

RESEARCH ARTICLE SUMMARY

SUSTAINABILITY

Planetary boundaries: Guiding human development on a changing planet

Will Steffen,* Katherine Richardson, Johan Rockström, Sarah E. Cornell, Ingo Fetzer, Elena M. Bennett, Reinette Biggs, Stephen R. Carpenter, Wim de Vries, Cynthia A. de Wit, Carl Folke, Dieter Gerten, Jens Heinke, Georgina M. Mace, Linn M. Persson, Veerabhadran Ramanathan, Belinda Meyers, Sverker Sörlin

INTRODUCTION: There is an urgent need for a new paradigm that integrates the continued development of human societies and the maintenance of the Earth system (ES) in a resilient and accommodating state. The planetary boundary (PB) framework contributes to such a paradigm by providing a science-based analysis of the risk that human perturbations will destabilize the ES at the planetary scale. Here, the scientific underpinnings of the PB framework are updated and strengthened.

RATIONALE: The relatively stable, 11,700-year-long Holocene epoch is the only state of the ES

that we know for certain can support contemporary human societies. There is increasing evidence that human activities are affecting ES functioning to a degree that threatens the resilience of the ES—its ability to persist in a Holocene-like state in the face of increasing human pressures and shocks. The PB framework is based on critical processes that regulate ES functioning. By combining improved scientific understanding of ES functioning with the precautionary principle, the PB framework identifies levels of anthropogenic perturbations below which the risk of destabilization of the ES is likely to remain low—a “safe operating

space” for global societal development. A zone of uncertainty for each PB highlights the area of increasing risk. The current level of anthropogenic impact on the ES, and thus the risk to the stability of the ES, is assessed by comparison with the proposed PB (see the figure).

RESULTS: Three of the PBs (climate change, stratospheric ozone depletion, and ocean acidification) remain essentially unchanged from the earlier analysis. Regional-level boundaries as well as globally aggregated PBs have now been developed for biosphere integrity (earlier “biodiversity loss”), biogeochemical flows, land-system change, and freshwater use. At present, only one regional boundary (south Asian monsoon) can be established for atmospheric aerosol loading. Although we cannot identify a single PB

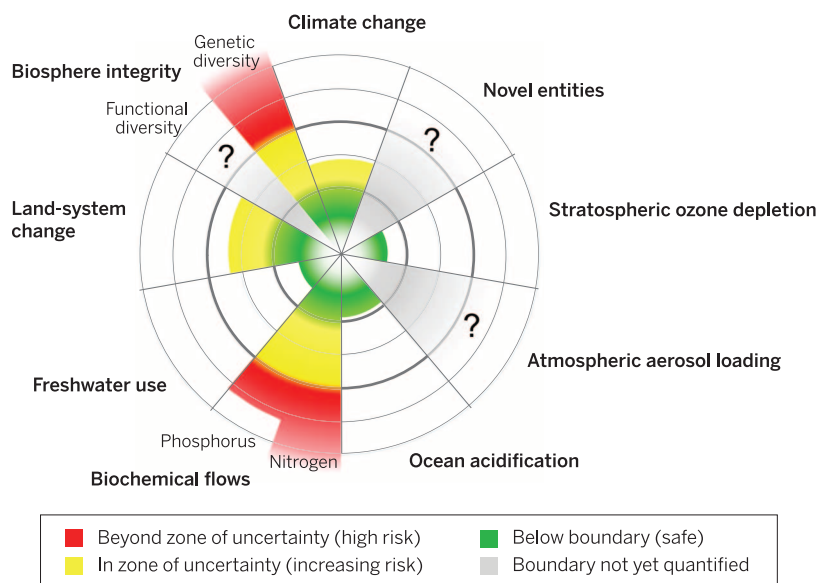
ON OUR WEB SITE

Read the full article at <http://dx.doi.org/10.1126/science.1259855>

for novel entities (here defined as new substances, new forms of existing substances, and modified life forms that have the potential for unwanted geo-

physical and/or biological effects), they are included in the PB framework, given their potential to change the state of the ES. Two of the PBs—climate change and biosphere integrity—are recognized as “core” PBs based on their fundamental importance for the ES. The climate system is a manifestation of the amount, distribution, and net balance of energy at Earth’s surface; the biosphere regulates material and energy flows in the ES and increases its resilience to abrupt and gradual change. Anthropogenic perturbation levels of four of the ES processes/features (climate change, biosphere integrity, biogeochemical flows, and land-system change) exceed the proposed PB (see the figure).

CONCLUSIONS: PBs are scientifically based levels of human perturbation of the ES beyond which ES functioning may be substantially altered. Transgression of the PBs thus creates substantial risk of destabilizing the Holocene state of the ES in which modern societies have evolved. The PB framework does not dictate how societies should develop. These are political decisions that must include consideration of the human dimensions, including equity, not incorporated in the PB framework. Nevertheless, by identifying a safe operating space for humanity on Earth, the PB framework can make a valuable contribution to decision-makers in charting desirable courses for societal development. ■



Current status of the control variables for seven of the planetary boundaries. The green zone is the safe operating space, the yellow represents the zone of uncertainty (increasing risk), and the red is a high-risk zone. The planetary boundary itself lies at the intersection of the green and yellow zones. The control variables have been normalized for the zone of uncertainty; the center of the figure therefore does not represent values of 0 for the control variables. The control variable shown for climate change is atmospheric CO₂ concentration. Processes for which global-level boundaries cannot yet be quantified are represented by gray wedges; these are atmospheric aerosol loading, novel entities, and the functional role of biosphere integrity.

The list of author affiliations is available in the full article online.

*Corresponding author. E-mail: will.steffen@anu.edu.au
Cite this article as W. Steffen et al., *Science* 347, 1259855 (2015). DOI: 10.1126/science.1259855

RESEARCH ARTICLE

SUSTAINABILITY

Planetary boundaries: Guiding human development on a changing planet

Will Steffen,^{1,2*} Katherine Richardson,³ Johan Rockström,¹ Sarah E. Cornell,¹ Ingo Fetzer,¹ Elena M. Bennett,⁴ Reinette Biggs,^{1,5} Stephen R. Carpenter,⁶ Wim de Vries,^{7,8} Cynthia A. de Wit,⁹ Carl Folke,^{1,10} Dieter Gerten,¹¹ Jens Heinke,^{11,12,13} Georgina M. Mace,¹⁴ Linn M. Persson,¹⁵ Veerabhadran Ramanathan,^{16,17} Belinda Reyers,^{1,18} Sverker Sörlin¹⁹

The planetary boundaries framework defines a safe operating space for humanity based on the intrinsic biophysical processes that regulate the stability of the Earth system. Here, we revise and update the planetary boundary framework, with a focus on the underpinning biophysical science, based on targeted input from expert research communities and on more general scientific advances over the past 5 years. Several of the boundaries now have a two-tier approach, reflecting the importance of cross-scale interactions and the regional-level heterogeneity of the processes that underpin the boundaries. Two core boundaries—climate change and biosphere integrity—have been identified, each of which has the potential on its own to drive the Earth system into a new state should they be substantially and persistently transgressed.

The planetary boundary (PB) approach (1, 2) aims to define a safe operating space for human societies to develop and thrive, based on our evolving understanding of the functioning and resilience of the Earth system. Since its introduction, the framework has been subject to scientific scrutiny [e.g., (3–7)] and has attracted considerable interest and discussions within the policy, governance, and business sectors as an approach to inform efforts toward global sustainability (8–10).

In this analysis, we further develop the basic PB framework by (i) introducing a two-tier approach for several of the boundaries to account for regional-level heterogeneity; (ii) updating the quantification of most of the PBs; (iii) identifying two core boundaries; and (iv) proposing a regional-level quantitative boundary for one of the two that were not quantified earlier (1).

The basic framework: Defining a safe operating space

Throughout history, humanity has faced environmental constraints at local and regional levels, with some societies dealing with these challenges more effectively than others (11, 12). More recently, early industrial societies often used local waterways and airsheds as dumping grounds for their waste and effluent from industrial processes. This eroded local and regional environmental quality and stability, threatening to undermine the progress made through industrialization by damaging human health and degrading ecosystems. Eventually, this led to the introduction of local or regional boundaries or constraints on what

could be emitted to and extracted from the environment (e.g., chemicals that pollute airsheds or waterways) and on how much the environment could be changed by direct human modification (land-use/cover change in natural ecosystems) (13). The regulation of some human impacts on the environment—for example, the introduction of chemical contaminants—is often framed in the context of “safe limits” (14).

These issues remain, but in addition we now face constraints at the planetary level, where the magnitude of the challenge is vastly different. The human enterprise has grown so dramatically since the mid-20th century (15) that the relatively stable, 11,700-year-long Holocene epoch, the only state of the planet that we know for certain can support contemporary human societies, is now being destabilized (figs. S1 and S2) (16–18). In fact, a new geological epoch, the Anthropocene, has been proposed (19).

The precautionary principle suggests that human societies would be unwise to drive the Earth system substantially away from a Holocene-like condition. A continuing trajectory away from the Holocene could lead, with an uncomfortably high probability, to a very different state of the Earth system, one that is likely to be much less hospitable to the development of human societies (17, 18, 20). The PB framework aims to help guide human societies away from such a trajectory by defining a “safe operating space” in which we can continue to develop and thrive. It does this by proposing boundaries for anthropogenic perturbation of critical Earth-system processes. Respecting these boundaries would greatly reduce the

risk that anthropogenic activities could inadvertently drive the Earth system to a much less hospitable state.

Nine processes, each of which is clearly being modified by human actions, were originally suggested to form the basis of the PB framework (1). Although these processes are fundamental to Earth-system functioning, there are many other ways that Earth-system functioning could be described, including potentially valuable metrics for quantifying the human imprint on it. These alternative approaches [e.g., (4)] often represent ways to explore and quantify interactions among the boundaries. They can provide a valuable complement to the original approach (1) and further enrich the broader PB concept as it continues to evolve.

The planetary boundary framework: Thresholds, feedbacks, resilience, uncertainties

A planetary boundary as originally defined (1) is not equivalent to a global threshold or tipping point. As Fig. 1 shows, even when a global- or continental/ocean basin-level threshold in an Earth-system process is likely to exist [e.g., (20, 21)], the proposed planetary boundary is not placed at the position of the biophysical threshold but rather upstream of it—i.e., well before reaching the threshold. This buffer between the boundary (the end of the safe operating space, the green zone in Fig. 1) and the threshold not only accounts for uncertainty in the precise position of the threshold with respect to the control variable

¹Stockholm Resilience Centre, Stockholm University, 10691 Stockholm, Sweden. ²Fenner School of Environment and Society, The Australian National University, Canberra, ACT 2601, Australia. ³Center for Macroecology, Evolution, and Climate, University of Copenhagen, Natural History Museum of Denmark, Universitetsparken 15, Building 3, 2100 Copenhagen, Denmark. ⁴Department of Natural Resource Sciences and McGill School of Environment, McGill University, 21, 111 Lakeshore Road, Ste-Anne-de-Bellevue, QC H9X 3V9, Canada. ⁵Centre for Studies in Complexity, Stellenbosch University, Private Bag X1, Stellenbosch 7602, South Africa. ⁶Center for Limnology, University of Wisconsin, 680 North Park Street, Madison WI 53706 USA. ⁷Alterra Wageningen University and Research Centre, P.O. Box 47, 6700AA Wageningen, Netherlands. ⁸Environmental Systems Analysis Group, Wageningen University, P.O. Box 47, 6700 AA Wageningen, Netherlands. ⁹Department of Environmental Science and Analytical Chemistry, Stockholm University, 10691 Stockholm, Sweden. ¹⁰Beijing Institute of Ecological Economics, Royal Swedish Academy of Sciences, SE-10405 Stockholm, Sweden. ¹¹Research Domain Earth System Analysis, Potsdam Institute for Climate Impact Research (PIK), Telegraphenberg A62, 14473 Potsdam, Germany. ¹²International Livestock Research Institute, P.O. Box 30709, Nairobi, 00100 Kenya. ¹³CSIRO (Commonwealth Scientific and Industrial Research Organization), St. Lucia, QLD 4067, Australia. ¹⁴Centre for Biodiversity and Environment Research (CBER), Department of Genetics, Evolution and Environment, University College London, Gower Street, London WC1E 6BT, UK. ¹⁵Stockholm Environment Institute, Linnégatan 87D, SE-10451 Stockholm, Sweden. ¹⁶Scripps Institution of Oceanography, University of California at San Diego, 8622 Kennel Way, La Jolla, CA 92037 USA. ¹⁷TERI (The Energy and Resources Institute) University, 10 Institutional Area, Vasant Kunj, New Delhi, Delhi 110070, India. ¹⁸Natural Resources and the Environment, CSIR, P.O. Box 320, Stellenbosch 7599, South Africa. ¹⁹Division of History of Science, Technology and Environment, KTH Royal Institute of Technology, SE-10044 Stockholm, Sweden. *Corresponding author. E-mail: will.steffen@anu.edu.au

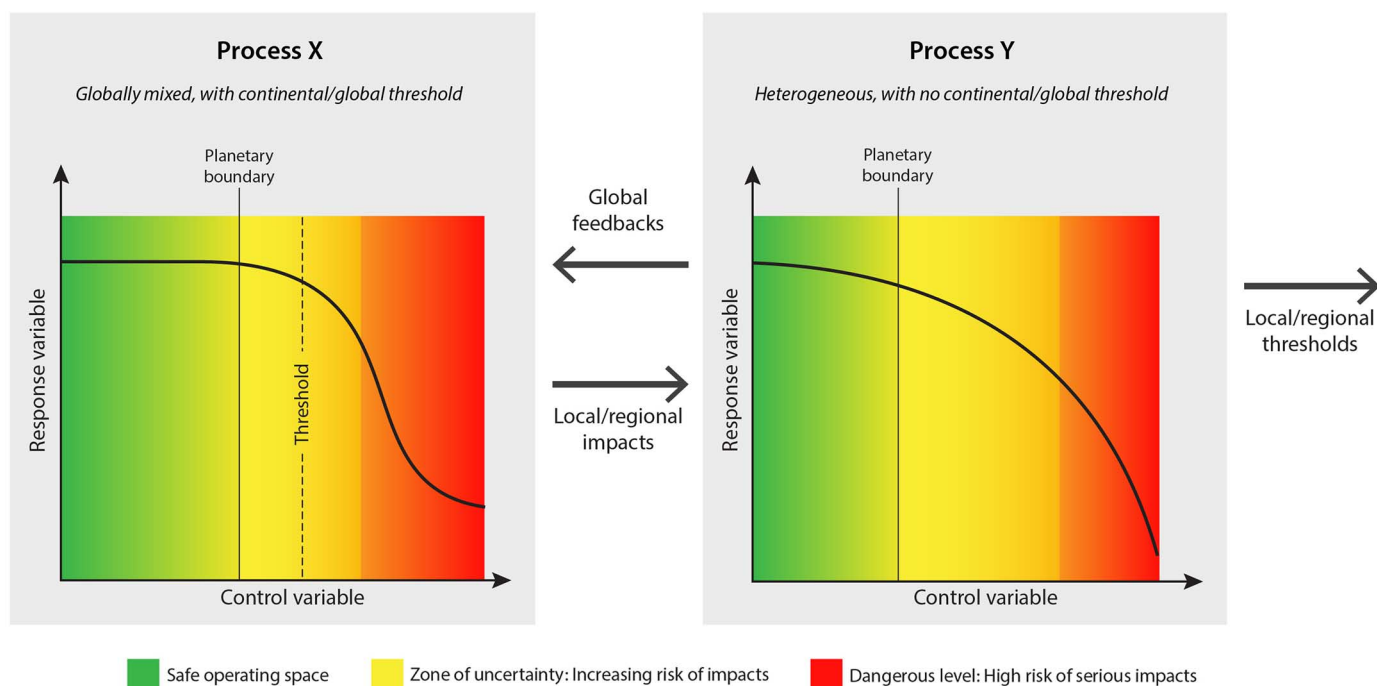


Fig. 1. The conceptual framework for the planetary boundary approach, showing the safe operating space, the zone of uncertainty, the position of the threshold (where one is likely to exist), and the area of high risk. Modified from (1).

but also allows society time to react to early warning signs that it may be approaching a threshold and consequent abrupt or risky change.

The developing science of early-warning signs can warn of an approaching threshold or a decrease in the capability of a system to persist under changing conditions. Examples include “critical slowing down” in a process (22), increasing variance (23), and flickering between states of the system (24–26). However, for such science to be useful in a policy context, it must provide enough time for society to respond in order to steer away from an impending threshold before it is crossed (27, 28). The problem of system inertia—for example, in the climate system (18)—needs to be taken into account in assessing the time needed for society to react to early-warning signs.

Not all Earth-system processes included in the PB approach have singular thresholds at the global/continental/ocean basin level (1). Nevertheless, it is important that boundaries be established for these processes. They affect the capacity of the Earth system to persist in a Holocene-like state under changing conditions (henceforth “resilience”) by regulating biogeochemical flows (e.g., the terrestrial and marine biological carbon sinks) or by providing the capacity for ecosystems to tolerate perturbations and shocks and to continue functioning under changing abiotic conditions (29, 30). Examples of such processes are land-system change, freshwater use, change in biosphere integrity [rate of biodiversity loss in (1, 2)], and changes in other biogeochemical flows in addition to carbon (e.g., nitrogen and phosphorus). Placing boundaries for these processes is more

difficult than for those with known large-scale thresholds (21) but is nevertheless important for maintaining the resilience of the Earth system as a whole. As indicated in Fig. 1, these processes, many of which show threshold behavior at local and regional scales, can generate feedbacks to the processes that do have large-scale thresholds. The classic example is the possible weakening of natural carbon sinks, which could further destabilize the climate system and push it closer to large thresholds [e.g., loss of the Greenland ice sheet (18)]. An interesting research question of relevance to the PB framework is how small-scale regime shifts can propagate across scales and possibly lead to global-level transitions (31, 32).

A zone of uncertainty, sometimes large, is associated with each of the boundaries (yellow zone in Fig. 1). This zone encapsulates both gaps and weaknesses in the scientific knowledge base and intrinsic uncertainties in the functioning of the Earth system. At the “safe” end of the zone of uncertainty, current scientific knowledge suggests that there is very low probability of crossing a critical threshold or substantially eroding the resilience of the Earth system. Beyond the “danger” end of the zone of uncertainty, current knowledge suggests a much higher probability of a change to the functioning of the Earth system that could potentially be devastating for human societies. Application of the precautionary principle dictates that the planetary boundary is set at the “safe” end of the zone of uncertainty. This does not mean that transgressing a boundary will instantly lead to an unwanted outcome but that the farther the boundary is transgressed, the higher the risk of regime shifts, destabilized sys-

tem processes, or erosion of resilience and the fewer the opportunities to prepare for such changes. Observations of the climate system show this principle in action by the influence of increasing atmospheric greenhouse gas concentrations on the frequency and intensity of many extreme weather events (17, 18).

Linking global and regional scales

PB processes operate across scales, from ocean basins/biomes or sources/sinks to the level of the Earth system as a whole. Here, we address the subglobal aspects of the PB framework. Rockström *et al.* (1) estimated global boundaries only, acknowledging that the control variables for many processes are spatially heterogeneous. That is, changes in control variables at the subglobal level can influence functioning at the Earth-system level, which indicates the need to define subglobal boundaries that are compatible with the global-level boundary definition. Avoiding the transgression of subglobal boundaries would thus contribute to an aggregate outcome within a planetary-level safe operating space.

We focus on the five PBs that have strong regional operating scales: biosphere integrity, biogeochemical flows [earlier termed “phosphorus (P) and nitrogen (N) cycles” (1, 2)], land-system change, freshwater use, and atmospheric aerosol loading. Table S1 describes how transgression of any of the proposed boundaries at the subglobal level affects the Earth system at the global level.

For those processes where subglobal dynamics potentially play a critical role in global dynamics, the operational challenge is to capture the importance of subglobal change for the functioning

of the Earth system. To do this, we propose the development of a two-level set of control variables and boundaries. The subglobal-level units of analysis for these six boundaries are not identical; they vary according to the role that the processes play in the Earth system: (i) changes in biosphere integrity occur at the level of land-based biomes, large freshwater ecosystems, or major marine ecosystems as the largest subglobal unit; (ii) the role of direct, human-driven land-system change in biophysical climate regulation is primarily related to changes in forest biomes; (iii) freshwater flows and use occur at the largest subglobal level in the major river basins around the world; and (iv) changes in biogeochemical flows, exemplified by phosphorus and nitrogen cycling, aggregate from relatively localized but very severe perturbations in intensive agricultural zones to affect global flows of nutrients. We recognize these as critical regions for Earth-system functioning. Where appropriate, the updates of the individual boundaries (see below) (33) now contain both the globally aggregated boundary value of the control variable and its regional distribution function. Figure 2 shows the distributions and current status of the control variables for three of the boundaries where subglobal dynamics are crit-

ical: biogeochemical cycles, land-system change, and freshwater use.

We emphasize that our subglobal-level focus is based on the necessity to consider this level to understand the functioning of the Earth system as a whole. The PB framework is therefore meant to complement, not replace or supersede, efforts to address local and regional environmental issues.

Updates of the individual boundaries

Brief updates of all nine of the PBs are given in this section, and more detailed descriptions of the updates for three of the PBs that have undergone more extensive revision can be found in (33). The geographical distribution issues discussed above are particularly important for five of the PBs, and their control variables and boundaries have been revised accordingly (Table 1). Figure 3 shows the current status of the seven boundaries that can be quantified at the global level.

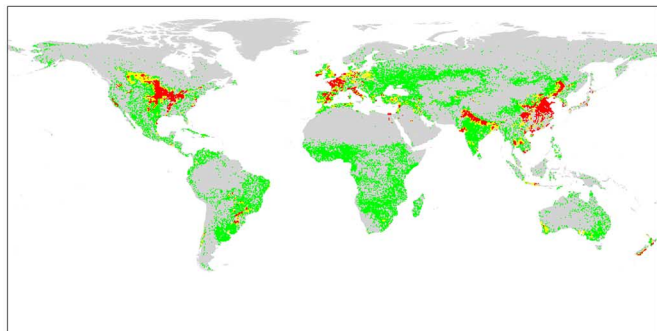
Climate change

We retain the control variables and boundaries originally proposed—i.e., an atmospheric CO₂ concentration of 350 parts per million (ppm) and an increase in top-of-atmosphere radiative forcing of +1.0 W m⁻² relative to preindustrial levels (1). The radiative forcing control variable is the more

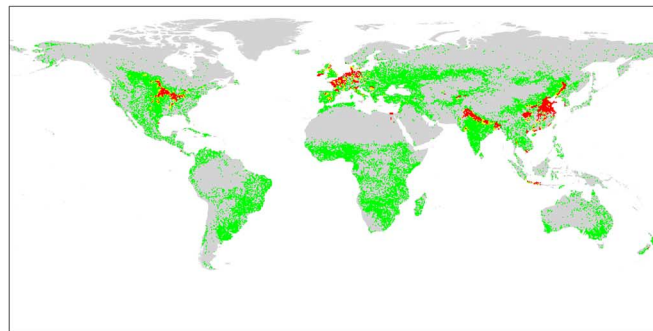
inclusive and fundamental, although CO₂ is important because of its long lifetime in the atmosphere and the very large human emissions. Human-driven changes to radiative forcing include all anthropogenic factors: CO₂, other greenhouse gases, aerosols, and other factors that affect the energy balance (18). Radiative forcing is generally the more stringent of the two boundaries, although the relationship between it and CO₂ can vary through time with changes in the relative importance of the individual radiative forcing factors.

Evidence has accumulated to suggest that the zone of uncertainty for the CO₂ control variable should be narrowed from 350 to 550 ppm to 350 to 450 ppm CO₂ (17, 18), while retaining the current zone of uncertainty for radiative forcing of +1.0 to 1.5 W m⁻² relative to preindustrial levels. Current values of the control variables are 399 ppm CO₂ (annual average concentration for 2014) (34) and +2.3 W m⁻² (1.1 to 3.3 W m⁻²) in 2011 relative to 1750 (18). Observed changes in climate at current levels of the control variables confirm the original choice of the boundary values and the narrowing of the zone of uncertainty for CO₂. For example, there has already been an increase in the intensity, frequency, and duration of heat waves globally (35); the number of heavy rainfall

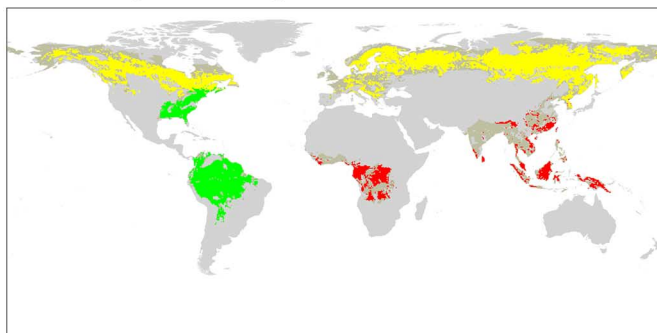
A Phosphorus



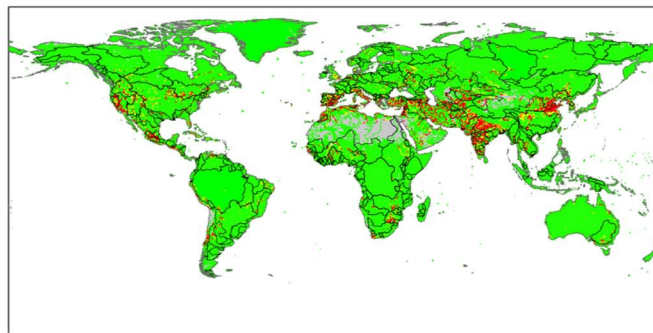
B Nitrogen



C Land-system change



D Freshwater use



■ Beyond zone of uncertainty (high risk) ■ In zone of uncertainty (increasing risk) ■ Below boundary (safe)

Fig. 2. The subglobal distributions and current status of the control variables for (A) biogeochemical flows of P; (B) biogeochemical flows of N; (C) land-system change; and (D) freshwater use. In each panel, green areas are within the boundary (safe), yellow areas are within the zone of uncertainty (increasing risk), and red areas are beyond the zone of uncertainty (high risk). Gray areas in (A) and (B) are areas where P and N fertilizers are not applied; in (C), they are areas not covered by major forest biomes; and in (D), they are areas where river flow is very low so that environmental flows are not allocated. See Table 1 for values of the boundaries and their zones of uncertainty and (33) for more details on methods and results.

Table 1. The updated control variables and their current values, along with the proposed boundaries and zones of uncertainty, for all nine planetary boundaries. In the first column, the name for the Earth-system process used in the original PB publication (R2009, reference 1) is given for comparison.

Earth-system process	Control variable(s)	Planetary boundary (zone of uncertainty)	Current value of control variable
Climate change (R2009: same)	Atmospheric CO ₂ concentration, ppm	350 ppm CO ₂ (350–450 ppm)	398.5 ppm CO ₂
	Energy imbalance at top-of-atmosphere, W m ⁻²	+1.0 W m ⁻² (+1.0–1.5 W m ⁻²)	2.3 W m ⁻² (1.1–3.3 W m ⁻²)
Change in biosphere integrity (R2009: Rate of biodiversity loss)	<i>Genetic diversity:</i> Extinction rate	< 10 E/MSY (10–100 E/MSY) but with an aspirational goal of ca. 1 E/MSY (the background rate of extinction loss). E/MSY = extinctions per million species-years	100–1000 E/MSY
	<i>Functional diversity:</i> Biodiversity Intactness Index (BII)	Maintain BII at 90% (90–30%) or above, assessed geographically by biomes/large regional areas (e.g. southern Africa), major marine ecosystems (e.g., coral reefs) or by large functional groups	84%, applied to southern Africa only
	Note: These are interim control variables until more appropriate ones are developed		
Stratospheric ozone depletion (R2009: same)	Stratospheric O ₃ concentration, DU	<5% reduction from pre-industrial level of 290 DU (5%–10%), assessed by latitude	Only transgressed over Antarctica in Austral spring (~200 DU)
Ocean acidification (R2009: same)	Carbonate ion concentration, average global surface ocean saturation state with respect to aragonite (Ω_{arag})	≥80% of the pre-industrial aragonite saturation state of mean surface ocean, including natural diel and seasonal variability (≥80%– ≥70%)	~84% of the pre-industrial aragonite saturation state
Biogeochemical flows: (P and N cycles) (R2009: Biogeochemical flows: (interference with P and N cycles))	<i>P Global:</i> P flow from freshwater systems into the ocean	11 Tg P yr ⁻¹ (11–100 Tg P yr ⁻¹)	~22 Tg P yr ⁻¹
	<i>P Regional:</i> P flow from fertilizers to erodible soils	6.2 Tg yr ⁻¹ mined and applied to erodible (agricultural) soils (6.2–11.2 Tg yr ⁻¹). Boundary is a global average but regional distribution is critical for impacts.	~14 Tg P yr ⁻¹
	<i>N Global:</i> Industrial and intentional biological fixation of N	62 Tg N yr ⁻¹ (62–82 Tg N yr ⁻¹). Boundary acts as a global 'valve' limiting introduction of new reactive N to Earth System, but regional distribution of fertilizer N is critical for impacts.	~150 Tg N yr ⁻¹

Earth-system process	Control variable(s)	Planetary boundary (zone of uncertainty)	Current value of control variable
Land-system change (R2009: same)	<i>Global:</i> Area of forested land as % of original forest cover	<i>Global:</i> 75% (75–54%) Values are a weighted average of the three individual biome boundaries and their uncertainty zones	62%
	<i>Biome:</i> Area of forested land as % of potential forest	<i>Biome:</i> Tropical: 85% (85–60%) Temperate: 50% (50–30%) Boreal: 85% (85–60%)	
Freshwater use (R2009: Global freshwater use)	<i>Global:</i> Maximum amount of consumptive blue water use ($\text{km}^3\text{yr}^{-1}$)	<i>Global:</i> $4000\text{ km}^3\text{ yr}^{-1}$ ($4000\text{--}6000\text{ km}^3\text{ yr}^{-1}$)	$\sim 2600\text{ km}^3\text{ yr}^{-1}$
	<i>Basin:</i> Blue water withdrawal as % of mean monthly river flow	<i>Basin:</i> Maximum monthly withdrawal as a percentage of mean monthly river flow. For low-flow months: 25% (25–55%); for intermediate-flow months: 30% (30–60%); for high-flow months: 55% (55–85%)	
Atmospheric aerosol loading (R2009: same)	<i>Global:</i> Aerosol Optical Depth (AOD), but much regional variation		0.30 AOD, over South Asian region
	<i>Regional:</i> AOD as a seasonal average over a region. South Asian Monsoon used as a case study	<i>Regional:</i> (South Asian Monsoon as a case study): anthropogenic total (absorbing and scattering) AOD over Indian subcontinent of 0.25 (0.25–0.50); absorbing (warming) AOD less than 10% of total AOD	
Introduction of novel entities (R2009: Chemical pollution)	No control variable currently defined	No boundary currently identified, but see boundary for stratospheric ozone for an example of a boundary related to a novel entity (CFCs)	

events in many regions of the world is increasing (17); changes in atmospheric circulation patterns have increased drought in some regions of the world (17); and the rate of combined mass loss from the Greenland and Antarctic ice sheets is increasing (36).

Changes in biosphere integrity

We propose a two-component approach, addressing two key roles of the biosphere in the Earth system. The first captures the role of genetically unique material as the “information bank” that ultimately determines the potential for life to

continue to coevolve with the abiotic component of the Earth system in the most resilient way possible. Genetic diversity provides the long-term capacity of the biosphere to persist under and adapt to abrupt and gradual abiotic change. The second captures the role of the biosphere in Earth-system functioning through the value, range, distribution, and relative abundance of the functional traits of the organisms present in an ecosystem or biota (7).

For the first role, the concept of phylogenetic species variability (PSV) (7, 33, 37) would be an appropriate control variable. However, because

global data are not yet available for PSV, we retain the global extinction rate as an interim control variable, although it is measured inaccurately and with a time lag. There may be a considerable risk in using extinction rate as a control variable, because phylogenetic (and functional) diversity may be more sensitive to human pressures than species-level diversity (38). In principle, the boundary should be set at a rate of loss of PSV no greater than the rate of evolution of new PSV during the Holocene. Because that is unknown, we must fall back on the (imperfectly) known extinction rate of well-studied organisms over the past several

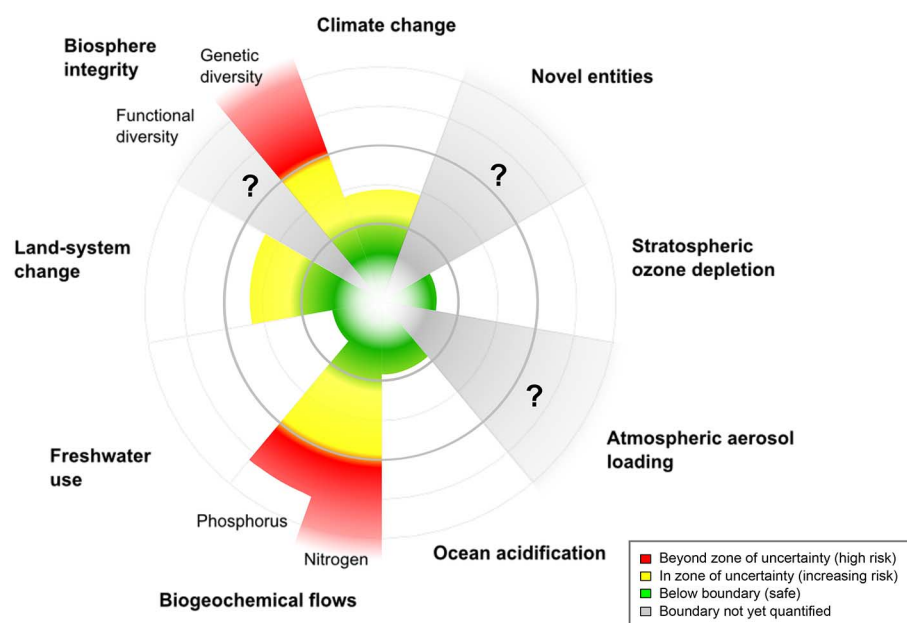


Fig. 3. The current status of the control variables for seven of the nine planetary boundaries. The green zone is the safe operating space (below the boundary), yellow represents the zone of uncertainty (increasing risk), and red is the high-risk zone. The planetary boundary itself lies at the inner heavy circle. The control variables have been normalized for the zone of uncertainty (between the two heavy circles); the center of the figure therefore does not represent values of 0 for the control variables. The control variable shown for climate change is atmospheric CO₂ concentration. Processes for which global-level boundaries cannot yet be quantified are represented by gray wedges; these are atmospheric aerosol loading, novel entities, and the functional role of biosphere integrity. Modified from (1).

million years—about 1 per million species-years (39)—and add a large uncertainty bound, raising the boundary to 10 per million species-years. The risk is that, although the Earth system can tolerate a higher-than-background level of extinctions for a time, we do not know what levels of, or types of, biodiversity loss may possibly trigger nonlinear or irreversible changes to the Earth system.

The second control variable aims to capture the role of the biosphere in Earth-system functioning and measures loss of biodiversity components at both global and biome/large ecosystem levels. Although several variables have been developed at local scales for measuring functional diversity [e.g., (40)], finding an appropriate control variable at regional or global levels is challenging. For the present, we propose an interim control variable, the Biodiversity Intactness Index (BII) (41). BII assesses change in population abundance as a result of human impacts, such as land or resource use, across a wide range of taxa and functional groups at a biome or ecosystem level using pre-industrial era abundance as a reference point. The index typically ranges from 100% (abundances across all functional groups at preindustrial levels) to lower values that reflect the extent and degree of human modification of populations of plants and animals. BII values for particular functional groups can go above 100% if human modifications to ecosystems lead to increases in the abundance of those species.

Due to a lack of evidence on the relationship between BII and Earth-system responses, we pro-

pose a preliminary boundary at 90% of the BII but with a very large uncertainty range (90 to 30%) that reflects the large gaps in our knowledge about the BII–Earth-system functioning relationship (42, 43). BII has been so far applied to southern Africa's terrestrial biomes only (see fig. S3 for an estimation of aggregated human pressures on the terrestrial biosphere globally), where the index (not yet disaggregated to functional groups) was estimated to be 84%. BII ranged from 69 to 91% for the seven countries where it has been applied (41). Observations across these countries suggest that decreases in BII adequately capture increasing levels of ecosystem degradation, defined as land uses that do not alter the land-cover type but lead to a persistent loss in ecosystem productivity (41).

In addition to further work on functional measures such as BII, in the longer term the concept of biome integrity—the functioning and persistence of biomes at broad scales (7)—offers a promising approach and, with further research, could provide a set of operational control variables (one per biome) that is appropriate, robust, and scientifically based.

Stratospheric ozone depletion

We retain the original control variable [O₃ concentration in DU (Dobson units)] and boundary (275 DU). This boundary is only transgressed over Antarctica in the austral spring, when O₃ concentration drops to about 200 DU (44). However, the minimum O₃ concentration has been

steady for about 15 years and is expected to rise over the coming decades as the ozone hole is repaired after the phasing out of ozone-depleting substances. This is an example in which, after a boundary has been transgressed regionally, humanity has taken effective action to return the process back to within the boundary.

Ocean acidification

This boundary is intimately linked with one of the control variables, CO₂, for the climate change PB. The concentration of free H⁺ ions in the surface ocean has increased by about 30% over the past 200 years due to the increase in atmospheric CO₂ (45). This, in turn, influences carbonate chemistry in surface ocean waters. Specifically, it lowers the saturation state of aragonite (Ω_{arag}), a form of calcium carbonate formed by many marine organisms. At $\Omega_{\text{arag}} < 1$, aragonite will dissolve. No new evidence has emerged to suggest that the originally proposed boundary ($\geq 80\%$ of the pre-industrial average annual global Ω_{arag}) should be adjusted, although geographical heterogeneity in Ω_{arag} is important in monitoring the state of the boundary around the world's oceans (fig. S4). Currently, Ω_{arag} is approximately equal to 84% of the preindustrial value (46). This boundary would not be transgressed if the climate-change boundary of 350 ppm CO₂ were to be respected.

Biogeochemical flows

The original boundary was formulated for phosphorus (P) and nitrogen (N) only, but we now propose a more generic PB to encompass human influence on biogeochemical flows in general. Although the carbon cycle is covered in the climate-change boundary, other elements, such as silicon (47, 48), are also important for Earth-system functioning. Furthermore, there is increasing evidence that ratios between elements in the environment may have impacts on biodiversity on land and in the sea (49–51). Thus, we may ultimately need to develop PBs for other elements and their ratios, although for now we focus on P and N only.

A two-level approach is now proposed for the P component of the biogeochemical flows boundary (see also the supplementary materials). The original global-level boundary, based on the prevention of a large-scale ocean anoxic event, is retained, with the proposed boundary set at a sustained flow of 11 Tg P year⁻¹ from freshwater systems into the ocean. Based on the analysis of Carpenter and Bennett (3), we now propose an additional regional-level P boundary, designed to avert widespread eutrophication of freshwater systems, at a flow of 6.2 Tg P year⁻¹ from fertilizers (mined P) to erodible soils.

Given that the addition of P to regional watersheds is almost entirely from fertilizers, the regional-level boundary applies primarily to the world's croplands. The current global rate of application of P in fertilizers to croplands is 14.2 Tg P year⁻¹ (52, 53). Observations point toward a few agricultural regions of very high P application rates as the main contributors to the transgression of this boundary (Fig. 2 and fig. S5A) and suggest that a redistribution of P from areas

where it is currently in excess to areas where the soil is naturally P-poor may simultaneously boost global crop production and reduce the transgression of the regional-level P boundary (3, 52, 54).

The N boundary has been taken from the comprehensive analysis of de Vries *et al.* (5), which proposed a PB for eutrophication of aquatic ecosystems of 62 Tg N year⁻¹ from industrial and intentional biological N fixation, using the most stringent water quality criterion. As for the P boundary, a few agricultural regions of very high N application rates are the main contributors to the transgression of this boundary (Fig. 2 and fig. S5B). This suggests that a redistribution of N could simultaneously boost global crop production and reduce the transgression of the regional-level boundary.

Because the major anthropogenic perturbation of both the N and P cycles arises from fertilizer application, we can analyze the links between the independently determined N and P boundaries in an integrated way based on the N:P ratio in the growing plant tissue of agricultural crops. Applying this ratio, which is on average 11.8 (55), to the P boundary (6.2 Tg P year⁻¹) gives an N boundary of 73 Tg N year⁻¹. Conversely, applying the ratio to the N boundary (62 Tg N year⁻¹) gives a P boundary of 5.3 Tg P year⁻¹. The small differences between the boundaries derived using the N:P ratio and those calculated independently, which are likely nonsignificant differences given the precision of the data available for the calculations, show the internal consistency in our approach to the biogeochemical boundaries.

More detail on the development of the P and N boundaries is given in (33), where we also emphasize that the proposed P and N boundaries may be larger for an optimal allocation of N (and P) over the globe.

Land-system change

The updated biosphere integrity boundary provides a considerable constraint on the amount and pattern of land-system change in all terrestrial biomes: forests, woodlands, savannas, grasslands, shrublands, tundra, and so on. The land-system change boundary is now focused more tightly on a specific constraint: the biogeophysical processes in land systems that directly regulate climate—exchange of energy, water, and momentum between the land surface and the atmosphere. The control variable has been changed from the amount of cropland to the amount of forest cover remaining, as the three major forest biomes—tropical, temperate and boreal—play a stronger role in land surface–climate coupling than other biomes (56, 57). In particular, we focus on those land-system changes that can influence the climate in regions beyond the region where the land-system change occurred.

Of the forest biomes, tropical forests have substantial feedbacks to climate through changes in evapotranspiration when they are converted to nonforested systems, and changes in the distribution of boreal forests affect the albedo of the land surface and hence regional energy exchange. Both have strong regional and global teleconnections.

The biome-level boundary for these two types of forest have been set at 85% (Table 1 and the supplementary materials), and the boundary for temperate forests has been proposed at 50% of potential forest cover, because changes to temperate forests are estimated to have weaker influences on the climate system at the global level than changes to the other two major forest biomes (56). These boundaries would almost surely be met if the proposed biosphere integrity boundary of 90% BII were respected.

Estimates of the current status of the land-system change boundary are given in Figs. 2 and 3 and fig. S6 and in (58).

Freshwater use

The revised freshwater use boundary has retained consumptive use of blue water [from rivers, lakes, reservoirs, and renewable groundwater stores (59)] as the global-level control variable and 4000 km³/year as the value of the boundary. This PB may be somewhat higher or lower depending on rivers' ecological flow requirements (6). Therefore, we report here a new assessment to complement the PB with a basin-scale boundary for the maximum rate of blue water withdrawal along rivers, based on the amount of water required in the river system to avoid regime shifts in the functioning of flow-dependent ecosystems. We base our control variable on the concept of environmental water flows (EWF), which defines the level of river flows for different hydrological characteristics of river basins adequate to maintain a fair-to-good ecosystem state (60–62).

The variable monthly flow (VMF) method (33, 63) was used to calculate the basin-scale boundary for water. This method takes account of intra-annual variability by classifying flow regimes into high-, intermediate-, and low-flow months and allocating EWF as a percentage of the mean monthly flow (MMF). Based on this analysis, the zones of uncertainty for the river-basin scale water boundary were set at 25 to 55% of MMF for the low-flow regime, 40 to 70% for the intermediate-flow regime, and 55 to 85% for the high-flow regime (table S2). The boundaries were set at the lower end of the uncertainty ranges that encompass average monthly EWF. Our new estimates of the current status of the water use boundary—computed based on grid cell-specific estimates of agricultural, industrial, and domestic water withdrawals—are shown in Figs. 2 and 3, with details in figs. S7 and S8.

Atmospheric aerosol loading

Aerosols have well-known, serious human health effects, leading to about 7.2 million deaths per year (64). They also affect the functioning of the Earth system in many ways (65) (fig. S9). Here, we focus on the effect of aerosols on regional ocean-atmosphere circulation as the rationale for a separate aerosols boundary. We adopt aerosol optical depth (AOD) (33) as the control variable and use the south Asian monsoon as a case study, based on the potential of widespread aerosol loading over the Indian subcontinent to switch the monsoon system to a drier state.

The background AOD over south Asia is ~0.15 and can be as high as 0.4 during volcanic events (66). Emissions of black carbon and organic carbon from cooking and heating with biofuels and from diesel transportation, and emission of sulfates and nitrates from fossil fuel combustion, can increase seasonal mean AODs to as high as 0.4 (larger during volcanic periods), leading to decreases of 10 to 15% of incident solar radiation at the surface (fig. S9). A substantial decrease in monsoon activity is likely around an AOD of 0.50, an increase of 0.35 above the background (67). Taking a precautionary approach toward uncertainties surrounding the position of the tipping point, we propose a boundary at an AOD of 0.25 (an increase due to human activities of 0.1), with a zone of uncertainty of 0.25 to 0.50. The annual mean AOD is currently about 0.3 (66), within the zone of uncertainty.

Introduction of novel entities

We define novel entities as new substances, new forms of existing substances, and modified life forms that have the potential for unwanted geophysical and/or biological effects. Anthropogenic introduction of novel entities to the environment is of concern at the global level when these entities exhibit (i) persistence, (ii) mobility across scales with consequent widespread distributions, and (iii) potential impacts on vital Earth-system processes or subsystems. These potentially include chemicals and other new types of engineered materials or organisms [e.g., (68–71)] not previously known to the Earth system, as well as naturally occurring elements (for example, heavy metals) mobilized by anthropogenic activities. The risks associated with the introduction of novel entities into the Earth system are exemplified by the release of CFCs (chlorofluorocarbons), which are very useful synthetic chemicals that were thought to be harmless but had unexpected, dramatic impacts on the stratospheric ozone layer. In effect, humanity is repeatedly running such global-scale experiments but not yet applying the insights from previous experience to new applications (72, 73).

Today there are more than 100,000 substances in global commerce (74). If nanomaterials and plastic polymers that degrade to microplastics are included, the list is even longer. There is also a “chemical intensification” due to the rapidly increasing global production of chemicals, the expanding worldwide distribution as chemical products or in consumer goods, and the extensive global trade in chemical wastes (75).

In recent years, there has been a growing debate about the global-scale effects of chemical pollution, leading to calls for the definition of criteria to identify the kinds of chemical substances that are likely to be globally problematic (76, 77). Persson *et al.* (73) proposed that there are three conditions that need to be fulfilled for a chemical to pose a threat to the Earth system: (i) the chemical has an unknown disruptive effect on a vital Earth-system process; (ii) the disruptive effect is not discovered until it is a problem at the global scale; and (iii) the effect is not readily

reversible. The challenge to the research community is to develop the knowledge base that allows the screening of chemicals, before they are released into the environment, for properties that may predispose them toward becoming global problems.

As a first step toward meeting this challenge, the three conditions outlined above have been used as the basis for identifying scenarios of chemical pollution that fulfill the conditions and as a next step for pinpointing chemical profiles that fit the scenarios (28). This proposal constitutes a first attempt at adding the Earth-system perspective when assessing hazard and risk of chemicals and offers a vision for a systematic approach to a complex management situation with many unknowns.

Despite this progress in developing an Earth-system-oriented approach, there is not yet an aggregate, global-level analysis of chemical pollution on which to base a control variable or a boundary value. It may also serve little purpose to define boundary values and control variables for a planetary boundary of this complexity. Nevertheless, there is a potential threat from novel entities to disrupt the functioning of the Earth-system and society needs to learn how to mitigate these unknown risks and manage chemicals under uncertainty (28, 73).

Some precautionary and preventive actions can be considered. These may include a stronger focus on green chemistry (78), finding synergies with risk-reducing interventions in other fields such as occupational health (79), paying more attention to learning from earlier mistakes (80, 81), and investing in science to better understand and monitor vital Earth-system processes in order to be able to detect disruptive effects from novel entities as early as possible.

Hierarchy of boundaries

An analysis of the many interactions among the boundaries (table S3 and fig. S10) suggests that two of them—climate change and biosphere integrity—are highly integrated, emergent system-level phenomena that are connected to all of the other PBs. They operate at the level of the whole Earth system (7) and have coevolved for nearly 4 billion years (82). They are regulated by the other boundaries and, on the other hand, provide the planetary-level overarching systems within which the other boundary processes operate. Furthermore, large changes in the climate or in biosphere integrity would likely, on their own, push the Earth system out of the Holocene state. In fact, transitions between time periods in Earth history have often been delineated by substantial shifts in climate, the biosphere, or both (82, 83).

These observations suggest a two-level hierarchy of boundaries, in which climate change and biosphere integrity should be recognized as core planetary boundaries through which the other boundaries operate. The crossing of one or more of the other boundaries may seriously affect human well-being and may predispose the transgression of a core boundary(ies) but does not by itself lead to a new state of the Earth system. This

hierarchical approach to classifying the boundaries becomes clearer by examining in more detail the roles of climate and biosphere integrity in the functioning of the Earth system.

The climate system is a manifestation of the amount, distribution, and net balance of energy at Earth's surface. The total amount of energy sets the overall conditions for life. In Earth's current climate, a range of global surface temperatures and atmospheric pressures allows the three phases of water to be present simultaneously, with ice and water vapor playing critical roles in the physical feedbacks of the climate system. The distribution of energy by latitude, over the land and sea surfaces, and within the ocean plays a major role in the circulation of the two great fluids, the ocean and the atmosphere. These systemic physical characteristics are key spatial determinants of the distribution of the biota and the structure and functioning of ecosystems and are controllers of biogeochemical flows.

Biosphere integrity is also crucial to Earth-system functioning, where the biosphere is defined as the totality of all ecosystems (terrestrial, freshwater, and marine) on Earth and their biota (32). These ecosystems and biota play a critical role in determining the state of the Earth system, regulating its material and energy flows and its responses to abrupt and gradual change (7). Diversity in the biosphere provides resilience to terrestrial and marine ecosystems (83, 84). The biosphere not only interacts with the other planetary boundaries but also increases the capacity of the Earth system to persist in a given state under changes in these other boundaries. The ultimate basis for the many roles that the biosphere plays in Earth-system dynamics is the genetic code of the biota, the basic information bank that defines the biosphere's functional role and its capacity to innovate and persist into the future.

Planetary boundaries in a societal context

A proposed approach for sustainable development goals (SDGs) (85) argues that the stable functioning of the Earth system is a prerequisite for thriving societies around the world. This approach implies that the PB framework, or something like it, will need to be implemented alongside the achievement of targets aimed at more immediate human needs, such as provision of clean, affordable, and accessible energy and the adequate supply of food. World development within the biophysical limits of a stable Earth system has always been a necessity [e.g., (86, 87)]. However, only recently, for a number of reasons, has it become possible to identify, evaluate, and quantify risks of abrupt planetary- and biome-level shifts due to overshoot of key Earth-system parameters: (i) the emergence of global-change thinking and Earth-system thinking (88); (ii) the rise of “the Planetary” as a relevant level of complex system understanding (89–92); and (iii) observable effects of the rapid increase in human pressures on the planet (16).

The PB approach is embedded in this emerging social context, but it does not suggest how to

maneuver within the safe operating space in the quest for global sustainability. For example, the PB framework does not as yet account for the regional distribution of the impact or its historical patterns. Nor does the PB framework take into account the deeper issues of equity and causation. The current levels of the boundary processes, and the transgressions of boundaries that have already occurred, are unevenly caused by different human societies and different social groups. The wealth benefits that these transgressions have brought are also unevenly distributed socially and geographically. It is easy to foresee that uneven distribution of causation and benefits will continue, and these differentials must surely be addressed for a Holocene-like Earth-system state to be successfully legitimated and maintained. However, the PB framework as currently construed provides no guidance as to how this may be achieved [although some potential synergies have been noted (54)], and it cannot readily be used to make choices between pathways for piecemeal maneuvering within the safe operating space or more radical shifts of global governance (93).

The nature of the PB framework implies that two important cautions should be observed when application of the framework to policy or management is proposed: boundary interactions and scale.

Boundary interactions

The planetary boundaries framework arises from the scientific evidence that Earth is a single, complex, integrated system—that is, the boundaries operate as an interdependent set [e.g., (94)] (table S1 and fig. S10). Although a systematic, quantitative analysis of interactions among all of the processes for which boundaries are proposed remains beyond the scope of current modeling and observational capacity, the Earth system clearly operates in well-defined states in which these processes and their interactions can create stabilizing or destabilizing feedbacks (16, 90, 95). This has profound implications for global sustainability, because it emphasizes the need to address multiple interacting environmental processes simultaneously (e.g., stabilizing the climate system requires sustainable forest management and stable ocean ecosystems).

Scale

The PB framework is not designed to be “downscaled” or “disaggregated” to smaller levels, such as nations or local communities. That said, the PB framework recognizes the importance of changes at the level of subsystems in the Earth system (e.g., biomes or large river basins) on the functioning of the Earth system as a whole. Also, there are strong arguments for an integrated approach coupling boundary definitions at regional and global levels with development goals to enable the application of “PB thinking” at levels (nations, basins, and regions) where policy action most commonly occurs [e.g., (85, 96)].

This update of the PB framework is one step on a longer-term evolution of scientific knowledge to

inform and support global sustainability goals and pathways. This evolution is needed more than ever before; there are severe implementation gaps in many global environmental policies relating to the PB issues, where problematic trends are not being halted or reversed despite international consensus about the urgency of the problems. The prospect of tighter resource constraints and rising environmental hazards is also unavoidably turning the focus onto global social equity and the planetary stewardship of Earth's life-support system. There is a need for a truly global evidence base, with much greater integration among issues, in order to respond to these global challenges. New research initiatives [e.g., Future Earth (www.futureearth.org)] provide evidence that science can respond to this need by applying Earth-system research to advance a new generation of integrated global analyses and to explore options for transformations toward sustainability. This is a clear sign that, as the risks of the Anthropocene to human well-being become clearer, research is maturing to a point where a systemic step-change is possible—and necessary—in exploring and defining a safe and just planetary operating space for the further development of human societies.

Methods summary

Our approach to building the planetary boundaries framework is described above. We have implemented the framework through an expert assessment and synthesis of the scientific knowledge of intrinsic biophysical processes that regulate the stability of the Earth system. Our precautionary approach is based on the maintenance of a Holocene-like state of the Earth system and on an assessment of the level of human-driven change that would risk destabilizing this state. For the climate change PB, there is already much literature on which to base such an assessment. For others, such as stratospheric ozone, ocean acidification, extinction rates, and P and N cycles, we have used estimates of preindustrial values of the control variable as a Holocene baseline. Where large, undesirable thresholds exist and have been studied (e.g., polar ice sheets, Amazon rainforest, aragonite dissolution, atmospheric aerosols, and the south Asian monsoon), quantitative boundaries can be readily proposed. For others, where the focus is on erosion of Earth-system resilience, the boundaries are more difficult (but not impossible) to quantify, as reflected in larger uncertainty zones.

We used large-scale assessments of the impacts of human activities on Earth-system functioning [e.g., Intergovernmental Panel on Climate Change (17, 18), the International Geosphere-Biosphere Programme synthesis (16), and chemicals (75, 80)] as sources of community-level understanding on which to propose PBs. Our update has also relied on post-2009 assessments of individual boundaries by the relevant expert research communities; examples include phosphorus (3), nitrogen (5), biosphere integrity (7), freshwater use (5, 63), and novel entities [with a focus on chemicals (28, 73)]. Finally, some new analyses have

been undertaken specifically for this paper: (i) a freshwater-use PB based on the EWF approach (33, 63); (ii) the linkage of the phosphorus and nitrogen boundaries via the N:P ratio in growing crop tissue (33); and (iii) the use of major forest biomes as the basis for the land-system change PB (33).

REFERENCES AND NOTES

1. J. Rockström *et al.*, Planetary boundaries: Exploring the safe operating space for humanity. *Ecol. Soc.* **14**, 32 (2009). <http://www.ecologyandsociety.org/vol14/iss2/art32/>
2. J. Rockström *et al.*, A safe operating space for humanity. *Nature* **461**, 472–475 (2009). doi: [10.1038/461472a](https://doi.org/10.1038/461472a); pmid: 19779433
3. S. R. Carpenter, E. M. Bennett, Reconsideration of the planetary boundary for phosphorus. *Environ. Res. Lett.* **6**, 014009 (2011). doi: [10.1088/1748-9326/6/1/014009](https://doi.org/10.1088/1748-9326/6/1/014009)
4. S. W. Running, Ecology. A measurable planetary boundary for the biosphere. *Science* **337**, 1458–1459 (2012). doi: [10.1126/science.1227620](https://doi.org/10.1126/science.1227620); pmid: 22997311
5. W. de Vries, J. Kros, C. Kroeze, S. P. Seitzinger, Assessing planetary and regional nitrogen boundaries related to food security and adverse environmental impacts. *Curr. Opin. Environ. Sust.* **5**, 392–402 (2013). doi: [10.1016/j.cosust.2013.07.004](https://doi.org/10.1016/j.cosust.2013.07.004)
6. D. Gerten *et al.*, Towards a revised planetary boundary for consumptive freshwater use: Role of environmental flow requirements. *Curr. Opin. Environ. Sust.* **5**, 551–558 (2013). doi: [10.1016/j.cosust.2013.11.001](https://doi.org/10.1016/j.cosust.2013.11.001)
7. G. M. Mace *et al.*, Approaches to defining a planetary boundary for biodiversity. *Glob. Environ. Change* **28**, 289–297 (2014). doi: [10.1016/j.gloenvcha.2014.07.009](https://doi.org/10.1016/j.gloenvcha.2014.07.009)
8. V. Galaz, *Global Environmental Governance, Technology and Politics: The Anthropocene Gap*. (Edward Elgar, Cheltenham, UK, 2014).
9. UN GSP (UN High-Level Panel on Global Sustainability). *Resilient People, Resilient Planet: A Future Worth Choosing* (Report for the 2012 Rio+20 Earth Summit, United Nations, New York, 2012).
10. WBCSD (World Business Council on Sustainable Development). *Action 2020 Overview* (WBCSD, Geneva, Switzerland, <http://action2020.org>, accessed 18 June 2014).
11. R. Costanza, L. Graumlich, W. Steffen, Eds., *Integrated History and Future of People on Earth* (MIT Press, Cambridge, MA USA, 2006).
12. S. Sörlin, P. Warde, in *Nature's End: History and the Environment*, S. Sörlin, P. Warde, Eds. (Palgrave MacMillan, London, 2009), pp. 1–19.
13. R. C. Bishop, Endangered species and uncertainty: The economics of a safe minimum standard. *Am. J. Agric. Econ.* **61**, 10–18 (1978). doi: [10.2307/1240156](https://doi.org/10.2307/1240156)
14. T. M. Crowards, Safe minimum standards: Costs and opportunities. *Ecol. Econ.* **25**, 303–314 (1998). doi: [10.1016/S0921-8009\(97\)00041-4](https://doi.org/10.1016/S0921-8009(97)00041-4)
15. W. Steffen, J. Crutzen, J. R. McNeill, The Anthropocene: Are humans now overwhelming the great forces of Nature? *Ambio* **36**, 614–621 (2007). doi: [10.1579/0044-7447\(2007\)36\[614:TAHNO\]2.0.CO;2](https://doi.org/10.1579/0044-7447(2007)36[614:TAHNO]2.0.CO;2); pmid: 18240674
16. W. Steffen *et al.*, *Global Change and the Earth System: A Planet Under Pressure* (The IGBP Book Series, Springer-Verlag, Berlin, Heidelberg, New York, 2004).
17. IPCC (Intergovernmental Panel on Climate Change). *Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of Working Groups I and II of the IPCC*. C.B. Field *et al.*, Eds. (Cambridge University Press, Cambridge, UK (2012). doi: [10.1017/CB09781139177245](https://doi.org/10.1017/CB09781139177245)
18. IPCC (Intergovernmental Panel on Climate Change). *Climate Change 2013: The Physical Science Basis. Summary for Policymakers*, L. Alexander *et al.*, Eds. (IPCC Secretariat, Geneva, Switzerland, 2013). doi: [10.1017/CB09781107415324](https://doi.org/10.1017/CB09781107415324)
19. P. J. Crutzen, Geology of mankind. *Nature* **415**, 23 (2002). doi: [10.1038/415023a](https://doi.org/10.1038/415023a); pmid: 11780095
20. K. Richardson, W. Steffen, D. Liverman, *Climate Change: Global Risks, Challenges and Decisions* (Cambridge Univ. Press, Cambridge, UK, 2011).
21. T. M. Lenton *et al.*, Tipping elements in the Earth's climate system. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 1786–1793 (2008). doi: [10.1073/pnas.0705414105](https://doi.org/10.1073/pnas.0705414105); pmid: 18258748
22. M. Scheffer *et al.*, Early-warning signals for critical transitions. *Nature* **461**, 53–59 (2009). doi: [10.1038/nature08227](https://doi.org/10.1038/nature08227); pmid: 19727193
23. S. R. Carpenter, W. A. Brock, Rising variance: A leading indicator of ecological transition. *Ecol. Lett.* **9**, 311–318 (2006). doi: [10.1111/j.1461-0248.2005.00877.x](https://doi.org/10.1111/j.1461-0248.2005.00877.x); pmid: 16958897
24. J. Bakke *et al.*, Rapid oceanic and atmospheric changes during the Younger Dryas cold period. *Nat. Geosci.* **2**, 202–205 (2009). doi: [10.1038/ngeo439](https://doi.org/10.1038/ngeo439)
25. M. Scheffer *et al.*, Anticipating critical transitions. *Science* **338**, 344–348 (2012). doi: [10.1126/science.1225244](https://doi.org/10.1126/science.1225244); pmid: 23087241
26. R. Wang *et al.*, Flickering gives early warning signals of a critical transition to a eutrophic lake state. *Nature* **492**, 419–422 (2012). doi: [10.1038/nature11655](https://doi.org/10.1038/nature11655); pmid: 23160492
27. R. Biggs, S. R. Carpenter, W. A. Brock, Turning back from the brink: Detecting an impending regime shift in time to avert it. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 826–831 (2009). doi: [10.1073/pnas.0811729106](https://doi.org/10.1073/pnas.0811729106); pmid: 19124774
28. M. MacLeod *et al.*, Identifying chemicals that are planetary boundary threats. *Environ. Sci. Technol.* **48**, 11057–11063 (2014). doi: [10.1021/es501893m](https://doi.org/10.1021/es501893m); pmid: 25181298
29. C. S. Holling, Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* **4**, 1–23 (1973). doi: [10.1146/annurev.es.04.110173.000245](https://doi.org/10.1146/annurev.es.04.110173.000245)
30. C. Folke *et al.*, Resilience thinking: Integrating resilience, adaptability and transformability. *Ecol. Soc.* **15**, 20 (2010). www.ecologyandsociety.org/vol15/iss4/art20
31. T. P. Hughes, S. Carpenter, J. Rockström, M. Scheffer, B. Walker, Multiscale regime shifts and planetary boundaries. *Trends Ecol. Evol.* **28**, 389–395 (2013). doi: [10.1016/j.tree.2013.05.019](https://doi.org/10.1016/j.tree.2013.05.019); pmid: 23769417
32. T. M. Lenton, H. T. P. Williams, On the origin of planetary-scale tipping points. *Trends Ecol. Evol.* **28**, 380–382 (2013). doi: [10.1016/j.tree.2013.06.001](https://doi.org/10.1016/j.tree.2013.06.001); pmid: 23777818
33. Supplementary text, figures, and tables are available on Science Online.
34. NOAA (National Oceanic and Atmospheric Administration). NOAA-ESRL Annual CO₂ Data, accessed at: <http://co2now.org/Current-CO2/CO2-Now/annual-co2.html> (2014).
35. S. E. Perkins, L. V. Alexander, J. Nairn, Increasing frequency, intensity and duration of observed global heat waves and warm spells. *Geophys. Res. Lett.* **39**, L20714 (2012). doi: [10.1029/2012GL053361](https://doi.org/10.1029/2012GL053361)
36. A. Shepherd *et al.*, A reconciled estimate of ice-sheet mass balance. *Science* **338**, 1183–1189 (2012). doi: [10.1126/science.1228102](https://doi.org/10.1126/science.1228102); pmid: 23197528
37. M. R. Helmus, T. J. Bland, C. K. Williams, A. R. Ives, Phylogenetic measures of biodiversity. *Am. Nat.* **169**, E68–E83 (2007). doi: [10.1086/511334](https://doi.org/10.1086/511334); pmid: 17230400
38. S. D'agata *et al.*, Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. *Curr. Biol.* **24**, 555–560 (2014). doi: [10.1016/j.cub.2014.01.049](https://doi.org/10.1016/j.cub.2014.01.049); pmid: 24560574
39. A. D. Barnosky *et al.*, Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51–57 (2011). doi: [10.1038/nature09678](https://doi.org/10.1038/nature09678); pmid: 21368823
40. N. W. Mason, F. de Bello, D. Mouillot, S. Pavoine, S. Dray, A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *J. Veg. Sci.* **24**, 794–806 (2013). doi: [10.1111/jvs.12013](https://doi.org/10.1111/jvs.12013)
41. R. J. Scholes, R. Biggs, A biodiversity intactness index. *Nature* **434**, 45–49 (2005). doi: [10.1038/nature03289](https://doi.org/10.1038/nature03289); pmid: 15744293
42. B. Cardinale, Ecology. Impacts of biodiversity loss. *Science* **336**, 552–553 (2012). doi: [10.1126/science.1222102](https://doi.org/10.1126/science.1222102); pmid: 22556243
43. D. U. Hooper *et al.*, A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* **486**, 105–108 (2012). doi: [10.1038/nature11118](https://doi.org/10.1038/nature11118); pmid: 22678289
44. BAS (British Antarctic Survey), "Antarctic ozone" www.antarctica.ac.uk/met/jds/ozone/index.html#data, J. Shanklin, British Antarctic Survey (2013).
45. Royal Society, *Ocean Acidification Due to Increasing Atmospheric Carbon Dioxide*. Policy Document 12/05 (The Royal Society, London, 2005).
46. J. M. Guinotte, V. J. Fabry, Ocean acidification and its potential effects on marine ecosystems. *Ann. N. Y. Acad. Sci.* **1134**, 320–342 (2008). doi: [10.1196/annals.1439.013](https://doi.org/10.1196/annals.1439.013); pmid: 18566099
47. D. J. Conley, Terrestrial ecosystems and the global biogeochemical silica cycle. *Global Biogeochem. Cycles* **16**, 681–688 (2002). doi: [10.1029/2002GB001894](https://doi.org/10.1029/2002GB001894)

48. F. Vandenne, E. Struyf, W. Clymans, P. Meire, Agricultural silica harvest: Have humans created a new loop in the global silica cycle? *Front. Ecol. Environ* **10**, 243–248 (2012). doi: [10.1890/110046](https://doi.org/10.1890/110046)
49. S. E. Gress, T. D. Nichols, C. C. Northcraft, W. T. Peterjohn, Nutrient limitation in soils exhibiting differing nitrogen availabilities: What lies beyond nitrogen saturation? *Ecol.* **88**, 119–130 (2007). doi: [10.1890/0012-9658\(2007\)88\[119:NUSED\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[119:NUSED]2.0.CO;2); pmid: [17489460](https://pubmed.ncbi.nlm.nih.gov/17489460/)
50. H. Hillebrand, V. Lehmppfuhl, Resource stoichiometry and consumers control the biodiversity-productivity relationship in pelagic metacommunities. *Am. Nat.* **178**, 171–181 (2011). doi: [10.1086/660831](https://doi.org/10.1086/660831); pmid: [21750381](https://pubmed.ncbi.nlm.nih.gov/21750381/)
51. C. M. Moore *et al.*, Processes and patterns of oceanic nutrient limitation. *Nat. Geosci.* **6**, 701–710 (2013). doi: [10.1038/ngeo1765](https://doi.org/10.1038/ngeo1765)
52. G. K. MacDonald, E. M. Bennett, P. A. Potter, N. Ramankutty, Agronomic phosphorus imbalances across the world's croplands. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 3086–3091 (2011). doi: [10.1073/pnas.1010808108](https://doi.org/10.1073/pnas.1010808108); pmid: [21282605](https://pubmed.ncbi.nlm.nih.gov/21282605/)
53. L. Bouwman *et al.*, Exploring global changes in nitrogen and phosphorus cycles in agriculture induced by livestock production over the 1900–2050 period. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 20882–20887 (2013). doi: [10.1073/pnas.1012878108](https://doi.org/10.1073/pnas.1012878108); pmid: [21576477](https://pubmed.ncbi.nlm.nih.gov/21576477/)
54. W. Steffen, M. Stafford Smith, Planetary boundaries, equity and global sustainability: Why wealthy countries could benefit from more equity. *Curr. Opin. Environ. Sust.* **5**, 403–408 (2013). doi: [10.1016/j.cosust.2013.04.007](https://doi.org/10.1016/j.cosust.2013.04.007)
55. D. J. Greenwood *et al.*, A unifying concept for the dependence of whole-crop N : P ratio on biomass: theory and experiment. *Ann. Bot. (Lond.)* **102**, 967–977 (2008). doi: [10.1093/aob/mcn188](https://doi.org/10.1093/aob/mcn188); pmid: [18840873](https://pubmed.ncbi.nlm.nih.gov/18840873/)
56. P. K. Snyder, C. Delire, J. A. Foley, Evaluating the influence of different vegetation biomes on the global climate. *Clim. Dyn.* **23**, 279–302 (2004). doi: [10.1007/s00382-004-0430-0](https://doi.org/10.1007/s00382-004-0430-0)
57. P. C. West, G. T. Narisma, C. C. Barford, C. J. Kucharik, J. A. Foley, An alternative approach for quantifying climate regulation by ecosystems. *Front. Ecol. Environ* **9**, 126–133 (2010). doi: [10.1890/0900015](https://doi.org/10.1890/0900015)
58. EPI (Earth Policy Institute), "Forest cover" www.earthpolicy.org/indicators/C56/forests_2012_ (2014).
59. M. Falkenmark, Meeting water requirements of an expanding world population. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **352**, 929–936 (1997). doi: [10.1098/rstb.1997.0072](https://doi.org/10.1098/rstb.1997.0072)
60. J. S. Wallace, M. C. Acreman, C. A. Sullivan, The sharing of water between society and ecosystems: From conflict to catchment-based co-management. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **358**, 2011–2026 (2003). doi: [10.1098/rstb.2003.1383](https://doi.org/10.1098/rstb.2003.1383); pmid: [14728795](https://pubmed.ncbi.nlm.nih.gov/14728795/)
61. N. L. Poff *et al.*, The natural flow regime: A paradigm for river conservation and restoration. *BioSci.* **47**, 769–784 (1997). doi: [10.2307/1313099](https://doi.org/10.2307/1313099)
62. N. L. Poff, J. K. H. Zimmerman, Ecological responses to altered flow regimes: A literature review to inform the science and management of environmental flows. *Biol.* **55**, 194–205 (2010). doi: [10.1111/j.1365-2427.2009.02272.x](https://doi.org/10.1111/j.1365-2427.2009.02272.x)
63. A. V. Pastor, F. Ludwig, H. Biemans, H. Hoff, P. Kabat, Accounting for environmental flow requirements in global water assessments. *Hydrol. Earth Syst. Sci.* **18**, 5041–5059 (2014). doi: [10.5194/hess-18-5041-2014](https://doi.org/10.5194/hess-18-5041-2014)
64. WHO (World Health Organization), *Burden of Disease from the Joint Effects of Household and Ambient Air Pollution for 2012* (www.who.int/phe/health_topics/outdoorair/databases/FINAL_HAP_AAP_BoD24March2014.pdf, accessed 23 June 2014; http://www.who.int/phe/health_topics/outdoorair/databases/en)
65. O. Boucher *et al.*, in *Climate Change 2013: The Physical Science Basis*. IPCC AR5 WGI report, T. Stocker *et al.*, Eds. (Cambridge Univ. Press, Cambridge, UK, 2013), chap. 7, pp. 571–657.
66. M. Chin *et al.*, Multi-decadal aerosol variations from 1980 to 2009: A perspective from observations and a global model. *Atmos. Chem. Phys.* **14**, 3657–3690 (2014). doi: [10.5194/acp-14-3657-2014](https://doi.org/10.5194/acp-14-3657-2014)
67. V. Ramanathan *et al.*, Atmospheric brown clouds: Impacts on South Asian climate and hydrological cycle. *Proc. Natl. Acad. Sci. U.S.A.* **102**, 5326–5333 (2005). doi: [10.1073/pnas.0500656102](https://doi.org/10.1073/pnas.0500656102); pmid: [15749818](https://pubmed.ncbi.nlm.nih.gov/15749818/)
68. M. Cole, P. Lindeque, C. Halsband, T. S. Galloway, Microplastics as contaminants in the marine environment: A review. *Mar. Pollut. Bull.* **62**, 2588–2597 (2011). doi: [10.1016/j.marpolbul.2011.09.025](https://doi.org/10.1016/j.marpolbul.2011.09.025); pmid: [22001295](https://pubmed.ncbi.nlm.nih.gov/22001295/)
69. EEA (European Environment Agency), *Genetically Modified Organisms (GMOs): The Significance of Gene Flow Through Pollen Transfer* (Environmental Issue Report 28, European Environment Agency, Copenhagen, Denmark, 2002).
70. J. A. Ivar do Sul, M. F. Costa, The present and future of microplastic pollution in the marine environment. *Environ. Pollut.* **185**, 352–364 (2014). doi: [10.1016/j.envpol.2013.10.036](https://doi.org/10.1016/j.envpol.2013.10.036); pmid: [24275078](https://pubmed.ncbi.nlm.nih.gov/24275078/)
71. R. Kessler, Engineered nanoparticles in consumer products: Understanding a new ingredient. *Environ. Health Perspect.* **119**, a120–a125 (2011). doi: [10.1289/ehp.119-a120](https://doi.org/10.1289/ehp.119-a120); pmid: [21356630](https://pubmed.ncbi.nlm.nih.gov/21356630/)
72. M. Rees, *Our Final Century. Will Civilisation Survive the Twenty-first Century?* (Arrow Books, London, 2003).
73. L. M. Persson *et al.*, Confronting unknown planetary boundary threats from chemical pollution. *Environ. Sci. Technol.* **47**, 12619–12622 (2013). doi: [10.1021/es402501c](https://doi.org/10.1021/es402501c); pmid: [23980998](https://pubmed.ncbi.nlm.nih.gov/23980998/)
74. P. P. Egeghy *et al.*, The exposure data landscape for manufactured chemicals. *Sci. Total Environ.* **414**, 159–166 (2012). doi: [10.1016/j.scitotenv.2011.10.046](https://doi.org/10.1016/j.scitotenv.2011.10.046); pmid: [22104386](https://pubmed.ncbi.nlm.nih.gov/22104386/)
75. UNEP (United Nations Environment Programme), *GCO Global Chemicals Outlook: Towards Sound Management of Chemicals* (United Nations Environment Programme, Nairobi, Kenya, 2013).
76. S. Stempel, M. Scheringer, C. A. Ng, K. Hungerbühler, Screening for PBT chemicals among the "existing" and "new" chemicals of the EU. *Environ. Sci. Technol.* **46**, 5680–5687 (2012). doi: [10.1021/es3002713](https://doi.org/10.1021/es3002713); pmid: [22494215](https://pubmed.ncbi.nlm.nih.gov/22494215/)
77. M. Scheringer *et al.*, How many persistent organic pollutants should we expect? *Atmos. Poll. Res.* **3**, 383–391 (2012). doi: [10.5094/APR.2012.044](https://doi.org/10.5094/APR.2012.044)
78. K. Sanderson, Chemistry: It's not easy being green. *Nature* **469**, 18–20 (2011). doi: [10.1038/469018a](https://doi.org/10.1038/469018a); pmid: [21209638](https://pubmed.ncbi.nlm.nih.gov/21209638/)
79. P. A. Schulte *et al.*, Occupational safety and health, green chemistry, and sustainability: A review of areas of convergence. *Environ. Health* **12**, 31 (2013). doi: [10.1186/1476-069X-12-31](https://doi.org/10.1186/1476-069X-12-31); pmid: [23587312](https://pubmed.ncbi.nlm.nih.gov/23587312/)
80. EEA (European Environment Agency), *Late Lessons from Early Warnings: The Precautionary Principle 1896-2000* (Environmental Issue Report 22/2001, Copenhagen, Denmark, 2001).
81. D. Gee, Late lessons from early warnings: Toward realism and precaution with endocrine-disrupting substances. *Environ. Health Perspect.* **114** (suppl. 1), 152–160 (2006). doi: [10.1289/ehp.8134](https://doi.org/10.1289/ehp.8134); pmid: [16818262](https://pubmed.ncbi.nlm.nih.gov/16818262/)
82. T. Lenton, A. Watson, A., *Revolutions That Made the Earth* (Oxford Univ. Press, Oxford UK, 2011).
83. R. Biggs *et al.*, Toward principles for enhancing the resilience of ecosystem services. *Annu. Rev. Environ. Resour.* **37**, 421–448 (2012). doi: [10.1146/annurev-environ-051211-123836](https://doi.org/10.1146/annurev-environ-051211-123836)
84. G. S. Cumming, P. Olsson, F. S. Chapin III, C. S. Holling, Resilience, experimentation and scale mismatches in social-ecological systems. *Landscape Ecol.* **28**, 1139–1150 (2013). doi: [10.1007/s10980-012-9725-4](https://doi.org/10.1007/s10980-012-9725-4)
85. D. Griggs *et al.*, Policy: Sustainable development goals for people and planet. *Nature* **495**, 305–307 (2013). doi: [10.1038/495305a](https://doi.org/10.1038/495305a); pmid: [23518546](https://pubmed.ncbi.nlm.nih.gov/23518546/)
86. R. Costanza, Ed., *Ecological Economics: The Science and Management of Sustainability* (Columbia Univ. Press, New York, 1991).
87. C. Folke, in *Linking the Natural Environment and the Economy: Essays from the Eco-Eco Group*, C. Folke, T. Kåberger, Eds. (Kluwer Academic Publishers, Dordrecht, Netherlands, 1991), pp. 77–94.
88. L. Robin, S. Sörin, P. Warde, Eds., *The Future of Nature: Documents of Global Change* (Yale Univ. Press, New Haven, CT, 2013).
89. U. Heise, *Sense of Place and Sense of Planet: The Environmental Imagination of the Global* (Oxford Univ. Press, Oxford, 2008).
90. M. Scheffer, *Critical Transitions in Nature and Society* (Princeton Univ. Press, Princeton, NJ, 2009).
91. J. Masco, Bad weather: On planetary crisis. *Soc. Stud. Sci.* **40**, 7–40 (2010). doi: [10.1177/0306312709341598](https://doi.org/10.1177/0306312709341598)
92. G. Pálsson *et al.*, Reconceptualizing the 'Anthropos' in the Anthropocene: Integrating the social sciences and humanities in global environmental change research. *Environ. Sci. Policy* **28**, 4 (2013). doi: [10.1016/j.envsci.2012.11.004](https://doi.org/10.1016/j.envsci.2012.11.004)
93. N. Castree *et al.*, Changing the intellectual climate. *Nature Clim. Change* **4**, 763–768 (2014). doi: [10.1038/nclimate2339](https://doi.org/10.1038/nclimate2339)
94. J. M. Anderies, S. R. Carpenter, W. Steffen, J. Rockström, The topology of non-linear global carbon dynamics: From tipping points to planetary boundaries. *Environ. Res. Lett.* **8**, 044048 (2013). doi: [10.1088/1748-9326/8/4/044048](https://doi.org/10.1088/1748-9326/8/4/044048)
95. S. E. Cornell, I. C. Prentice, J. I. House, C. J. Downy, *Understanding the Earth System. Global Change Science for Application* (Cambridge Univ. Press, Cambridge, 2012).
96. J. A. Dearing *et al.*, Safe and just operating spaces for regional social-ecological systems. *Glob. Environ. Change* **28**, 227–238 (2014). doi: [10.1016/j.gloenvcha.2014.06.012](https://doi.org/10.1016/j.gloenvcha.2014.06.012)

ACKNOWLEDGMENTS

We thank J. Foley and N. Ramankutty for contributions to the land-system change boundary; A. Pastor for analytical work on the PB for freshwater; B. Armstrong, C. Butler, T. McMichael, and A. Woodward for contributions to the novel entities boundary; and B. Scholes for comments on an earlier version of the manuscript. Data associated with the paper are located at the Stockholm Resilience Centre, Sweden (<http://www.stockholmresilience.org/21/research/research-programmes/planetary-boundaries.html>). The planetary boundaries research at the Stockholm Resilience Centre is made possible through a core grant from MISTRA (Swedish Foundation for Strategic Environmental Research). S.E.C. is supported by the Swedish Research Council, E.M.B. is supported by the Natural Sciences and Engineering Research Council of Canada and by the Trottier Institute for Science and Public Policy, R.B. is supported by a Branco Weiss Fellowship, C.F. is supported by the Family Erling Persson Academy Programme on Global Economic Dynamics and the Biosphere, I.F. is supported by the Stordalen Foundation (Norway), S.S. is supported by the Riksbankens Jubileumsfond and the Institute for Advanced Study, Princeton NJ, and S.R.C. and V.R. are supported by the U.S. National Science Foundation.

SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/347/6223/1259855/suppl/DC1
Methods
Figs. S1 to S10
Tables S1 to S3
References (97–158)

11 August 2014; accepted 8 January 2015
Published online 15 January 2015;
[10.1126/science.1259855](https://doi.org/10.1126/science.1259855)

This copy is for your personal, non-commercial use only.

If you wish to distribute this article to others, you can order high-quality copies for your colleagues, clients, or customers by [clicking here](#).

Permission to republish or repurpose articles or portions of articles can be obtained by following the guidelines [here](#).

The following resources related to this article are available online at www.sciencemag.org (this information is current as of March 16, 2015):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/content/347/6223/1259855.full.html>

Supporting Online Material can be found at:

<http://www.sciencemag.org/content/suppl/2015/01/14/science.1259855.DC1.html>

A list of selected additional articles on the Science Web sites **related to this article** can be found at:

<http://www.sciencemag.org/content/347/6223/1259855.full.html#related>

This article **cites 120 articles**, 27 of which can be accessed free:

<http://www.sciencemag.org/content/347/6223/1259855.full.html#ref-list-1>

This article appears in the following **subject collections**:

Ecology

<http://www.sciencemag.org/cgi/collection/ecology>