REVIEW

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Approaching a state shift in Earth's biosphere

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Localized ecological systems are known to shift abruptly and irreversibly from one state to another when they are forced across critical thresholds. Here we review evidence that the global ecosystem as a whole can react in the same way and is approaching a planetary-scale critical transition as a result of human influence. The plausibility of a planetary-scale 'tipping point' highlights the need to improve biological forecasting by detecting early warning signs of critical transitions on global as well as local scales, and by detecting feedbacks that promote such transitions. It is also necessary to address root causes of how humans are forcing biological changes.

Humans now dominate Earth, changing it in ways that threaten its ability to sustain us and other species[1–3]. This realization has led to a growing interest in forecasting biological responses on all scales from local to global[4–7].

However, most biological forecasting now depends on projecting recent trends into the future assuming various environmental pressures[5], or on using species distribution models to predict how climatic changes may alter presently observed geographic ranges[8,9]. Present work recognizes that relying solely on such approaches will be insufficient to characterize fully the range of likely biological changes in the future, especially because complex interactions, feedbacks and their hard-to-predict effects are not taken into account[6,8–11].

Particularly important are recent demonstrations that 'critical transitions' caused by threshold effects are likely[12]. Critical transitions lead to state shifts, which abruptly override trends and produce unanticipated biotic effects. Although most previous work on threshold-induced state shifts has been theoretical or concerned with critical transitions in localized ecological systems over short time spans[12–14], planetary-scale critical transitions that operate over centuries or millennia have also been postulated[3,12,15–18]. Here we summarize evidence that such planetary-scale critical transitions have occurred previously in the biosphere, albeit rarely, and that humans are now forcing another such transition, with the potential to transform Earth rapidly and irreversibly into a state unknown in human experience.

Two conclusions emerge. First, to minimize biological surprises that would adversely impact humanity, it is essential to improve biological forecasting by anticipating critical transitions that can emerge on a planetary scale and understanding how such global forcings cause local changes. Second, as was also concluded in previous work, to prevent a global-scale state shift, or at least to guide it as best we can, it will be necessary to address the root causes of human-driven global change and to improve our management of biodiversity and ecosystem services[3,15–17,19].

Basics of state shift theory

It is now well documented that biological systems on many scales can shift rapidly from an existing state to a radically different state[12]. Biological 'states' are neither steady nor in equilibrium; rather, they are characterized by a defined range of deviations from a mean condition over a prescribed period of time. The shift from one state to another can be caused by either a 'threshold' or 'sledgehammer' effect. State shifts resulting from threshold effects can be difficult to anticipate, because the critical threshold is reached as incremental changes accumulate and the threshold value generally is not known in advance. By contrast, a state shift caused by a sledgehammer effect—for example the clearing of a forest using a bulldozer—comes as no surprise. In both cases, the state shift is relatively abrupt and leads to new mean conditions outside the range of fluctuation evident in the previous state.

Threshold-induced state shifts, or critical transitions, can result from 'fold bifurcations' and can show hysteresis[12]. The net effect is that once a critical transition occurs, it is extremely difficult or even impossible for the system to return to its previous state. Critical transitions can also result from more complex bifurcations, which have a different character from fold bifurcations but which also lead to irreversible changes[20].

Recent theoretical work suggests that state shifts due to fold bifurcations are probably preceded by general phenomena that can be characterized mathematically: a deceleration in recovery from perturbations ('critical slowing down'), an increase in variance in the pattern of within-state fluctuations, an increase in autocorrelation between fluctuations, an increase in asymmetry of fluctuations and rapid back-and-forth shifts ('flickering') between states[12,14,18]. These phenomena can theoretically be

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assessed within any temporally and spatially bounded system. Although such assessment is not yet straightforward[12,18,20], critical transitions and in some cases their warning signs have become evident in diverse biological investigations[21], for example in assessing the dynamics of disease outbreaks[22,23], populations[14] and lake ecosystems[12,13]. Impending state shifts can also sometimes be determined by parameterizing relatively simple models[20,21].

In the context of forecasting biological change, the realization that critical transitions and state shifts can occur on the global scale[3,12,15–18], as well as on smaller scales, is of great importance. One key question is how to recognize a global-scale state shift. Another is whether global-scale state shifts are the cumulative result of many smaller-scale events that originate in local systems or instead require global-level forcings that emerge on the planetary scale and then percolate downwards to cause changes in local systems. Examining past global-scale state shifts provides useful insights into both of these issues.

Hallmarks of global-scale state shifts

Earth's biosphere has undergone state shifts in the past, over various (usually very long) timescales, and therefore can do so in the future (Box 1). One of the fastest planetary state shifts, and the most recent, was the transition from the last glacial into the present interglacial condition[12,18], which occurred over millennia[24]. Glacial conditions had prevailed for ~100,000 yr. Then, within ~3,300 yr, punctuated by episodes of abrupt, decadal-scale climatic oscillations, full interglacial conditions were attained. Most of the biotic change—which included extinctions, altered diversity patterns and new community compositions—occurred within a period of 1,600 yr beginning ~12,900 yr ago. The ensuing interglacial state that we live in now has prevailed for the past ~11,000 yr.

Occurring on longer timescales are events such as at least four of the 'Big Five' mass extinctions[25], each of which represents a critical transition that spanned several tens of thousands to 2,000,000 yr and changed the course of life's evolution with respect to what had been normal for the previous tens of millions of years. Planetary state shifts can also substantially increase biodiversity, as occurred for example at the 'Cambrian explosion'[26], but such transitions require tens of millions of years, timescales that are not meaningful for forecasting biological changes that may occur over the next few human generations (Box 1).

Despite their different timescales, past critical transitions occur very quickly relative to their bracketing states: for the examples discussed here, the transitions took less than ~5% of the time the previous state had lasted (Box 1). The biotic hallmark for each state change was, during the critical transition, pronounced change in global, regional and local assemblages of species. Previously dominant species diminished or went extinct, new consumers became important both locally and globally, formerly rare organisms proliferated, food webs were modified, geographic ranges reconfigured and resulted in new biological communities, and evolution was initiated in new directions. For example, at the Cambrian explosion large, mobile predators became part of the food chain for the first time. Following the K/T extinction, mammalian herbivores replaced large archosaur herbivores. And at the last glacial–interglacial transition, megafaunal biomass switched from being dominated by many species to being dominated by *Homo sapiens* and our domesticated species[27].

All of the global-scale state shifts noted above coincided with global-scale forcings that modified the atmosphere, oceans and climate (Box 1). These examples suggest that past global-scale state shifts required global-scale forcings, which in turn initiated lower-level state changes that local controls do not override. Thus, critical aspects of biological forecasting are to understand whether present global forcings are of a magnitude sufficient to trigger a global-scale critical transition, and to ascertain the extent of lower-level state changes that these global forcings have already caused or are likely to cause.

Present global-scale forcings

Global-scale forcing mechanisms today are human population growth with attendant resource consumption[3], habitat transformation and fragmentation[3], energy production and consumption[28,29], and climate change[3,18]. All of these far exceed, in both rate and magnitude, the forcings evident at the most recent global-scale state shift, the last glacial–interglacial transition (Box 1), which is a particularly relevant benchmark for comparison given that the two global-scale forcings at that time—climate change

BOX 1
Past planetary-scale critical transitions and state shifts

Last glacial–interglacial transition[18,24]. The critical transition was a rapid warm–cold–warm fluctuation in climate between 14,300 and 11,000 yr ago, and the most pronounced biotic changes occurred between 12,900 and 11,300 yr ago[24,27,30,54].

The major biotic changes were the extinction of about half of the species of large-bodied mammals, several species of large birds and reptiles, and a few species of small animals[30]; a significant decrease in local and regional biodiversity as geographic ranges shifted individualistically, which also resulted in novel species assemblages[37,49,53,54]; and a global increase in human biomass and spread of humans to all continents[27].

The pre-transition global state was a glacial stage that lasted about 100,000 yr and the post-transition global state is an interglacial that Earth has been in for approximately 11,000 yr. The global forcings were orbitally induced, cyclic variations in solar insolation that caused rapid global warming. Direct and indirect of effects of humans probably contributed to extinctions of megafauna and subsequent ecological restructuring.

'Big Five' mass extinctions[25]. The respective critical transitions ended at ~443,000,000, ~359,000,000, ~251,000,000, ~200,000,000 and ~65,000,000 yr ago. They are each thought to have taken at most 2,000,000 yr to complete but could have been much shorter; the limitations of geological dating preclude more precision. The most recent transition (the K/T extinction, which occurred at the end of the Cretaceous period) may have been the catastrophic result of a bolide impact, and could have occurred on a timescale as short as a human lifetime.

The major biotic changes were the extinction of at least 75% of Earth's species; a major reorganization of global and local ecosystems as previously rare lifeforms gained evolutionary dominance; and the return to pre-extinction levels of biodiversity over hundreds of thousands to millions of years.

The pre- and post-transition global states lasted ~50,000,000–100,000,000 yr. We are now 65,000,000 yr into the present state on this scale, in an era known as the Cenozoic or the Age of Mammals. The global forcings all corresponded to unusual climate changes and shifts in ocean and atmospheric chemistry, especially in concentrations of carbon dioxide and, in one case, hydrogen sulphide. Intense volcanic activity seems to have been important at some extinction events. A bolide impact is well documented as a cause of the K/T event and has been postulated as a cause of some of the others.

Cambrian explosion[26,81]. The critical transition began ~540,000,000 yr ago and lasted about 30,000,000 yr.

The major biotic changes were evolutionary innovations resulting in all phyla known today; a conversion of the global ecosystem from one based almost solely on microbes to one based on complex, multicellular life; and diversity increased, but on a timescale that is far too long to be meaningful in predicting the biotic future over human generations.

The pre-transition global state lasted ~2,000,000,000 yr and was characterized by primary lifeforms consisting of prokaryotic and eukaryotic microbes. The post-transition global state is about 540,000,000 yr old and ongoing. The global forcings were the increase of atmospheric oxygen to levels sufficient for the metabolic processes required to sustain complex, multicellular life, and evolutionary innovations that included large size, predation and complex locomotion.

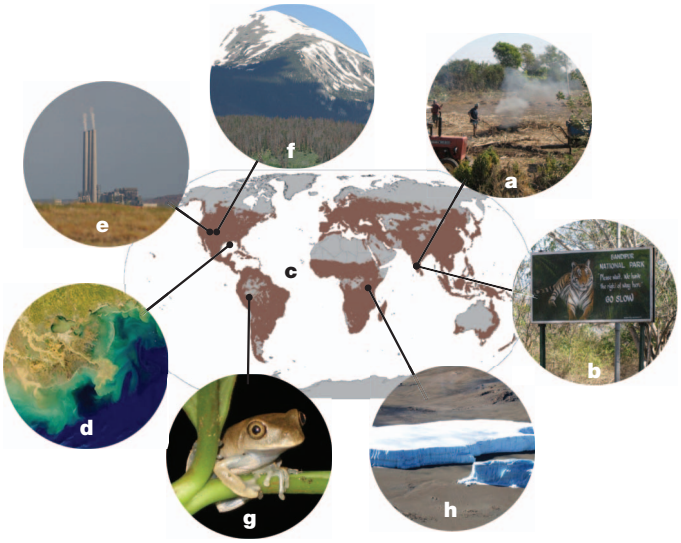

Figure 1 | Drivers of a potential planetary-scale critical transition. **a**, Humans locally transform and fragment landscapes. **b**, Adjacent areas still harbouring natural landscapes undergo indirect changes. **c**, Anthropogenic local state shifts accumulate to transform a high percentage of Earth's surface drastically; brown colouring indicates the approximately 40% of terrestrial ecosystems that have now been transformed to agricultural landscapes, as explained in ref. 34. **d**, Global-scale forcings emerge from accumulated local human impacts, for example dead zones in the oceans from run-off of agricultural pollutants. **e**, Changes in atmospheric and ocean chemistry from the release of greenhouse gases as fossil fuels are burned. **f**–**h**, Global-scale forcings emerge to cause ecological changes even in areas that are far from human population concentrations. **f**, Beetle-killed conifer forests (brown trees) triggered by seasonal changes in temperature observed over the past five decades. **g**, Reservoirs of biodiversity, such as tropical rainforests, are projected to lose many species as global climate change causes local changes in temperature and precipitation, exacerbating other threats already causing abnormally high extinction rates. In the case of amphibians, this threat is the human-facilitated spread of chytrid fungus. **h**, Glaciers on Mount Kilimanjaro, which remained large throughout the past 11,000 yr, are now melting quickly, a global trend that in many parts of the world threatens the water supplies of major population centres. As increasing human populations directly transform more and more of Earth's surface, such changes driven by emergent global-scale forcings increase drastically, in turn causing state shifts in ecosystems that are not directly used by people. Photo credits: E.A.H. and A.D.B. (**a**–**c**, **e**–**h**); NASA (**d**).

and human population growth[27,30]—are also primary forcings today. During the last glacial–interglacial transition, however, these were probably separate, yet coincidental, forcings. Today conditions are very different because global-scale forcings including (but not limited to) climate change have emerged as a direct result of human activities.

Human population growth and per-capita consumption rate underlie all of the other present drivers of global change. The growth in the human population now (~77,000,000 people per year) is three orders of magnitude higher than the average yearly growth from ~10,000–400 yr ago (~67,000 people per year), and the human population has nearly quadrupled just in the past century[31–33]. The most conservative estimates suggest that the population will grow from its present value, 7,000,000,000, to 9,000,000,000 by 2045[31] and to 9,500,000,000 by 2050[31,33].

As a result of human activities, direct local-scale forcings have accumulated to the extent that indirect, global-scale forcings of biological change have now emerged. Direct forcing includes the conversion of ~43% of Earth's land to agricultural or urban landscapes, with much of the remaining natural landscapes networked with roads[1,2,34,35]. This exceeds the physical transformation that occurred at the last global-scale critical transition, when ~30% of Earth's surface went from being covered by glacial ice to being ice free.

The indirect global-scale forcings that have emerged from human activities include drastic modification of how energy flows through the global ecosystem. An inordinate amount of energy now is routed through one species, *Homo sapiens*. Humans commandeer ~20–40% of global net primary productivity[1,2,35] (NPP) and decrease overall NPP through habitat degradation. Increasing NPP regionally through atmospheric and agricultural deposition of nutrients (for example nitrogen and phosphorus) does not make up the shortfall[2]. Second, through the release of energy formerly stored in fossil fuels, humans have substantially increased the energy ultimately available to power the global ecosystem. That addition does not offset entirely the human appropriation of NPP, because the vast majority of that 'extra' energy is used to support humans and their domesticates, the sum of which comprises large-animal biomass that is far beyond that typical of pre-industrial times[27]. A decrease in this extra energy budget, which is inevitable if alternatives do not compensate for depleted fossil fuels, is likely to impact human health and economies severely[28], and also to diminish biodiversity[27], the latter because even more NPP would have to be appropriated by humans, leaving less for other species[36].

By-products of altering the global energy budget are major modifications to the atmosphere and oceans. Burning fossil fuels has increased atmospheric CO_2 concentrations by more than a third (~35%) with respect to pre-industrial levels, with consequent climatic disruptions that include a higher rate of global warming than occurred at the last global-scale state shift[37]. Higher CO_2 concentrations have also caused the ocean rapidly to become more acidic, evident as a decrease in pH by ~0.05 in the past two decades[38]. In addition, pollutants from agricultural run-off and urban areas have radically changed how nutrients cycle through large swaths of marine areas[16].

Already observable biotic responses include vast 'dead zones' in the near-shore marine realm[39], as well as the replacement of >40% of Earth's formerly biodiverse land areas with landscapes that contain only a few species of crop plants, domestic animals and humans[3,40]. Worldwide shifts in species ranges, phenology and abundances are concordant with ongoing climate change and habitat transformation[41]. Novel communities are becoming widespread as introduced, invasive and agricultural species integrate into many ecosystems[42]. Not all community modification is leading to species reductions; on local and regional scales, plant diversity has been increasing, owing to anthropogenic introductions[42], counter to the overall trend of global species loss[5,43]. However, it is unknown whether increased diversity in such locales will persist or will eventually decrease as a result of species interactions that play out over time. Recent and projected[5,44] extinction rates of vertebrates far exceed empirically derived background rates[25]. In addition, many plants, vertebrates and invertebrates have markedly reduced their geographic ranges and abundances to the extent that they are at risk of extinction[43]. Removal of keystone species worldwide, especially large predators at upper trophic levels, has exacerbated changes caused by less direct impacts, leading to increasingly simplified and less stable ecological networks[39,45,46].

Looking towards the year 2100, models forecast that pressures on biota will continue to increase. The co-opting of resources and energy use by humans will continue to increase as the global population reaches 9,500,000,000 people (by 2050), and effects will be greatly exacerbated if per capita resource use also increases. Projections for 2100 range from a population low of 6,200,000,000 (requiring a substantial decline in fertility rates) to 10,100,000,000 (requiring continued decline of fertility in countries that still have fertility above replacement level) to 27,000,000,000 (if fertility remains at 2005–2010 levels; this population size is not thought to be supportable; ref. 31). Rapid climate change shows no signs of slowing. Modelling suggests that for ~30% of Earth, the speed at which plant species will have to migrate to keep pace with projected climate change is greater than their dispersal rate when Earth last shifted from a glacial to an interglacial climate[47], and that dispersal will be thwarted by highly fragmented landscapes. Climates found at present on 10–48% of the planet are projected to disappear within a century, and climates that contemporary organisms have never experienced are likely to cover 12–39% of Earth[48]. The mean global temperature by 2070 (or possibly a few decades earlier) will be higher than it has been since the human species evolved.

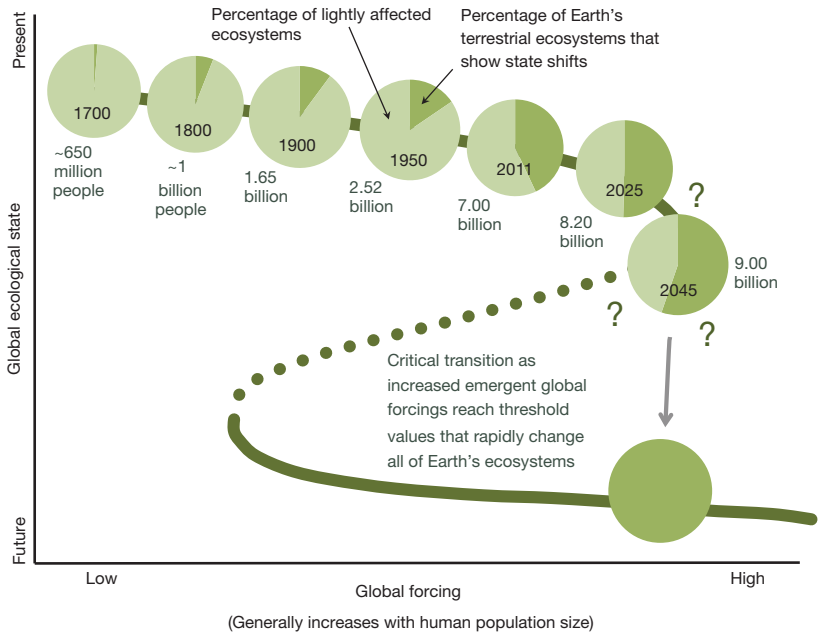

Figure 2 | Quantifying land use as one method of anticipating a planetary state shift. The trajectory of the green line represents a fold bifurcation with hysteresis[12]. At each time point, light green represents the fraction of Earth's land that probably has dynamics within the limits characteristic of the past 11,000 yr. Dark green indicates the fraction of terrestrial ecosystems that have unarguably undergone drastic state changes; these are minimum values because they count only agricultural and urban lands. The percentages of such transformed lands in 2011 come from refs 1, 34, 35, and when divided by 7,000,000,000 (the present global human population) yield a value of approximately 2.27 acres (0.92 ha) of transformed land for each person. That value was used to estimate the amount of transformed land that probably existed in the years 1800, 1900 and 1950, and which would exist in 2025 and 2045 assuming conservative population growth and that resource use does not become any more efficient. Population estimates are from refs 31–33. An estimate of 0.68 transformed acres (0.28 ha) per capita (approximately that for India today) was used for the year 1700, assuming a lesser effect on the global landscape before the industrial revolution. Question marks emphasize that at present we still do not know how much land would have to be directly transformed by humans before a planetary state shift was imminent, but landscape-scale studies and theory suggest that the critical threshold may lie between 50 and 90% (although it could be even lower owing to synergies between emergent global forcings). See the main text for further explanation. Billion, 10^9.

Expecting the unexpected

The magnitudes of both local-scale direct forcing and emergent global-scale forcing are much greater than those that characterized the last global-scale state shift, and are not expected to decline any time soon. Therefore, the plausibility of a future planetary state shift seems high, even though considerable uncertainty remains about whether it is inevitable and, if so, how far in the future it may be. The clear potential for a planetary-scale state shift greatly complicates biotic forecasting efforts, because by their nature state shifts contain surprises. Nevertheless, some general expectations can be gleaned from the natural experiments provided by past global-scale state shifts. On the timescale most relevant to biological forecasting today, biotic effects observed in the shift from the last glacial to the present interglacial (Box 1) included many extinctions[30,49–51]; drastic changes in species distributions, abundances and diversity; and the emergence of novel communities[49,50,52–54]. New patterns of gene flow triggered new evolutionary trajectories[55–58], but the time since then has not been long enough for evolution to compensate for extinctions.

At a minimum, these kinds of effects would be expected from a global-scale state shift forced by present drivers, not only in human-dominated regions but also in remote regions not now heavily occupied by humans (Fig. 1); indeed, such changes are already under way (see above[5,25,39,41–44]). Given that it takes hundreds of thousands to millions of years for evolution to build diversity back up to pre-crash levels after major extinction episodes[25], increased rates of extinction are of particular concern, especially because global and regional diversity today is generally lower than it was 20,000 yr ago as a result of the last planetary state shift[37,50,51,54,59]. This large-scale loss of diversity is not overridden by historical increases in plant species richness in many locales, owing to human-transported species homogenizing the world's biota[42]. Possible too are substantial losses of ecosystem services required to sustain the human population[60]. Still unknown is the extent to which human-caused increases in certain ecosystem services—such as growing food—balances the loss of 'natural' ecosystem services, many of which already are trending in dangerous directions as a result of overuse, pollutants and climate change[3,16]. Examples include the collapse of cod and other fisheries[45,61,62]; loss of millions of square kilometres of conifer forests due to climate-induced bark-beetle outbreaks;[63] loss of carbon sequestration by forest clearing[60]; and regional losses of agricultural productivity from desertification or detrimental land-use practices[1,35]. Although the ultimate effects of changing biodiversity and species compositions are still unknown, if critical thresholds of diminishing returns in ecosystem services were reached over large areas and at the same time global demands increased (as will happen if the population increases by 2,000,000,000 within about three decades), widespread social unrest, economic instability and loss of human life could result[64].

Towards improved biological forecasting and monitoring

In view of potential impacts on humanity, a key need in biological forecasting is the development of ways to anticipate a global critical transition, ideally in time to do something about it[65]. It is possible to imagine qualitative aspects of a planetary state shift given present human impacts (Fig. 1), but criteria that would indicate exactly how close we might be to a planetary-scale critical transition remain elusive. Three approaches should prove helpful in defining useful benchmarks and tracking progression towards them.

Tracking global-scale changes

The first approach acknowledges the fact that local-scale state changes—whether they result from sledgehammer or threshold effects—trigger critical transitions over regions larger than the directly affected area, as has been shown both empirically and theoretically[66–70]. On the landscape scale, tipping points in undisturbed patches are empirically evident when 50–90% of the surrounding patches are disturbed. Simulations indicate that critical transitions become much more likely when the probability of connection of any two nodes in a network (ecological or otherwise) drops

below ~59% (refs 66–70). More generally, dense human populations, roads and infrastructure, and land transformation are known to cause ecological changes outside the areas that have actually undergone sledgehammer state changes[68]. Translating these principles to the planetary scale would imply that once a sufficient proportion of Earth's ecosystems have undergone transformation, the remainder can change rapidly (Fig. 2), especially because emergent, larger-scale forcings (for instance changes in atmospheric and ocean chemistry, nutrient and energy cycling, pollution and so on) multiply and interact to exacerbate local forcings[21] (Fig. 1). It is still unknown, however, what percentage of Earth's ecosystems actually have to be transformed to new states by the direct action of humans for rapid state changes to be triggered in remaining 'natural' systems. That percentage may be knowable only in retrospect, but, judging from landscape-scale observations and simulations[66–70], it can reasonably be expected to be as low as 50% (ref. [68]), or even lower if the interaction effects of many local ecosystem transformations cause sufficiently large global-scale forcings to emerge.

In that context, continued efforts to track global-scale changes by remote sensing and other techniques will be essential in assessing how close we are to tipping the balance towards an Earth where most ecosystems are directly altered by people. This is relatively straightforward for land and it has already been demonstrated that at least 43% of Earth's terrestrial ecosystems have undergone wholesale transformation[1,2,34,40], on average equating to ~2.27 transformed acres (0.92 ha) per capita for the present human population. Assuming that this average rate of land transformation per capita does not change, 50% of Earth's land will have undergone state shifts when the global population reaches 8,200,000,000, which is estimated to occur by the year 2025[31]. Under the same land-use assumption and according to only slightly less conservative population growth models, 70% of Earth's land could be shifted to human use (if the population reaches 11,500,000,000) by 2060[31].

Assessing the percentage change to new states in marine systems, and the direct human footprint on the oceans, is much more challenging, but available data suggest widespread effects[38,39]. More precise quantification of ecosystem state shifts in the oceans is an important task, to the extent that ocean ecosystems cover most of the planet.

Tracking local-scale changes caused by global forcings

The second approach is the direct monitoring of biological change in local study systems caused by external forcing. Such monitoring will be vital, particularly where the human footprint is thought to be small. Observing unusual changes in such areas, as has occurred recently in Yellowstone Park, USA, which has been protected since 1872[71], and in many remote watersheds[72], would indicate that larger-scale forcings[38,73] are influencing local ecological processes.

A key problem has been how to recognize 'unusual' change, because biological systems are dynamic and shifting baselines have given rise to many different definitions of 'normal', each of which can be specified as unusual within a given temporal context. However, identifying signals of a global-scale state shift in any local system demands a temporal context that includes at least a few centuries or millennia, to encompass the range of ecological variation that would be considered normal over the entire ~11,000-yr duration of the present interglacial period. Identifying unusual biotic changes on that scale has recently become possible through several different approaches, which are united by their focus on integrating spatial and temporal information (Box 2). Breakthroughs include characterizing ecosystems using taxon-independent metrics that can be tracked with palaeontological data through pre-anthropogenic times and then compared with present conditions and monitored into the future; recognizing macro-ecological patterns that indicate disturbed systems; combining phylochronologic and phylogeographic information to trace population dynamics over several millennia; and assessing the structure and stability of ecological networks using theoretical and empirical methods. Because all of these approaches benefit from time series data, long-term monitoring efforts and existing palaeontological and natural history museum collections will become particularly valuable[74].

BOX 2

Integrating spatio-temporal data on large scales to detect planetary state shifts

- Palaeontology uses historical, fossil and geological information to calibrate normal levels of fluctuation in biodiversity, species composition and abundance[80], food webs[82], ecomorphology[83], extinction[25] and so on. Recent work shows that some lightly populated ecosystems still operate within bounds that would be considered normal for the present interglacial period, but that others have been disturbed[80].
- Macroecology provides quantitative ways to identify when a particular ecosystem has unusual characteristics in such metrics as the species–area relationship, species abundance distributions, spatial aggregation patterns[84,85], the distribution of metabolic rates over individuals in a community[85,86], the inverse power-law relation between abundance and body size[87], and the distribution of linkages across species in a trophic network[88]. Recent advances in formalizing the maximum entropy (MaxEnt) theory of ecology[85,86] provide a theoretical means of accurately predicting such patterns in undisturbed ecosystems; significant departures from the predictions of MaxEnt probably indicate disturbed systems[85].
- Population biology uses life history, abundance, genetics and numerical modelling to assess population dynamics and viability. Recent advances in obtaining ancient DNA from samples several thousand years old, plus newly developed analytical models that take into account temporal (phylochronologic) as well as spatial (phylogeographic) patterning, increase power in testing whether genetic patterning on the modern landscape deviates significantly from patterns that arise on the scale of centuries to millennia[10,89].
- Ecological network theory regards ecosystems as complex networks of species connected by different interactions. Recent work identifies persistent and stabilizing characteristics of networks on different geographic and temporal scales[81,82] (both current and palaeontological), such as consumer–resource body size ratios[90], allometric scaling effects[91] and skewed distributions for connectivity[81,92,93] and interaction strengths[94–96]. Alteration in such characteristics signals perturbation of the normal network structure. Theoretical work also is revealing where information about species-specific traits such as body size[46,90,91], trophic generality[91], trophic uniqueness[97], non-trophic interactions[98] and phylogenetic information[99] may help predict when ecosystem services degrade as networks destabilize[46,100] and disassemble[97].

Synergy and feedbacks

Thresholds leading to critical transitions are often crossed when forcings are magnified by the synergistic interaction of seemingly independent processes or through feedback loops[3,16]. Given that several global-scale forcings are at work today, understanding how they may combine to magnify biological change is a key challenge[3,15–17]. For example, rapid climate change combined with highly fragmented species ranges can be expected to magnify the potential for ecosystem collapse, and wholesale landscape changes may in turn influence the biology of oceans.

Feedback loops also occur among seemingly discrete systems that operate at different levels of the biological hierarchy[6,8,37] (genotype, phenotype, populations, species distributions, species interactions and so on). The net effect is that a biological forcing applied on one scale can cause a critical transition to occur on another scale. Examples include inadvertent, anthropogenic selection for younger maturation of individual cod as a result of heavy fishing pressure[61]; population crashes due

to decreased genetic diversity[75]; mismatch in the phenology of flowering and pollination resulting from interaction of genetic factors, temperature, photoperiod and/or precipitation[76]; and cascades of ecological changes triggered by the removal of top predators[62]. In most cases, these 'scale-jumping' effects, and the mechanisms that drive them, have become apparent only in hindsight, but even so they take on critical importance in revealing interaction effects that can now be incorporated into the next generation of biological forecasts.

Finally, because the global-scale ecosystem comprises many smaller-scale, spatially bounded complex systems (for instance the community within a given physiographic region), each of which overlaps and interacts with others, state shifts of the small-scale components can propagate to cause a state shift of the entire system[21]. Our understanding of complexity at this level can be increased by tracking changes within many different ecosystems in a parallel fashion, from landscape-scale studies of state-shifts[12,21] and from theoretical work that is under way[20]. Potential interactions between overlapping complex systems, however, are proving difficult to characterize mathematically, especially when the systems under study are not well known and are heterogeneous[20]. Nevertheless, one possibility emerging from such work is that long-term transient behaviours, where sudden changes in dynamics can occur after periods of relative stasis even in the absence of outside forces, may be pervasive at the ecosystem level[20], somewhat analogously to delayed metapopulation collapse as a result of extinction debt[77]. This potential 'lag-time' effect makes it all the more critical rapidly to address, where possible, global-scale forcings that can push the entire biosphere towards a critical transition.

Guiding the biotic future

Humans have already changed the biosphere substantially, so much so that some argue for recognizing the time in which we live as a new geologic epoch, the Anthropocene[3,16,78]. Comparison of the present extent of planetary change with that characterizing past global-scale state shifts, and the enormous global forcings we continue to exert, suggests that another global-scale state shift is highly plausible within decades to centuries, if it has not already been initiated.

As a result, the biological resources we take for granted at present may be subject to rapid and unpredictable transformations within a few human generations. Anticipating biological surprises on global as well as local scales, therefore, has become especially crucial to guiding the future of the global ecosystem and human societies. Guidance will require not only scientific work that foretells, and ideally helps to avoid[65], negative effects of critical transitions, but also society's willingness to incorporate expectations of biological instability[64] into strategies for maintaining human well-being.

Diminishing the range of biological surprises resulting from bottom-up (local-to-global) and top-down (global-to-local) forcings, postponing their effects and, in the optimal case, averting a planetary-scale critical transition demands global cooperation to stem current global-scale anthropogenic forcings[3,15–17,19]. This will require reducing world population growth[31] and per-capita resource use; rapidly increasing the proportion of the world's energy budget that is supplied by sources other than fossil fuels while also becoming more efficient in using fossil fuels when they provide the only option[79]; increasing the efficiency of existing means of food production and distribution instead of converting new areas[34] or relying on wild species[39] to feed people; and enhancing efforts to manage as reservoirs of biodiversity and ecosystem services, both in the terrestrial[80] and marine realms[39], the parts of Earth's surface that are not already dominated by humans. These are admittedly huge tasks, but are vital if the goal of science and society is to steer the biosphere towards conditions we desire, rather than those that are thrust upon us unwittingly.

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