human system' analogous to the climate system. As with the climate system, which shapes the dynamics of energy and material flow across the atmosphere, hydrosphere and other Earth spheres, human systems shape the dynamics of energy, material, biotic and information flow across the biosphere, the anthroposphere (human societies and their material cultures) and other Earth spheres. The dynamics of the human system and the anthroposphere are driven primarily by changes in social organisation, exchange relationships, ecosystem engineering, and energy systems, and by feedbacks with other Earth systems. Over the long-term, changes in the patterns and processes of human systems as a force shaping the Anthropocene biosphere are the product of sociocultural evolution of human sociocultural niche construction (Ellis, 2015). Social behaviour and interactions are subject to rapid evolution and changes due to events, value systems, economic conditions, demography and other factors. New frameworks of global thinking, such as the need for environmental protection, sustainability, post-anthropocentric approaches and the Anthropocene idea itself, have arisen in recent decades and have begun to influence individual and collective behaviour (UN Millennium Development Goals, UN biodiversity targets etc.; see for example, Steffen et al., 2015b). A coherent response of the technosphere to changes in behaviour occurring amongst its small parts requires that small-part behaviour be collective (i.e. extending over technospheric scale; see discussion of rule of reciprocity in Haff, 2014b). To the extent that the impact of atmospheric warming on human wellbeing is a global force, it has the potential to exert large-scale influence on human behaviour and thus on technospheric dynamics in a way that reduces the effects of the driving force. The growth of large-scale social movements that act to diminish the impact of such adverse global forcings would represent the emergence in the technosphere of a kind of global thermostat (Haff, 2014b; see also Kellie-Smith and Cox, 2011).

The technosphere currently remains dependent on its human component, and if that component fails catastrophically and terminally for any reason, then the technosphere will collapse. Certainly, the current global trajectory of human population growth, materials and energy use and associated environmental feedbacks seems unsustainable, not least because the technosphere is much less effective in recycling its component materials than is the biosphere (Haff, 2014a). Thus, the increasing atmospheric CO₂ burden is a reflection of an inability to recycle the amount of carbon that is released by burning fossil fuels. If the technosphere were to collapse what would remain is physical evidence of its history, as a preserved stratigraphic signal in the rocks. This will include a short-lived event bed of 'urban strata' and related deposits, recording rapid technospheric evolution and deep roots via preserved tunnels, mines and boreholes; a climate perturbation that might last 0.1–0.2 Ma, perhaps comparable with the Palaeocene–Eocene Thermal Maximum (see Haywood et al., 2011 for a summary); and a permanent reconfiguration of the biosphere (and hence of the fossil record) resulting from the effect of trans-global species invasions and a moderate- to large-scale mass extinction event. If catastrophic failure happens today, then the changes may broadly equate to an epoch-level event (though with some quite unique features) of the deep time record; if it develops in a more gradual way over the next century or two, then the changes will likely be of period- to era-scale, provided there is a continued accumulation of substantial modifications to the biosphere (e.g. Barnosky et al., 2011, 2012). A comparison might then be made between the Anthropocene stage of biosphere evolution and some of the 'short-lived' (from a geological perspective) biosphere innovations of the past, such as the Ediacaran biota, though on a much more compressed timescale. Nevertheless, after this, if geologic history is a guide, and even if humans never recovered their present level of influence over Earth function, the biosphere will recover into a new pattern of species groups over the next 3-10 million years (e.g. see Hart, 1996 and references therein), in which case the manifestation of the Anthropocene biosphere would be as a trigger of major biotic change.

Or it may be that future technological change will favour more or less continued growth and development of a distinctive Anthropocene biosphere, with technology providing a means of solving some of the problems associated with its explosive development (Sharp, 2014). These might include straightforward steps such as the increasing deployment of environmental monitoring technology (Hanrahan et al., 2004); agroecological innovations, large-scale ecosystem regeneration and restoration projects; design of cities and the food system as bio-diverse ecosystems; full recyclability of materials; expansion of non-carbon-based energy sources; and more effective means of resource allocation and conflict resolution between different communities (Falk, 2014a, 2014b); as well as risky planetary-scale emergency measures such as geoengineering to lower mean global surface temperature (Crutzen, 2006). Aimed at paving the way for a sustainable Anthropocene Earth, some combination of these and other approaches may result in a technosphere that is stably integrated with the biosphere in a truly commensal relationship, producing a 'techno-biosphere' where the two are virtually inseparable but sustainable and co-evolve, rather than the present situation, in which the technosphere in effect is parasitising the biosphere. Should continued anthropogenic innovation result in a commensal techno-biosphere, the probability of biosphere (or technosphere) collapse is likely to be greatly reduced. In that case, the four characteristics that we identify as unique to the Anthropocene biosphere's existence would potentially herald a new era in the planet's history which would have the potential of persisting over geological timescales.

Conclusions

The Anthropocene biosphere is characterised by four unique physical components: (1) a global signal of marine and terrestrial neobiota that in many cases have displaced indigenous forms, that

have often taken advantage of the modified anthromes of humans, and that have reset the structure of many terrestrial ecosystems and that are profoundly modifying the marine realm; (2) a single species, Homo sapiens, dominating the net primary production and energy flow; (3) the humandirected evolution of plants and animals; and (4) the increasing interaction of the biosphere with an ever more rapidly evolving technosphere. Currently the degree of change induced by humans would show in the rock record as a boundary broadly comparable in scale with those that mark epoch/series boundaries in the geological record, albeit one with some entirely novel geological characters. We are now living through a phase of rapid acceleration in many geologically significant processes, notably as regards climate, ocean chemistry and biodiversity, and the changes that already have occurred in the Earth System approach those evident in the lead-up to the Cambrian Explosion. Hence, current trends, if maintained, would likely result in period- or even era-scale changes to the Earth System. However, sustained evolution of an intertwined biosphere and technosphere will require a shift from the present situation of the technosphere essentially parasitising the biosphere, to a commensal relationship between the two. Should that happen, anthropogenic influence would be responsible for a lasting change to the Earth System, initiating a new trajectory for the biosphere that could last over geological timescales.

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