Focus Issue: Is there a global tipping point for planet Earth?

Multiscale regime shifts and planetary boundaries

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Life on Earth has repeatedly displayed abrupt and massive changes in the past, and there is no reason to expect that comparable planetary-scale regime shifts will not continue in the future. Different lines of evidence indicate that regime shifts occur when the climate or biosphere transgresses a tipping point. Whether human activities will trigger such a global event in the near future is uncertain, due to critical knowledge gaps. In particular, we lack understanding of how regime shifts propagate across scales, and whether local or regional tipping points can lead to global transitions. The ongoing disruption of ecosystems and climate, combined with unprecedented breakdown of isolation by human migration and trade, highlights the need to operate within safe planetary boundaries.

Escalating human–biosphere interactions

The extent and scale of human–biosphere interactions in recent centuries is unprecedented, altering the dynamics of ecosystems throughout the world [1–7], and even changing the climate of the Earth, illustrated, for example, by rising temperatures, changes in rainfall, retreat of polar ice and glaciers, and declining ocean pH [8–12]. In response to anthropogenic activities, many ecosystems exhibit regime shifts to a different assemblage of species, such as the transitions between clear and turbid lakes [13], grassland and forest [14,15], or from kelp beds to sea urchin barren [16]. Although these transitions are often described and studied as local and recent phenomena, collectively they amount to a slow and on-going global transformation. According to one estimate [4], humans had already significantly altered 50% of the terrestrial habitats of the world by 1750, and 75% were transformed by 2000. These ubiquitous regime shifts are important because they often result in profound changes in ecosystem services, biodiversity, and esthetic values, are hard to predict and avoid, and are often costly, difficult, or even impossible to reverse (e.g., [17]). Importantly, because of the way in which we perceive gradual global change, many people today are unaware, or do not care, that the changes to the climate and biosphere of the Earth as a result of anthropogenic activities are sufficient to invoke the concept of a new geological epoch, the ‘Anthropocene’ (e.g., [18–20]).

Here, we explore whether the global extent of human activity could give rise to planetary-scale thresholds and regime shifts, as proposed recently by Barnosky et al. [21], but disputed by others [22,23]. We first outline the theory of regime shifts in the context of global change, highlighting some common misconceptions that confuse the speed of ecological change with the presence or absence of tipping points that generate large-scale regime shifts. We also discuss the related concept of planetary boundaries [24,25], recently proposed as a framework for achieving global sustainability and for avoiding irreparable damage to planetary systems and the societies that they support. In particular, we highlight the important distinctions between planetary boundaries and planetary tipping points, which has been a source of confusion in recent debates (e.g., [26], Box 1). We then review the evidence for planetary-scale tipping points, or threshold behavior, revealed by the evolutionary history of ecosystems, and in elements of the climate of the Earth, which is a primary driver of past and contemporary ecological shifts. Finally, we discuss ways in which regime shifts unfold and spread across multiple scales, highlighting numerous gaps in current research on regional- and planetary-scale dynamics.

Regime shifts, thresholds, and feedbacks

Regime shifts, or major changes in ecosystems, have multiple causes. Desertification of a landscape, for example, involves gradual changes in climate, slowly unfolding changes in interactions of the land surface and the atmosphere, complex shifting patterns of vegetation, movements of grazing animals, and changing behavior of pastoralists. When a regime shift occurs, it is easy to attribute the change to a recent short-term event, such as an exceptionally dry year. A deeper analysis, however, shows interacting causal networks of slow and fast processes that have eroded the
Box 1. Coping with uncertainty: planetary boundaries

The global influence of human actions raises questions about the amount of change in large-scale processes that can be accommodated without severely damaging the biosphere, while still maintaining or improving human well-being. In the past, some global shifts, such as loss of biodiversity from mass extinctions or shifting biomes during an ice age, were quickly reversed on a geological timescale, but such changes today would be catastrophic for humans. In the face of this risk and uncertainty, Rockström et al. [24] developed the concept of establishing planetary boundaries (as distinct from identifying tipping points) for maintaining safe levels of anthropogenic drivers, to avoid long-term damage to planetary systems and to the societies that depend on them (Figure 1). The concept neither assumes, nor rules out, the existence of tipping points in Earth system behavior. Instead, it takes a rational approach to weighing up the expected future costs of unwanted regime shifts versus the benefits of identifying safe levels of drivers that can be sustained. Often, there are strong social and economic incentives to increase drivers closer to a tipping point. Intuitively, planetary boundaries should be set at lower level for a set of drivers whose safe levels are uncertain.

![Figure 1](https://example.com/figure1.png)

**Figure 1.** The planetary boundary or ‘safe operating space’ concept, expressed in two ways. In (A), the equilibrail response (e.g., of the climate of a region or by an ocean basin) is plotted as a function of the strength of multiple, interacting anthropogenic drivers, such as overharvesting or ocean acidification. Uncertainty over the eventual, equilibrail impact of high levels of drivers is indicated by considering three potential system responses at equilibrail: smooth, a step function, and hysteretic (or folded, creating two basins of attraction). The latter two constitute threshold effects. To reduce the likelihood of surpassing a threshold or of severely impacting the system even if a threshold does not exist, the safe boundary is placed, as a precaution, at an intermediate level of drivers. Note that this depiction does not illustrate the pace of change in the drivers, or the speed of response by the system to a small or large change in drivers. In (B), the response of the system to escalating drivers is plotted over time. At regional and global scales, the temporal trajectory is always gradual over human time scales, regardless of the shape of the equilibrail response [shown in (A)], because change takes time and even threshold responses at regional to global scales are typically lagged by centuries, millennia, or millions of years.

resilience of the system, thereby making it more vulnerable to shocks or disturbances.

Major shifts in ecosystems can be visualized heuristically in a graphical model where the position of a rolling ball represents the current ecosystem state in a landscape with valleys and peaks (e.g., [27–29]). An ecosystem is resilient to change if it can sustain human activities and shocks. In this case, the ball remains within the same valley (often described as a basin of attraction in a stability landscape), returning towards its original equilibrium after a disturbance or reduction in human pressures, rather than flipping into a new regime or state represented by a different valley. The peaks separating valleys depict unstable thresholds between two or more alternate ecosystem states, such as a forest and an urbanized landscape. Anthropogenic activities interact with the stability landscape, changing the shape and depth of valleys, and moving the thresholds, making a regime shift to a new state either more, or less, likely (e.g., [29,30]).

A tipping point or threshold is a nonlinear relation between a driver (e.g., climate change or pollution) and the eventual state of the ecosystem when it finally equilibrails. The slope of the relation becomes steeper if destabilizing positive feedbacks result (eventually) in a disproportionate ecological change arising from a relatively small increase in driver. Strong destabilizing feedbacks bend the curve even further, producing two alternate states over the same range of driver (see Figure 1A in Box 1). A common mistake is to confuse the rate of change of an ecosystem through time, with the nonlinear relation between the strength of drivers and equilibrail ecosystem state or states [31]. Thus, a smooth, slow, or incremental ecological change through time may simply be the lagged transient response of an ecosystem that nonetheless has tipping points and alternate stable states.

Ecologists tend to focus on fast changes that are easy to observe and measure in the time frame of a thesis project, a research grant, or during a 40-year career. However, many regional- and planetary-scale responses progress slowly during regime shifts and appear to be incremental on human time scales. For example, the response by terrestrial ecosystems to global warming at the end of the last ice age took millennia to unfold, long after the ice sheets had melted [32]. Consequently, transgressing global tipping thresholds is unlikely to manifest as sudden and synchronous collapses worldwide, a criterion proposed by some researchers to reject the possibility of planetary-scale tipping points [22]. The key issue is not the speed of transition, but rather the presence or absence of tipping points in the equilibrail response of the biosphere to anthropogenic drivers.

**Learning from ancient regime shifts**

Our understanding of the regime shifts that punctuate the history of the Earth is necessarily fragmentary; nonetheless, the geological and paleontological records provide
valuable insights into irreversible planetary-scale dynamics that unfold and spread slowly on human time scales. The history and tempo of life on Earth is characterized by short bursts of extinction and speciation, interspersed with longer periods of relative stasis when turnover of species is slower (e.g., [33]). Profound and relatively sudden changes in species composition are recorded in successive geological strata, and their worldwide occurrence (which led to the establishment of the geological timescale) is well recognized, despite huge variation in local- and regional-scale environments. Over evolutionary time frames, planetary-scale ecological change has been driven by environmental shifts and shocks (e.g., global warming and cooling, ocean acidification, habitat loss from geological processes, anoxia, and meteor impacts [19]), as well as by intrinsically generated instabilities (i.e., destabilizing feedbacks) that have led to runaway bouts of extinction and speciation. Thus, an emerging paradigm favored by a growing number of paleoecologists is that the punctuated history of life represents consecutive basins of attraction or alternate stable states, analogous to the threshold dynamics caused by destabilizing feedbacks that we see more clearly today in many contemporary ecosystem shifts [21,29,34,35]. An alternative hypothesis, that the Earth then and now is in constant flux due to waxing and waning drivers and, therefore, lacks clearly definable states, can be rejected.

Early during the history of the Earth, the paucity of oxygen in the atmosphere and sea, coupled with repeated global ice ages and periods of intense volcanic activity, constrained the evolution of life for billions of years. The first ecosystems were likely to have been those formed by marine sulfur-metabolizing bacteria, dating from 3.4 billion years ago, when the atmosphere was rich in methane [36]. After a threshold level of oxygen had developed, more complex marine life forms evolved during the Pre-Cambrian, followed by the Cambrian Explosion, when many new phyla evolved during a brief transitional period lasting approximately 30 million years. One theory proposes that a threshold in genetic complexity was reached during the Cambrian, and that changes in gene regulation opened an explosion of novelty, generating a regime shift that was global in scale [37]. Furthermore, rapid diversification must have greatly increased the potential for biological interactions to shape and accelerate the pace of evolution (e.g., between newly evolved predators and their prey), creating reinforcing feedbacks that promoted even greater diversity across ancient biomes.

Similarly, land plants underwent a massive radiation during the Devonian, followed by the diversification of angiosperms during the Cretaceous, transforming terrestrial ecosystems. Early angiosperms were restricted to sites that were highly disturbed, aquatic, or extremely dry, representing a stable state dominated by gymnosperms [38]. One hypothesis to explain the subsequent radiation and spread of angiosperms is that their leaf litter increased nutrient supply, helping them to outcompete gymnosperms and ferns. New innovations including radiating angiosperms included pollination and seed dispersal by land animals, and diversification of life histories. These relatively rapid shifts could have also generated positive feedbacks once angiosperms reached a critical level of abundance and diversity as they dispersed from their former strongholds, promoting regime shifts that spread across biotic and climatic zones, leading to a radically different array of terrestrial ecosystems around the world [38].

The extinction of nonavian dinosaurs at the end of the Cretaceous and the radiation of mammals represents another radical and irreversible transition, which has recently been reinterpreted by paleontologists as a planetary-scale regime shift [34]. As with adaptive radiations, internal feedbacks during mass extinctions, such as the loss of a predator or symbiont following the extirpation of its prey or host, could contribute to self-propagation of species loss. In this case, an external shock (the Chicxulub bolide impact in Mexico) in combination with climate change, may have been the final event that tipped the world into a new basin of attraction or alternate stable state. After millions of years of greenhouse conditions, the end of the Cretaceous experienced multiple cycles of climatic cooling of up to 8 °C, and sea level rose and fell in association with the waxing and waning of the polar ice sheets. These instabilities in climate and habitats may have pushed Cretaceous ecosystems closer to a global tipping point that was finally breached by the meteor impact [34]. There are striking analogies between this regime-shift scenario and the better studied dynamics of contemporary ecosystems, such as lakes and coral reefs. Slowly escalating rates of harvesting, global warming, and added nutrients from pollution can push these contemporary ecosystems closer to a tipping point, which is often finally exceeded by an external disturbance, such as a flood, heat wave, or an introduced species (e.g., [39,40]).

Paleoclimates and regime shifts

The climate of the Earth, a key driver of evolutionary and ecological regime shifts, also exhibits a range of dynamic behaviors, including tipping-point dynamics leading to sudden climate shifts (e.g., [9,41]). The interconnection and feedbacks between climate subsystems and ecosystems around the world is a key element in the historical and contemporary dynamics of the biosphere (e.g., [42,43]). One hallmark of tipping points is increased autocorrelation in time series, illustrating a slowing down in system responses as a threshold is approached (e.g., [44]). Analysis of past episodes of abrupt climate change shows this early warning signal remarkably clearly, confirming that the climate itself undergoes multiscale regime shifts [41].

Importantly, all of these ancient climate changes and paleoecological shifts were global in scale and influence, even though the world then, as now, was not a uniform place and climatic elements and distant ecosystems were only weakly interconnected. Change takes time, and the transitory phase of global regime shifts takes a lot of time to play out before equilibrating. To a human observer, even a mass extinction or burst of speciation appears as a slow, smooth trajectory. Similarly, rapid shifts in climate over the past few decades are perceived by humans as glacially slow and hard to distinguish from background variability. Arguably, there would be fewer climate change skeptics if the 4–6°C rise in temperatures predicted by the Inter-governmental Panel on Climate Change (IPCC) by 2100
(under business-as-usual greenhouse gas emissions) were to occur over just a few years. The difficulty of observing a slow regime shift over short periods, or the speed with which a regime shift unfolds, are not valid arguments for refuting them.

**Drivers of change and ecological responses**

The major regional and global drivers of ecological regime shifts today and in the foreseeable future are climate change, land-use change and harvesting, direct manipulation of biogeochemical cycles, toxin release, and invasive species. Some of these drivers are global (climate and biogeochemical cycles), whereas others act more locally but are nonetheless globally pervasive syndromes (land use, harvesting, toxins, and invasive species). For example, almost 1000 introduced species now occur in the Mediterranean Sea, with approximately 25 new ones arriving annually in recent years [45]. Half a world away, the Galapagos Islands, famous for the evolutionary novelty arising from their (former) isolation, are now home to more than 1400 invasive species [46]. At a given location, it can take centuries for a newly introduced species to reach its full spatial extent and density [47]. Thus, invasive species are now a ubiquitous and slowly unfolding phenomenon around the world, because anthropogenic drivers, such as expanding transport and trade networks, globalization of markets, and mass migration of humans, continue to strengthen the linkages between far-flung locations [7,48]. Similarly, the harvesting and depletion of apex predators and large herbivores by humans since the Pleistocene are now so pervasive that they have affected the ecological functioning, trophic structure, and resilience of most ecosystems globally [3].

Much of the controversy over the evidence for or against planetary-scale regime shifts and tipping points in the biosphere arises from a failure to distinguish clearly external drivers of change from the internal responses of ecosystems [49]. For example, some studies (e.g., [22,50]) have regarded habitat fragmentation, loss of biodiversity, emergent diseases, and other native population explosions, as the causes (or proximate drivers) of change, when these phenomena are in fact the responses of ecosystems to larger-scale anthropogenic drivers, such as climate change and overharvesting. The distinction between drivers and responses is important, because one is cause and the other effect, and management interventions work best when they tackle causes rather than symptoms. For example, on coral reefs across the Indo-Pacific, outbreaks of predatory starfish, coral bleaching, and rising diseases are symptoms of ecosystem change (due to increasing pollution, overfishing, and global warming) rather than the causes of the widespread decline of reefs. Many management interventions and restoration efforts are doomed to failure if they focus only on quick-fix solutions to disparate symptoms, while ignoring ongoing or recurrent drivers that are the root cause of ecological regime shifts. Part of the problem is that biologists tend to seek biological explanations, when the crux of the issue are human–climate–ecosystem interactions. Defining biodiversity loss, for example, as a proximate driver (when it is caused primarily by habitat fragmentation, harvesting, and climate change, which in turn are driven ultimately by human population growth and consumption) effectively downscales and simplifies the problem from a complex social–ecological challenge into a purely biological analysis. The human dimensions of regional and global regime shifts are important and intimately linked to societal sharing of power, equity, and governance (Box 2). Therefore, coping with large-scale change, protecting ecosystem functions, and achieving sustainable development will all require a more rigorous integration of multiple research disciplines [51,52] (Box 3).

### Box 2. Global governance

Governance, at all scales (but especially global), is failing to grapple with the rate and extent of change in the biosphere. The governance challenge lies in inducing cooperation among disparate players when all would benefit if they cooperated, where the temptation to free ride on the cooperation of others is strong. Many institutions focus solely on single drivers and systems, and cannot adequately address the influential interactions among them [65]. Moreover, progress to date has been slow and incremental, rather than fast and transformational.

Nation states have been a powerful force in uplifting many people, but individual countries often trade off national benefits at the cost of reduced global resilience (e.g., the wealth of Australia improves as it exports vast amounts of coal that pollute the atmosphere). The urgent need is for a system of global governance that overcomes free riding by providing incentives that reward cooperation and sanction violations. Such a system can only be maintained by a global-scale social contract, supported and enforced by the major sovereign powers. However, power play and hegemony among these major states is the main stumbling block to achieving effective global governance [67].

The Program for Earth System Governance [69] is an emerging proposal that could address the challenges highlighted by the planetary boundaries concept. The Program has identified targeted areas, where major changes are needed for tackling planetary-scale problems [88]. These include strengthening existing international treaties, negotiating new ones, upgrading the relevant United Nations programs, strengthening accountability and legitimacy, and addressing equity and the sharing of responsibilities and power. Collective progress on all of these fronts will be needed to achieve the necessary speed and scale of transformative change in global governance.

### Connectivity and the domino effect

Escalating connections, or connectivity, is a critical issue for planetary resilience because of its potential to increase the likelihood of contagious spreading or scaling-up of local regime shifts to larger scales [53–57]. In ecology, connectivity between metapopulations or metacommunities is often perceived to be advantageous for promoting resilience and recovery; for example, if depleted local populations receive a recruitment or immigration subsidy from elsewhere (e.g., [58]). Similarly, the rationale for establishing networks of protected areas is that a region peppered with parks is more resilient than one without them. The spacing of parks and the connections between them and the broader landscape are key issues for managing heterogeneous land- and seascapes [58].

However, connectivity is a two-edged sword, and more connection among ecosystems through human action can also spread disease, introduce new species, increase harvesting and access to markets, erode indigenous stewardship, distort foodwebs, and eliminate spatial refuges,
gradually eroding resilience at larger and larger scales (e.g., [56,59]). An emerging area of research examines how local regime shifts can propagate to larger scales, analogous to the political science concept of the domino effect, where a regime shift to communism might spread from country to country, or to the cascading collapse of financial systems or a national power grid (e.g., [60]). For example, many individual reefs and islands in the Caribbean, on the Great Barrier Reef, and elsewhere have undergone local regime shifts due to human impacts over the past century. A key issue is the circumstances under which a higher-order threshold could arise from a sufficient amount of local regime shifts, triggering a system-wide collapse (e.g., [55–57]).

The climate and array of biomes on Earth are two highly connected systems, each one comprising multiple subsystems. Changes in vegetation due to shifts in climate, land use, and urbanization can create feedbacks that reinforce climate drivers, generating nonlinear or threshold responses [61,62]. For example, in the Arctic, global warming over the past century has promoted the expansion northwards of boreal forests, causing a reduction in the surface albedo, which in turn leads to further climate changes [63]. Similarly, in the Amazon Basin, changing El Niño–Southern Oscillations (ENSO), lower rainfall, and more frequent fires, are driving a shift to sharply diminished forest cover that is reinforced by logging, while loss of vegetation is further reducing the rainfall [42]. Climate modeling predicts that ongoing deforestation in the tropics could have global impacts on climate through land–atmosphere feedbacks, for example, causing an increase in storm activity in Europe and reinforcing the long-term warming trend across Eurasia [43]. These interconnections are analogous to two interdependent networks, such as the Internet and power grids. A spectacular nation-wide blackout in Italy [60] demonstrates that failure of nodes or clusters in one network (e.g., the computers that control electricity grids) can cascade through the other (e.g., the electricity grid that powers computers) leading to a system-wide collapse in both networks.

Humans are now the unprecedented connectors, imposing more and more demands on ecosystems, near and afar, and changing the climate of the world. With limited connections, ecological collapses might be contained locally, but as connectivity grows due to anthropogenic action, there is greater risk of regional and global regime shifts [56]. Thus, the role that escalating connectivity plays in coalescing scattered, ostensibly local, syndromes into global problems is a major challenge for future research on planetary dynamics (Box 3).

Concluding remarks

One of the shortcomings of predicting the future is that we can not assess the accuracy of our projections until they finally come to pass, or fail to eventuate [64]. Today, we might surmise that anthropogenic activities are already slowly pushing many elements of the biosphere closer to regional- and planetary-scale thresholds. Clearly, there are many uncertainties, warranting a precautionary approach to guiding future planetary trajectories (Box 1). For example, as atmospheric concentrations of CO2 slip past 400 ppm in 2013, and rise even higher over coming decades, the eventual worldwide consequences for ecosystems and humanity are poorly understood. The existence of thresholds and alternate states in many ecosystems at more local scales is not in doubt (e.g., [13–15]). Similarly, tipping points also occur in societies [29], in climate systems [9], and in coupled combinations of all three (e.g., [25,62,64]). At this stage in the evolution of the Earth, changes in society, ecosystems, and climate are intimately interconnected, and large-scale shifts in one become a driver of another.

Two common misconceptions cloud the controversy surrounding planetary-scale tipping points. The first is confusing the rate of change of a system, which may be fast and synchronous or slow and incremental, with the presence or absence of a tipping point. Crucially, a gradual ecological change through time can easily represent the lagged transient response of an ecosystem that has already passed a tipping point from one basin of attraction (i.e., alternate state) to another [31]. The second mistake is failure to differentiate between drivers (i.e., causes), feedbacks, and system responses. Avoiding detrimental consequences of planetary-scale regime shifts will require a clear focus on the drivers and feedbacks, not just on piecemeal efforts to control some of the biological consequences.

One of the areas of high uncertainty in future outcomes is how human-altered ecosystems are changing the climate, and visa versa, increasing the likelihood of transitions that could cascade and eventually spread globally. Arguably, the escalating impact of multiple anthropogenic drivers on ecosystems and climate may soon reach levels that in the past have triggered long-lasting global responses (e.g., [19,21]). In some cases, we may have already passed unrecognized global tipping points, and a

**Box 3. Key issues for future research**

**Regime shifts and tipping points**

- How do multiple drivers interact?
- How do feedback interactions influence threshold dynamics?
- What negative feedbacks could be promoted that weaken threshold behavior?
- How can tipping points be detected or anticipated?
- How do pulse and/or press disturbances contribute to regime shifts?
- How do we identify regime shifts that unfold slowly and smoothly?

**Connectivity and domino effects**

- How do local and regional-scale regime shifts spread to larger scales?
- In the context of increasing connectivity, what role do introduced species play in promoting or dampening regime shifts?
- How do tipping points cascade across linked social–ecological–climate systems?

**Governance**

- How can power and hegemony be incorporated in an evolving set of global institutions?
- How can adaptive governance be implemented at the global scale?
- How can incentives for cooperation and sanctions for violation be designed to minimize free riding in managing the global commons?
slow trajectory to a new regime could have already begun [40].

Undoubtedly, the greatest challenge for the future is incorporating the dynamics of tipping points and alternate states into global governance of the environment, food, and energy (e.g., [65–69]), and the concept of planetary boundaries is one potential framework that could help guide future approaches to policy and management actions (Box 2). We stress, however, that the strong opinions expressed on either side of the debate on planetary tipping points (e.g., [21,22]) are sometimes based on assertions or unproven assumptions, and there are many knowledge gaps in our understanding of large-scale transformations (Box 3).

Acknowledgments

This research was supported by the Australian Research Council’s Centre of Excellence Program. We thank Matt Young for technical assistance.

References

15 Staver, A.C. et al. (2011) Tree cover in sub-Saharan Africa: rainfall and fire constrain forest and savanna as alternative stable states. Ecology 92, 1063–1072
22 Brook, B.W. et al. (2013) Does the terrestrial biosphere have planetary tipping points? Trends Ecol. Evol. 28, 396–401

32 Minckley, T.A. et al. (2012) Resilience and regime change in a southern Rocky Mountain ecosystem during the past 17 000 years. Ecol. Monogr. 82, 49–68
42 Malhi, Y. et al. (2008) Climate change, deforestation, and the fate of the Amazon. Science 319, 169–172
47 Gasso, N. et al. (2010) Spreading to a limit: the time required for a neophyte to reach its maximum range. Divers. Distrib. 16, 310–311
52 Carpenter, S. et al. (2012) General resilience to cope with extreme events. Sustainability 4, 3248–3259