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The development of Anthropocene biotas

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Abstract

Biodiversity has always responded dynamically to environmental perturbations in the geological past, through changes to the abundances and distributions of genes and species, to the composition of biological communities, and to the cover and locations of different ecosystem types. This is how the 'nature' that exists today has survived.   The same is true in the Anthropocene. The entire planet surface has been altered by humans, ranging from direct vegetation transformation and removal of most of the world's megafauna, through to atmospheric changes in greenhouse gasses and consequent climatic changes and ocean acidification. These anthropogenic perturbations have led to the establishment of genes and species in new locations, thus generating novel communities and ecosystems. In this historical context, recent biological changes should be seen as responses to multiple drivers of change, rather than being a problem *per se*. These changes are the means by which the biosphere is adjusting to and will ultimately survive the Anthropocene. Thus, management and conservation of the biological world, and our place in it, requires a transition from trying to minimise biological change to one in which we facilitate dynamism that accelerates the rates at which species and ecosystems adjust to human-associated drivers of change.

Key words: Anthropocene, biodiversity, biological invasions, climate change, conservation, land use change

1. Introduction

Humans are generating novel combinations of physical and biological conditions across the world
(Steffen *et al.* 2011, Ellis 2018). These perturbations include: the removal of most terrestrial
megafaunal diversity and over-exploitation of fisheries; the conversion of more than a third of the
world's terrestrial ecosystems for agriculture, livestock (replacement megafauna) grazing and human
dwellings; doubling global nitrogen fixation and the release of a wide array of novel chemicals into
the environment; and the transfer of species around the planet at an unprecedented rate. Other
rapid perturbations also include the release of greenhouse gasses, especially CO_2, resulting in altered
photosynthetic rates for plants, climate change, and ocean acidification. Both the high speed of
change (e.g., rate of atmospheric CO_2 increase) and the destination (e.g., potential future CO_2
concentrations not seen for 20 million years) are important to biotic responses, as well as the fact
that multiple pressures are acting together (Sala *et al*., 2000, Thomas *et al.* 2004, Hoegh-Guldberg *et
al.* 2007, Chen *et al.* 2011). The global extent of these changes means that essentially every location
on the Earth has already been influenced by human activity, save for an unknown proportion of
microbial communities within geological substrates. The result has been the decline and
extermination of some genes, populations and species, a loss which has been characterised as 'the
biodiversity crisis'. However, the new anthropogenic conditions simultaneously favour other genes,
populations and species, increases of which can be thought of as biological gains. These gains, as
well as losses, are so extensive that it is no longer possible to disentangle human and non-human
contributions to gene frequencies, geographic distributions, the composition of biological
communities or ecosystem functions (Thomas 2017, Bleige Bird & Nimmo 2018). Humans and
human-related activities are integral to the biological processes of the Earth system, arising from the
unlikely evolution and then social and technological development of the human ape, ushering in the
Anthropocene (Ellis 2018).

45   Despite the prevalence of human influences, the fundamental processes that underpin

biological change remain qualitatively unaltered across the world's surface – at least, so far.

Changes to the abundances and distributions of genes, populations and species are still achieved by

the birth, death and movement of individuals, and their interactions determine community

composition and ecosystem processes. They are simply doing so in the context of human

50   modification of the physical and biotic environment (including humans both influencing the variation

that comes into existence and acting as selective agents), reshuffling the Earths biotic 'building

blocks' as a faster rate than usual.

From an evolutionary perspective, individuals of each organism (bearing different

combinations of genes and capacity for plasticity) still vary in their survival and reproduction in

55   different environments, albeit in human-modified ones. Mutation, recombination, gene flow,

hybridisation (i.e., gene flow between less closely-related entities) and horizontal gene transfer

determine the variation available for evolution to act upon in new anthropogenic environments

(Carroll *et al.* 2007). This includes any genetic variation accidentally or deliberately generated by

humans, and recognises that the human animal is an important selective force. Evolutionary change

60   can also be thought of as operating at a range of micro- to macroevolutionary levels: from mutations

and changes in gene frequencies within populations and metapopulations, to the relative success or

failure of evolutionarily distinct populations and races within species, the success or failure of

different species, through to differences in the origination and extinction rates of different clades or

functional types. Thus, declines and extinctions, and also the success of alleles, populations, races,

65   species and higher taxa – all of which have been observed in the Anthropocene – represent

evolutionary changes taking place at multiple taxonomic, spatial and temporal scales (e.g., Jablonski

2001, Thomas *et al.* 2001, Isaac *et al.* 2007, Barnosky *et al.* 2011, Hill *et al.* 2011, Bridle *et al.* 2014).

These processes (generation of variation and selection acting upon it) are fundamentally the same as

they have been in previous epochs, whilst accepting that the rates of change in the Anthropocene

70   are exceptionally high.

In what follows, I am attempting here to extract broad biological generalisations, rather than to describe the situation in every location or region. Regions differ in their biological histories, climates, geologies, and human social and economic situations, resulting in a wide variety of specific changes. I am also not passing any value judgements, at least not until section 6 of the paper! Our human opinions about the relative worth of different species, about the ecosystem services we derive from historic versus novel ecosystems, and about the importance of diversity levels on different spatial and temporal scales are societal issues for which there cannot be universal 'correct' answers. Whatever our individual perspective, biological diversity (with both inputs of new species arriving and the disappearance of species that were present previously) is changing at all spatial scales, and dynamic change is going to continue. It is our attitudes and responses to these changes, and how we might attempt to influence future trajectories of change, that are a matter for debate. Anthropocene change is commonly perceived as being characterised by biological collapse, with an emphasis on the need for humanity to 'save biodiversity' and the ecosystem services that it provides (e.g., Barnosky *et al.* 2012, Pimm *et al.* 2014, Cavicchioli *et al.* 2019, Dinerstein *et al.* 2019, IPBES 2019). I agree that we should. However, we have to work with biological, human and physical planetary systems as they are, rather than as we might wish them to be. My focus here, therefore, is on the dynamism of biological systems, and hence that maintaining biodiversity in the long term requires us to embrace rather than reject or repel many of the processes of biological change (Thomas 2017). To this end, sections 2 to 5 represent my interpretation of biological changes that have taken place in response to environmental perturbation in the recent and more distant past, while section 6 discusses the implications of these changes for the conservation of biodiversity.

2. Biological communities are especially dynamic during periods of environmental change

The Pleistocene climatic switchback between frigid glacial conditions (such as the last glacial maximum, ~26,500 years ago) and relatively warm interglacials (as for the last ~11,700 years of the

Holocene) has generated drastic and repeated changes to the composition of local biological communities and regional biotas, during which some species have been extirpated (extinction at the local or regional scale) while others have arrived and their populations grown (Atkinson *et al.* 1987, Hewitt 2000, Davis & Shaw 2001). There are potential lags both in times to extirpation ('extinction

100   debt') and the arrival and increases of species that will subsequently thrive under the new conditions ('colonisation deficits') (Davis 1989, Menéndez *et al.* 2006). There are also slow community and ecosystem development processes (e.g., population dynamics of long-lived trees, soil development), such that we observed trajectories of community change over decades to millennia (Miettinen *et al.* 2017, Talluto *et al.* 2017, Esquivel-Muelbert *et al.* 2019). Lags are difficult to determine precisely,

105   partly because of the temporal resolution and spatial incompleteness of paleo-records, and partly because it is hard to distinguish between delayed responses to an earlier perturbation and immediate responses to a later stimulus. Nonetheless, delays can be substantial. For example, the distributions of some European tree species may not have fully 'caught up' with climatic changes that took place over 10,000 years ago (Svenning & Skov 2004). At a global scale, the relatively cold

110   2.6 Ma of the Pleistocene has seen both species-level extinctions of warm-adapted species, such as frost sensitive trees that lived in Europe during the warmer Pliocene (Svenning 2003), and diversification of cold-adapted and colonising lineages, including lupins in the Andes (Hughes & Eastwood 2006). Changes in precipitation played an equally important role, especially in the tropics. Thus, the Quaternary (Pleistocene plus Holocene) and earlier episodes of climate instability

115   (including the Paleocene-Eocene Thermal Maximum ~55 Mya; Wing *et al.* 2005) have consistently been associated with high rates of distribution and community composition changes at local, regional and larger scales. Today, rates of warming are even faster, at a global scale.

More generally, biological changes within any given region – be that an island, landscape, seascape, or present-day human administrative unit such as a county or country – are generated by

120   changes to the physical environment, the arrival of new species from outside, and the disappearance of species that are no longer able to survive under the new physical and biological conditions.

Within each region, the populations of species present develop altered abundances and local distributions (as a result of birth, death and movement), evolve in relation to the new physical environment, and co-evolve in relation to one another. Delayed arrivals, delayed extirpations, and

125   feedback loops involving community composition, ecosystem processes and evolutionary adjustments generate lags in the system (Jackson & Sax 2010).

It is helpful to consider the parallels between evolutionary and ecological change (Vellend & Geber 2005, Rosindell *et al.* 2015, Vellend 2016). The rate of evolutionary change in a population commonly increases with the strength of selection, with the level of relevant genetic variation within

130   that population, and with gene flow that increases the variation that is available for selection to act on. This is uncontroversial. The same is inevitably true at the community level: changes to the identities and relative abundances of species within communities (equivalent to changes in allele frequencies, or rate of evolution) accelerate with the rate of environmental change (equivalent to the strength of selection), and also increase with the diversity of species within the initial community

135   (equivalent to the standing genetic diversity within a population) and with the immigration of new taxa (equivalent to gene flow).

Note that compositional (i.e. community) change is not equivalent to ecosystem change, and the functional attributes of an ecosystem may either be stabilised (e.g., a forest remains a forest through increases in drought-resistant species) or destabilised by community changes (e.g., a forest

140   becomes a savanna through increases in drought-resistant species that are flammable). This is again equivalent to evolutionary change in a population, where selection, gene flow and evolution at particular loci may provide resilience and stability to the rest of that population's genome (adaptive introgression), or where gene flow may effectively replace (swamp) the previously-resident genome (Ellstrand & Rieseberg 2016). Thus, an ecosystem type may be stabilised (e.g., maintained as forest)

145   or disrupted (e.g., becomes another ecosystem) by changes to the species composition of a biological community, and a 'locally adapted' population type may be stabilised or disrupted

(replaced) by the arrival of new alleles, depending on circumstances. However, in each case, the biotic change is normally generating populations, communities and ecosystems that are now 'better adjusted' to the *new* physical and biological reality of the location that is under consideration. I am

150   using the term 'adjusted' as a very broad term to refer to any alteration, be that evolutionary or ecological, which increases some definable metric of individual, population or ecosystem performance, such as individual fitness, population growth rate or primary productivity.

Whilst mutation is evidently central to the evolution and ecology of life on Earth in the long run, the immediate response to rapid environmental change is predominantly achieved by re-

155   arrangements of those elements (genes and species – the latter can be thought of as bundles of genes) that existed previously. Changes to the abundances of alleles and species in space and time are what permit the global biotic system to adjust to rapid environmental change, generating successions of new populations, communities, and functioning ecosystems. This means that certain genes and species have been rare or localised under some environmental circumstances but

160   relatively common and widespread at other times, generating overall flexibility and resilience of biological systems at regional and global scales. For example, European warm-adapted tree species become confined to climatically-suitable refugia in southern Europe during glacial maximum conditions but expand during interglacials (Huntley & Birks 1983, Bennett *et al.* 1991), whereas cold-adapted bird species do the reverse, becoming confined to relatively cold refugia at high elevations

165   and in northern Europe during warmer interglacial conditions (Smith *et al.* 2013).

In conclusion, all past biological communities and ecosystems have been constructed dynamically from combinations of genes and species. This remains the case today, and all future biological systems will be constructed from the descendants of today's species, unless humans generate entirely new life forms.

170

3. Plus ça change in the Anthropocene

The new biological and physical reality of the Earth surface includes humans, who have collectively exterminated megafauna, increased atmospheric CO_2 concentrations, changed the climate and increased the acidity of the oceans even in the remotest locations. The existence of areas without

175   human influence passed into history long ago. All notions of wilderness, protected areas, saving a 'half Earth' for nature, or rewilding must be seen in this context. Our human abundance, consumption and functional capabilities (including cultural development and desires) have triggered environmental change everywhere.

The basic processes by which biotic systems have responded to these changes remain broadly

180   similar, however, with inputs and departures of genes and species at any given location, and new interactions then taking place among the novel set of organisms that establish in that location (figure 1). Some genotypes, populations, entire species (in endemic-containing regions) and ecosystem types are extirpated as a result. Humans are also instrumental in biological gains. Species have colonised new areas because the human-altered environment is more suitable for

185   them. For example, the climate has become more suitable in new locations for many warmth-associated species, as evidenced by polewards range expansions of a majority of temperate zone animal species (Parmesan & Yohe 2003, Hickling *et al.* 2006, Chen *et al.* 2011), and new human-derived habitats have become available for grassland and disturbance-dependent species in regions that were previously forested. Species have also spread because humans actively accelerate the

190   rates at which species immigrate into new areas through accidental and deliberate introductions. A wide range of human-associated and non-human changes to the environment can trigger new arrivals and disappearances, and figure 1 simply illustrates three major anthropogenic impacts. As with Pleistocene perturbations of the climate, there are time lags in the delayed arrival and extirpation of genes and species, as well as ecological and evolutionary feedbacks (Jackson & Sax

195   2010). Even if all humans were to disappear tomorrow, the past human-mediated transfer of

species between continents, for example, will still affect the biological future of every region on

Earth for an indefinite period. The Anthropocene represents multiple trajectories of change, not a

new categorical state.

FIGURE 1 NEAR HERE

200   The re-mixed sets of species interact ecologically and evolve in relation to the new physical

environment, and co-evolve in relation to one another. Local evolution, population declines,

population increases, distribution changes, changes to communities and regional biotas, and

changes to ecosystems are all being observed within novel anthropogenic environments (e.g., IPCC

2014, Thomas 2017). As during previous epoch-changing events, the net result is generating

205   populations, communities and ecosystems that are more resilient under the new, albeit transient,

conditions than were the biological communities that preceded them (the previous sets of

organisms were in most cases better adjusted to the previous non-anthropogenic set of conditions).

Some of these changes are regarded as beneficial by humanity, and some negative. For example,

the development of pollinator communities associated with urban gardens and ruderal communities

210   is typically seen as beneficial, as are increases in specific insects that pollinate widespread crop

plants, whereas declines in other pollinators because of land use changes and pesticides are seen as

negative (Hanson 2018, Baldock *et al.* 2019; Powney *et al.* 2019). But this is a human perspective.

The net result of both the gains and losses is an improved match between the distributions and

abundances of pollinators and the current human-altered environment (including nectar and pollen

215   resource availability, places to nest or otherwise reproduce, and insecticides as one aspect of the

chemistry of the modern environment), not a failure of basic biological processes.

4. '*Local diversity stays about the same, regional diversity increases, and global diversity declines*'

(Thomas 2013a)

220   The net balance of the human-driven gains and losses depicted in figure 1 depends on the temporal

and spatial scale considered. These differences emerge because patterns of colonisation and

extirpation themselves vary in space and time. There are different spatial and temporal signatures

of key processes, such as human-caused habitat change, over-exploitation (including megafaunal

extinctions), humans acting as a vector for the transport of species around the world and,

225   increasingly, climate change. Scaling difference are also linked to the *relative* importance of

different population dynamic processes at different spatial scales (Thomas & Kunin 1999). Changes

to the number of species at a very local scale primarily depend on the birth, death and movement of

individuals, while (meta-) population-level colonisation and extirpation are also important at

regional scales, as are extinction and speciation at the global scale. Similarly, patterns of change

230   may vary through time, depending on the durations over which extinction debts, colonisation lags

and community reassembly take place. These differences make it possible for diversity to increase

at some spatial scales and decline at others (McGill et al 2015) and to increase on some time scales

and decline at others, depending on the temporal schedules of arrivals and departures. Diversity

can, therefore, decline in response to some human-mediated perturbations at first and then

235   increase later as species gradually colonise novel environments (transient diversity troughs), or *vice*

versa if initial arrival rates exceed subsequent extirpation rates (Suggitt *et al.* in press).

Consider the evidence, first in relation to spatial scale. An increasingly large literature

suggests that the *average* number of species in local biological communities (i.e., for relatively small

sample areas) has been fairly stable or has even increased slightly in recent decades (Vellend *et al.*

240   2013, 2017a, Dornelas *et al.* 2014). In other words, the rate of arrival of new species matches the

rate of disappearance of others when averaged across many sites, although some individual sites

exhibit net increases while others show declines. The exception is when there is a 'one-off'

reduction associated with major land use change or intensification (Newbold *et al.* 2015). These

observations (little or no net change despite one-off diversity reductions) are compatible because

245   only a modest percentage of the world's land surface experiences fundamental diversity-reducing

land use change each year, and the transformed lands may then gradually accumulate species that are suited to the new environments. Inputs to these novel habitats include, for example, the colonisation of urban areas by former cliff-dwelling birds, the establishment of disturbance-dependent communities of plants and insects, and the range expansions of introduced species.

250 Given time, derived environments can potentially support substantial numbers of species, such as 'semi-natural' calcareous grasslands (livestock pastures) in parts of Europe, domestic parks and gardens in many parts of world, and the development of reefs on human structures in marine systems. Anthropogenic climate change can also contribute to the growth of local species richness whenever range shifts take place along species-richness gradients, for example when the expansions

255 of warm-associated species outnumber the retreats of cold-associated species (e.g., Menéndez *et al.* 2006, Chen *et al.* 2011, Thomas 2017, Vellend *et al.* 2017b, Suggitt *et al.* in press). The trickle of species accumulating in novel environments and under altered climates counteract (but do not necessarily match) the more easily attributable losses taking place in the subset of localised areas where land use transformation or intensification is taking place.

260   In contrast, if we increase the sample area considered, the number of species has substantially increased in recent centuries for most regions of the world (e.g., per country- or state-sized area of land, or per island group; Sax *et al.* 2002, Sax & Gaines 2003, Ellis *et al.* 2012, McGill *et al.* 2015, Vellend *et al.* 2017b). At this larger spatial scale, the number of species establishing has exceeded the number of extirpations and extinctions, and hence the 'input' arrows are shown as wider than

265 the departure arrows in figure 1. These increases have predominantly been associated with the formation of novel anthropogenic habitats within each region, which provide new opportunities for colonisation, and with the deliberate and accidental transport of immigrant species (Seebens *et al.* 2017).

However, humans have been responsible for reducing the total number of species (and

270 presumably unique alleles) on Earth. At this very large spatial scale, the rate of extinction has

exceeded the rate of speciation in recent centuries, for animals at least (Barnosky *et al.* 2011, Pimm *et al.* 2014, De Vos *et al.* 2015, Humphreys *et al.* 2019), despite a human-associated acceleration in the speciation rate (Thomas 2015, Bull & Maron 2016).

A consistent pattern is emerging. Measured species richness change shows a hump-shaped

275   relationship with increasing 'plot' size. Local diversity has remained relatively stable (increasing in some locations, declining in others), regional diversity has generally increased, and global diversity has declined (Sax & Gaines 2003, Thomas 2013a, McGill *et al.* 2015, Vellend *et al* 2017b). These conclusions are based on observed changes to the numbers of species, given that this is the information that is most readily available. Nonetheless, the same principles of the arrival and

280   disappearance of genes will apply and, since species bear genes, we might generally expect similar results (considering total genetic variation at the assemblage level). There are inputs of new genetic variation to biological assemblages through gene flow, as well as through the establishment of colonising species. Losses are associated with selection and the extirpation of individual alleles, populations and species. Newly-arriving species might initially be expected to hold relatively low

285   within- and among-population levels of variation arising from founder bottlenecks, but the addition of new species (especially unrelated ones from distant continents) also introduces genetic variation and functions not present in the original species within a particular site or broader region. At a global scale, allele extinction (associated with population, race and species-level extinctions) almost certainly exceeds the establishment of novel mutations. Even so, the many examples of populations

290   undertaking evolutionary adaptation to anthropogenic environments imply that novel mutations are also establishing (Carroll *et al.* 2007, Thomas 2017). Thus, I hypothesise that there is also likely to be a humped-shaped relationship for total genetic diversity, with a net loss at a global scale, net increase at a regional level (mainly associated with the net increase in species richness and the taxonomic diversity of colonising and imported species), and intermediate change at local scales.

295   Net genetic diversity will undoubtedly have increased in some locations and declined in others, at a local scale, but insufficient data are available to deduce the overall average direction of change.

Contrary to the common perception of biodiversity decline, the positive trend in the number of species per region is very likely to continue as the processes that have driven the growth of regional richness are still operating (international transport more so than ever), notwithstanding

300 that there will be exceptions in some regions. The postulated slight upwards trend in species richness at a local scale can also be expected to continue. There is generally a positive correlation between the size of the regional pool of species and the species-richness of local communities (Cornell & Lawton 1992, Ricklefs & He 2016), such that recent increases in regional diversity place 'upwards pressure' on the average species richness of local communities. However, fresh land

305 conversion and intensification will generate 'downwards pressure' on those locations directly affected (Newbold *et al.* 2015), and hence any possible growth in local richness is expected to be much slower than that of regional richness. At a global scale, species extinctions are expected to continue to exceed speciation (Thomas *et al.* 2004, Pimm *et al.* 2014), but not necessarily for higher plants (Thomas 2013b, 2015, Humphreys *et al.* 2019).

310

5. The composition of communities

Differences in the identities of species and genetic variation at different locations (beta diversity) are equally important, and the scaling effects are reminiscent of those for species richness. The transport of species has reduced beta diversity at a global and continental scales: biotas more than,

315 say, 2,000 km apart are usually more similar to one another than they used to be (Winter *et al.* 2009, McGill *et al.* 2015, Capinha *et al*. 2015), and the same must be true for the unique genetic variation associated with these species. For example, Great Britain and New Zealand share many more species than they did 1000 years ago, and the extinction of New Zealand endemics has also eroded the difference.

320   In contrast, beta diversity has increased *within* each region for two reasons. First, 'naturally

colonising' and introduced species have disproportionately established populations in human-

transformed ecosystems (Hobbs *et al.* 2006, Maskell *et al.* 2006, Chytrý *et al.* 2008, Beniak *et al.*

2015) over the course of recent centuries and millennia, leaving higher proportions of 'native'

species in less disturbed locations, thereby contributing to increased beta diversity between

325   ecosystem types (Hiley *et al.* 2016, Newbold *et al.* 2016; although this can reverse with extreme

intensification, Birks *et al.* 2016, Thomas 2017, cf. McGill *et al.* 2015). Secondly, despite the linguistic

implications of terms such as 'invasive species', immigrant 'non-native' species tend to have smaller

geographic range sizes within regions than do the longer-established 'native' species, at least for

arrivals within the last 500 years (Williamson *et al.* 2009, Thomas & Palmer 2015). This again

330   increases compositional differences between locations. Within-region beta diversity of genetic

variation is also likely to have increased, linked to the species-level differences and to different

selection pressures operating in anthropogenic versus less disturbed ecosystems. Quite how beta

diversity is changing at very local scales is less clear, but there is some indication that it could be

declining (McGill *et al.* 2015). If so, we also see a hump-shaped relationship for beta diversity

335   change, with the greatest increases taking place at intermediate (within-region) spatial scales, and

declines at very local (potentially) and global scales.

        Turnover in the composition of biological communities through time is also highly relevant,

and is known to have accelerated during periods of rapid environmental change, in the Pleistocene

and before (see above). It is no surprise, therefore, that the rate of turnover in species composition

340   in any given location or region has increased in recent centuries (Vellend *et al.* 2013, 2017a,

Dornelas *et al.* 2014, 2019). This is likely to be true at all spatial scales (McGill *et al.* 2015), even at

the global scale, where both extinction and speciation rates have apparently accelerated (Mallet

2007, Barnosky *et al.* 2011, Pimm *et al.* 2014, De Vos *et al.* 2015, Thomas 2013, 2015, Bull & Maron

2016, Humphreys *et al.* 2019). Genetic turnover is also likely to have increased at all spatial scales,

345   with increased selection in favour of adaptations to novel environments, allele extinction (associated

with population, race and species-level extinctions), gene flow (including establishment of species in new locations), and the establishment of novel mutations which provide increased fitness in anthropogenic environments. We can confidently predict that species and gene turnover will continue apace in coming decades, as they respond to multiple human-associated drivers of change

350   – and show lagged responses to events that have already taken place.

6. Managing dynamic systems

Human actions will continue to affect the establishment as well as the loss of biological diversity at all spatial scales in the future, and it is inevitable than we will wish to manage biodiversity at local,

355   regional and global scales to minimise risks of harm and maximise potential benefits, including the benefit of simply enjoying nature. However, this is challenging when nature is dynamic (Jackson 2016), and when human-caused changes to the atmosphere, land, freshwaters and seas are in the process of accelerating change. It is not straightforward to determine priorities in a dynamic system (figure 1), given that different individuals and interest groups will take different perspectives and

360   imagine different futures.

If nature was 'nearly static' relative to human lifetimes and cultures, it might seem appropriate to define environmental and biodiversity 'baselines', representing either the current condition of ecosystems or some historical state that could in principle be maintained. But this approach eventually fails in a dynamic system. Baseline thinking implicitly holds that all ecological

365   and evolutionary change up to the baseline date or condition is 'good' (including the immigration of species and genes up to that time), whereas all subsequent deviations (including the immigration of additional species and in some instances genes) are deemed to be undesirable, in the sense that they represent departures from that 'preferred' state. This is philosophically and practically flawed. It is inevitable that every location will gradually depart from its baseline, without necessarily

370   degrading the local, regional or global system, especially during episodes of rapid climate change. Such is the history of life on Earth.

To illustrate how these social attitudes can play out, England has adopted several biodiversity indicators representing changes to the status of priority 'native' species and one representing the spread of selected 'non-native' species (Defra 2018). Both the decreasing trend for 'native' species

375   (most of which have colonised Britain in the last 12,000 years) and increasing trend for 'non-native' species (which have arrived in the last 500 years) are deemed to be negative. The net result is a near-universal perception that biodiversity is declining in Britain (it is by some metrics), even though it is unequivocally true that the total number of species in Britain is increasing, if we add all losses and all gains together (Roy *et al.* 2014; see above). The rate of arrival and establishment of species

380   exceeds the rate of extirpation of others. This is not just a UK-centric perspective. For example, Sala *et al.*'s (2000) renowned global scenarios for future biodiversity explicitly exclude gains of 'exotic' species and omit biological communities that are 'maintained by regular human intervention', thereby implicitly assuming both that there is a correct distribution of species and that contributions of anthropogenic ecosystems to biodiversity are negligible (despite the fact that all ecosystems are

385   somewhat modified). Neither assumption is consistent with the past, recent and future dynamics of species and ecosystems during a period of environmental change and human influence.

This apparent preference for what we already have, or used to have, is reflected in the UN Sustainable Development Goals, the Convention on Biological Diversity Aichi targets, the legislation of individual countries, and the mission statements of numerous global and national NGOs and

390   corporations. In contrast, the same conventions, legislatures and organisations typically refer to recently-successful species in condemnatory language (for example, as weeds, pests, adventives, non-natives or invasive aliens) and urge individuals, institutions and nations to take action against them. The establishment of successful species in new locations is commonly interpreted as further evidence that the Earth system is departing from a more desirable state, located somewhere in the

395   historical past. However, the reality is that we always have been, are, and will continue to live with

dynamic systems, in which gains are as much a reality as losses.

Aligned with this policy emphasis, most ongoing conservation effort focusses on retaining

existing ecosystems (retarding change in the central part of figure 1) and reducing extirpations

(right-hand side of figure 1), with an element of re-introduction of previously-extirpated species. In

400   contrast, the inputs of new genes and species associated with novel environments is largely left to

happenstance, with inputs from far afield (introductions of non-native species) commonly regarded

or defined as negative (left-hand side of figure 1). Instead, actions and expenditure concentrate on

repelling new arrivals. This is puzzling, given that inputs of new functional elements (genes, species)

facilitate adjustments of ecosystems, and potentially generate ecosystem transformations that

405   increase longer-term resilience.

Facilitating the arrival of species and genes that provide benefits (ecosystem goods and

services, including pleasure from the presence of new species) is just as legitimate – no more, no less

– an intervention in a dynamic system as managing existing biodiversity or attempting to avoid

extirpations. Indeed, it is already widely applied in agriculture, forestry and, on occasion, in

410   conservation (e.g., Hamilton & Miller 2016). Facilitating arrivals may also be easier. When large-

scale external forces cannot be counteracted locally or regionally, it could be less costly and more

practical to introduce new elements that thrive under the new conditions than attempt to save the

last few individuals of species that will inevitably die out from that location (provided that they are

can survive elsewhere). Yet, the inputs of new genes and species commonly remain off the radar –

415   at least as a specific approach to conservation management. Arrivals are still going to take place as

conditions change, but this generates angst as often as it is perceived as an opportunity. In contrast,

environmental mangers and conservationists *could* intervene to increase the rate of arrival of

desirable organisms, as we already have in the contexts of agriculture, horticulture and forestry.

TABLE 1 NEAR HERE

420   Given that climatic and other ongoing environmental changes are inevitable, conservation

bodies are re-adjusting to the new reality (table 1). For example, 'connectivity conservation' is

perceived as increasingly important, in the contexts of both minimising negative impacts of habitat

fragmentation and facilitating distributional responses to climate change (Crooks & Sanjayan 2006,

Hodgson *et al.* 2009, Isaac *et al.* 2009). However, setting goals for dynamic systems is genuinely

425   challenging. Priority setting requires a shift away from "how do I save my country's species and

ecosystems?" (which will eventually fail because of ongoing environmental and distribution changes)

to a more global perspective of "how can my site, county, or country contribute most effectively to

global conservation in the long run?". With the latter perspective, citizens who live in countries that

contain many narrowly-distributed endemic species are likely to maintain and develop existing

430   priorities, but with increased flexibility, because the national 'good' (saving species x in country y) is

similar to the global 'good' (saving entire species from extinction). Elsewhere – over most of the

land and oceans because areas of high endemism are localised – it is possible to take a more relaxed

attitude to the precise identities and abundances of the species present in each location because a

recently-arrived species can have as much global significance (in terms of rarity, functions and

435   contributions to ecosystem services) as one that has been present in the region for longer. A far

greater emphasis can be placed on facilitating adaptive change, including *trans situ* conservation

(table 1), the notion of enabling genes and species to reach locations where they might survive,

thrive and contribute to ecosystem processes. *Trans situ* conservation can be enhanced by the

redesign of landscapes and by the designation of protected areas to maintain existing habitat

440   continuity along environmental gradients, so as to facilitate large scale distribution changes. It can

also be enhanced by the deliberate transport of genes and species. The logic is to save rare and

endangered genes and species *somewhere* within the global system so that they have the potential

to contribute to additional ecosystem functions, resilience and services in the recipient regions

either in the near future (benefiting current and near-future generations) or in the longer term (the

445   equity of generations).

At present, there is a lack of accepted national and international guidelines and legal frameworks to facilitate prioritisation and decision-making to bring about *trans situ* conservation (although a number of approaches and methodologies have been proposed: e.g., Hoegh-Guldberg *et al.* 2006, IUCN 2013, Nuñez *et al.* 2013, Foden *et al.* 2018). Achieving an increased consensus on

450 assessing risks and opportunities (from actions and inactions) on *trans situ* conservation is a growing priority. Otherwise, the default position will be to leave the inputs of biodiversity to chance. Or rather, conservationists will simply be leaving the identities of new arrivals to be influenced by the actions of other sectors of society.

455 **7. Concluding remarks**

The gains in biological diversity that have been taking place at local and regional scales generally illustrate resilience of the global biological system to human perturbation, and change *per se* should not be defined as negative. Biological change is what maintains biodiversity and functioning ecosystems during periods of perturbation to the Earth system. Thus, we should think twice before

460 embarking on the forever treatment of the biological symptoms of change, many of which are indications of biological resilience, rather than of forthcoming collapse. Trying to stop biological change is often ineffective, and sometimes counter-productive. We require a paradigm shift from any concepts that are still inspired by a notional 'balance of nature' to a dynamic perspective of nature at multiple temporal and spatial scales (Pickett 2013, Thomas 2017). If we wish to slow

465 change, we should concentrate more on its causes than on the consequences – this should be the focus of human choices. In the meantime, biological communities will continue to change, and they are likely to do so at an accelerating rate until at least the end of this century. By that time, we will have stored up a millennium or more's worth of lagged changes, in extinction debt, colonisation lags and community reassembly. Given that change is inevitable, we need to contemplate the benefits

470 and opportunities that might be associated with the arrival of new species in changing ecosystems,

as well as the harms and risks, and then decide whether, when and how to intervene so as to

accelerate new arrivals and rates of biological change.

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705 Figure 1. Inputs and losses of biological diversity in the Anthropocene, from a regional perspective (the region can be small or large). The schema is illustrative rather than exhaustive. The larger 'arrival' than 'departure' arrows reflect that regional diversity (number of species per country or island) has increased for most parts of the world, over the last 300 years. Humans affect changes taking place within each region, the arrival of new species, and the losses of ones that die out. The questions (bottom of figure) relate to what our targets should be for any regions when systems are

710 dynamic (centre); who, why and how we should decide to import additional species deliberately (left); and why and how we might try to retain species for which the region is no longer suitable for their survival (right).
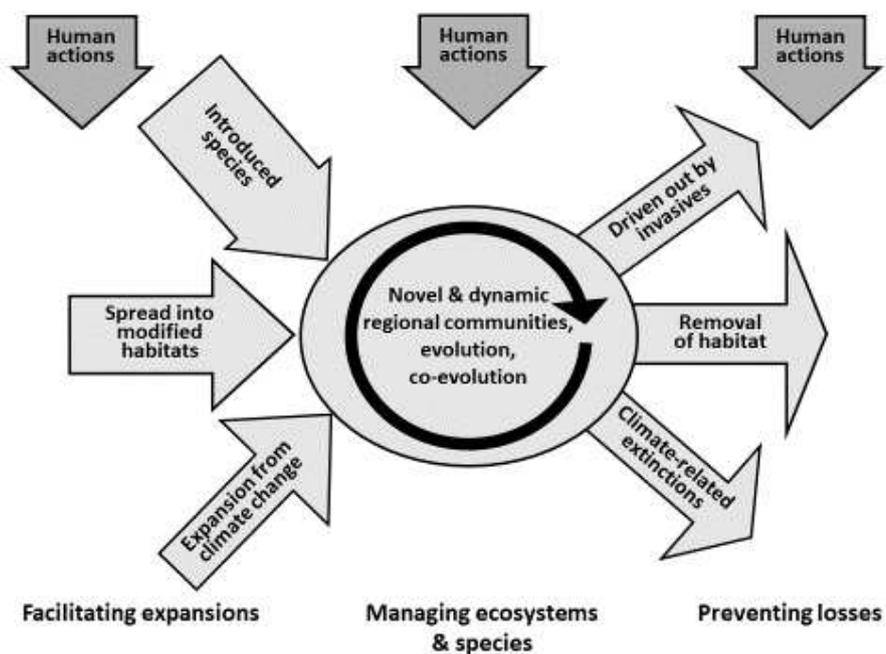
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Table 1: Conservation Strategies. Caricatures of 'recent' and 'emerging' conservation strategies, in the context of climatic and other drivers of environmental change. In dynamic systems, increasing emphasis needs to be on balancing the global and regional importance of any actions, and on *trans situ* conservation, enabling genes and species to survive somewhere, even if that is not within their historical distributions.

BROAD STRATEGY	RECENT EMPHASIS	EMERGING EMPHASIS
planning	**mainly static**, with priority areas, holding the line, and some attempts to reverse past changes	**dynamic**, with mental shift to accept and encourage dynamic ranges and novel ecosystems, co-benefits
in situ reserves, ecosystem protection & management	**primary approach**, often local, protecting species in existing ranges and ecosystems, restoration and reintroduction	**primary approach**, regional & global perspectives, refugia, heterogeneous environments, engineered ecosystems
ex situ zoos, botanic gardens, gene/seed banks	**modest contribution**, largely back-up collections, also for reintroductions (mainly of vertebrates and plants)	**increased contribution**, but still modest, for *trans situ* conservation, with gene banks (DNA code) for lost causes
trans situ facilitating movement to new locations	**trivial contribution**, mainly associated with landscape-scale conservation and ecological corridors	**major role**, connectivity (stepping-stones, corridors), translocation, managing ecosystem transitions

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