

FEATURE

A safe operating space for humanity

Identifying and quantifying planetary boundaries that must not be transgressed could help prevent human activities from causing unacceptable environmental change, argue Johan Rockström and colleagues.

Although Earth has undergone many periods of significant environmental change, the planet's environment has been unusually stable for the past 10,000 years¹⁻³. This period of stability - known to geologists as the Holocene - has seen human civilizations arise, develop and thrive. Such stability may now be under threat. Since the Industrial Revolution, a new era has arisen, the Anthropocene⁴, in which human actions have become the main driver of global environmental change⁵. This could see human activities push the Earth system outside the stable environmental state of the Holocene, with consequences that are detrimental or even catastrophic for large parts of the world.

During the Holocene, environmental change occurred naturally and Earth's regulatory capacity maintained the conditions that enabled human development. Regular temperatures, freshwater availability and biogeochemical flows all stayed within a relatively narrow range. Now, largely because of a rapidly growing reliance on fossil fuels and



SUMMARY

- New approach proposed for defining preconditions for human development
- Crossing certain biophysical thresholds could have disastrous consequences for humanity
- Three of nine interlinked planetary boundaries have already been overstepped

industrialized forms of agriculture, human activities have reached a level that could damage the systems that keep Earth in the desirable Holocene state. The result could be irreversible and, in some cases, abrupt environmental change, leading to a state less conducive to human development⁶. Without pressure from humans, the Holocene is expected to continue for at least several thousands of years⁷.

Planetary boundaries

To meet the challenge of maintaining the Holocene state, we propose a framework based on 'planetary boundaries'. These

boundaries define the safe operating space for humanity with respect to the Earth system and are associated with the planet's biophysical subsystems or processes. Although Earth's complex systems sometimes respond smoothly to changing pressures, it seems that this will prove to be the exception rather than the rule. Many subsystems of Earth react in a nonlinear, often abrupt, way, and are particularly sensitive around threshold levels of certain key variables. If these thresholds are crossed, then important subsystems, such as a monsoon system, could shift into a new state, often with deleterious or potentially even disastrous consequences for humans^{8,9}.

Most of these thresholds can be defined by a critical value for one or more control variables, such as carbon dioxide concentration. Not all processes or subsystems on Earth have well-defined thresholds, although human actions that undermine the resilience of such processes or subsystems - for example, land and water degradation - can increase the risk that thresholds will also be crossed in other processes, such as the climate system.

We have tried to identify the Earth-system processes and associated thresholds which, if crossed, could generate unacceptable environmental change. We have found nine such processes for which we believe it is necessary to define planetary boundaries: climate change; rate of biodiversity loss (terrestrial and marine); interference with the nitrogen and phosphorus cycles; stratospheric ozone depletion; ocean acidification; global freshwater use; change in land use; chemical pollution; and atmospheric aerosol loading (see Fig. 1 and Table).

In general, planetary boundaries are values for control variables that are either at a 'safe' distance from thresholds - for processes with evidence of threshold behaviour - or at dangerous levels - for processes without

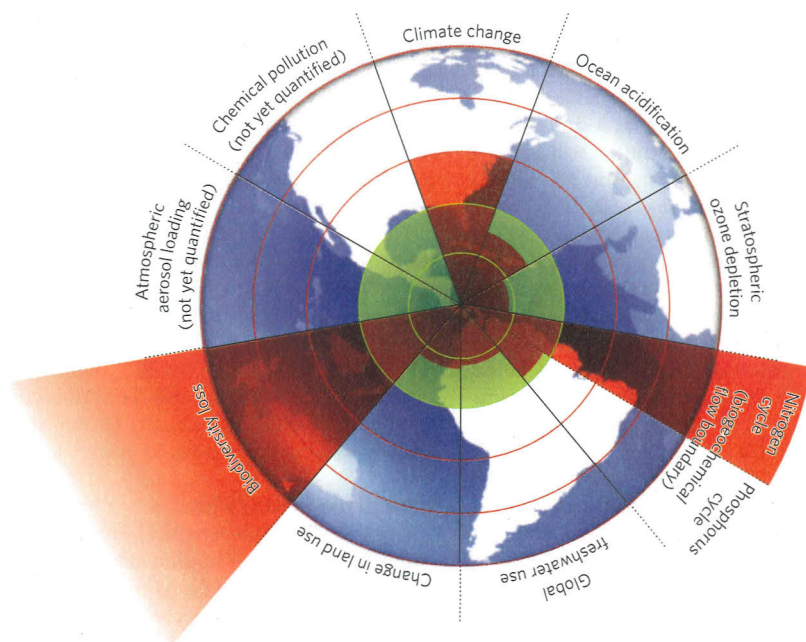


Figure 1 | Beyond the boundary. The inner green shading represents the proposed safe operating space for nine planetary systems. The red wedges represent an estimate of the current position for each variable. The boundaries in three systems (rate of biodiversity loss, climate change and human interference with the nitrogen cycle), have already been exceeded.

evidence of thresholds. Determining a safe distance involves normative judgements of how societies choose to deal with risk and uncertainty. We have taken a conservative, risk-averse approach to quantifying our planetary boundaries, taking into account the large uncertainties that surround the true position of many thresholds. (A detailed description of the boundaries - and the analyses behind them - is given in ref. 10.)

Humanity may soon be approaching the boundaries for global freshwater use, change in land use, ocean acidification and interference with the global phosphorous cycle (see Fig. 1). Our analysis suggests that three of the Earth-system processes - climate change, rate of biodiversity loss and interference with the nitrogen cycle - have already transgressed their boundaries. For the latter two of these, the control variables are the rate of species loss and the rate at which N_2 is removed from the atmosphere and converted to reactive nitrogen for human use, respectively. These are rates of change that cannot continue without significantly eroding the resilience of major components of Earth-system functioning. Here we describe these three processes.

Climate change

Anthropogenic climate change is now beyond dispute, and in the run-up to the climate negotiations in Copenhagen this December, the international discussions on targets for climate mitigation have intensified. There is a growing convergence towards a '2°C guard-rail' approach, that is, containing the rise in global mean temperature to no more than 2°C above the pre-industrial level.

Our proposed climate boundary is based on two critical thresholds that separate qualitatively different climate-system states. It has two parameters: atmospheric concentration of carbon dioxide and radiative forcing (the rate of energy change per unit area of the globe as measured at the top of the atmosphere). We propose that human changes to atmospheric CO_2 concentrations should not exceed 350 parts per million by volume, and that radiative forcing should not exceed 1 watt per square metre above pre-industrial levels. Transgressing these boundaries will increase the risk of irreversible climate change, such as the loss of major ice sheets, accelerated sea-level rise and abrupt shifts in forest and agricultural systems. Current CO_2 concentration stands at 387 p.p.m.v. and the change in radiative forcing is $1.5 W m^{-2}$ (ref. 11).

There are at least three reasons for our proposed climate boundary. First, current climate models may significantly underestimate the severity of long-term climate change for

PLANETARY BOUNDARIES

Earth-system process	Parameters	Proposed boundary	Current status	Pre-industrial value
Climate change	(i) Atmospheric carbon dioxide concentration (parts per million by volume)	350	387	280
	(ii) Change in radiative forcing (watts per metre squared)	1	1.5	0
Rate of biodiversity loss	Extinction rate (number of species per million species per year)	10	>100	0.1-1
Nitrogen cycle (part of a boundary with the phosphorus cycle)	Amount of N_2 removed from the atmosphere for human use (millions of tonnes per year)	35	121	0
Phosphorus cycle (part of a boundary with the nitrogen cycle)	Quantity of P flowing into the oceans (millions of tonnes per year)	11	8.5-9.5	-1
Stratospheric ozone depletion	Concentration of ozone (Dobson unit)	276	283	290
Ocean acidification	Global mean saturation state of aragonite in surface sea water	2.75	2.90	3.44
Global freshwater use	Consumption of freshwater by humans (km^3 per year)	4,000	2,600	415
Change in land use	Percentage of global land cover converted to cropland	15	11.7	Low
Atmospheric aerosol loading	Overall particulate concentration in the atmosphere, on a regional basis	To be determined		
Chemical pollution	For example, amount emitted to, or concentration of persistent organic pollutants, plastics, endocrine disrupters, heavy metals and nuclear waste in, the global environment, or the effects on ecosystem and functioning of Earth system thereof	To be determined		

Boundaries for processes in red have been crossed. Data sources: ref. 10 and supplementary information

a given concentration of greenhouse gases¹². Most models¹¹ suggest that a doubling in atmospheric CO_2 concentration will lead to a global temperature rise of about 3°C (with a probable uncertainty range of 2-4.5°C) once the climate has regained equilibrium. But these models do not include long-term reinforcing feedback processes that further warm the climate, such as decreases in the surface area of ice cover or changes in the distribution of vegetation. If these slow feedbacks are included, doubling CO_2 levels gives an eventual temperature increase of 6°C (with a probable uncertainty range of 4-8°C). This would threaten the ecological life-support systems that have developed in the late Quaternary environment, and would severely challenge the viability of contemporary human societies.

The second consideration is the stability of the large polar ice sheets. Palaeoclimate data from the past 100 million years show that CO_2 concentrations were a major factor in the long-term cooling of the past 50 million years. Moreover, the planet was largely ice-free until CO_2 concentrations fell below 450 p.p.m.v.

(± 100 p.p.m.v.), suggesting that there is a critical threshold between 350 and 550 p.p.m.v. (ref. 12). Our boundary of 350 p.p.m.v. aims to ensure the continued existence of the large polar ice sheets.

Third, we are beginning to see evidence that some of Earth's subsystems are already moving outside their stable Holocene state. This includes the rapid retreat of the summer sea ice in the Arctic ocean¹³, the retreat of mountain glaciers around the world¹¹ the loss of mass from the Greenland and West Antarctic ice sheets¹⁴ and the accelerating rates of sea-level rise during the past 10-15 years¹⁵.

Rate of biodiversity loss

Species extinction is a natural process, and would occur without human actions. However, biodiversity loss in the Anthropocene has accelerated massively. Species are becoming extinct at a rate that has not been seen since the last global mass-extinction event¹⁶.

The fossil record shows that the background extinction rate for marine life is 0.1-1 extinctions per million species per year; for

mammals it is 0.2–0.5 extinctions per million species per year¹⁶. Today, the rate of extinction of species is estimated to be 100 to 1,000 times more than what could be considered natural. As with climate change, human activities are the main cause of the acceleration. Changes in land use exert the most significant effect. These changes include the conversion of natural ecosystems into agriculture or into urban areas; changes in frequency, duration or magnitude of wildfires and similar disturbances; and the introduction of new species into land and freshwater environments¹⁷. The speed of climate change will become a more important driver of change in biodiversity this century, leading to an accelerating rate of species loss¹⁸. Up to 30% of all mammal, bird and amphibian species will be threatened with extinction this century¹⁹.

Biodiversity loss occurs at the local to regional level, but it can have pervasive effects on how the Earth system functions, and it interacts with several other planetary boundaries. For example, loss of biodiversity can increase the vulnerability of terrestrial and aquatic ecosystems to changes in climate and ocean acidity, thus reducing the safe boundary levels of these processes. There is growing understanding of the importance of functional biodiversity in preventing ecosystems from tipping into undesired states when they are disturbed²⁰. This means that apparent redundancy is required to maintain an ecosystem's resilience. Ecosystems that depend on a few or single species for critical functions are vulnerable to disturbances, such as disease, and at a greater risk of tipping into undesired states^{8,21}.

From an Earth-system perspective, setting a boundary for biodiversity is difficult. Although it is now accepted that a rich mix of species underpins the resilience of ecosystems^{20,21}, little is known quantitatively about how much and what kinds of biodiversity can be lost before this resilience is eroded²². This is particularly true at the scale of Earth as a whole, or for major subsystems such as the Borneo rainforests or the Amazon Basin. Ideally, a planetary boundary should capture the role of biodiversity in regulating the resilience of systems on Earth. Because science cannot yet provide such information at an aggregate level, we propose extinction rate as an alternative (but weaker) indicator. As a result, our suggested planetary boundary for biodiversity often times the background rates of extinction is only a very preliminary estimate. More research is required to pin down this boundary with greater certainty. However, we can say with some confidence that Earth cannot sustain the current rate of loss without Significant erosion of ecosystem resilience.

Nitrogen and phosphorus cycles

Modern agriculture is a major cause of environmental pollution, including large-scale nitrogen- and phosphorus-induced environmental change²³. At the planetary scale, the additional amounts of nitrogen and phosphorus activated by humans are now so large that they significantly perturb the global cycles of these two important elements^{24,25}.

Human processes – primarily the manufacture of fertilizer for food production and the cultivation of leguminous crops – convert around 120 million tonnes of N₂ from the atmosphere per year into reactive forms – which is more than the combined effects from all Earth's terrestrial processes. Much of this new reactive nitrogen ends up in the environment, polluting waterways and the coastal zone, accumulating in land systems and adding a number of gases to the atmosphere. It slowly erodes the resilience of important Earth subsystems. Nitrous oxide, for example, is one of the most important non-CO₂ greenhouse gases and thus directly increases radiative forcing.

Anthropogenic distortion of the nitrogen cycle and phosphorus flows has shifted the state of lake systems from clear to turbid water²⁶. Marine ecosystems have been subject to similar shifts, for example, during periods of anoxia in the Baltic Sea caused by excessive nutrients²⁷. These and other nutrient-generated impacts justify the formulation of a planetary boundary for nitrogen and phosphorus flows, which we propose should be kept together as one boundary given their close interactions with other Earth-system processes.

Setting a planetary boundary for human modification of the nitrogen cycle is not straightforward. We have defined the boundary by considering the human fixation of N₂ from the atmosphere as a giant 'valve' that controls a massive flow of new reactive nitrogen into Earth. As a first guess, we suggest that this valve should contain the flow of new reactive nitrogen to 25% of its current value, or about 35 million tonnes of nitrogen per year. Given the implications of trying to reach this target, much more research and synthesis of information is required to determine a more informed boundary.

Unlike nitrogen, phosphorus is a fossil mineral that accumulates as a result of geological processes. It is mined from rock and its uses range from fertilizers to toothpaste. Some 20 million tonnes of phosphorus is mined every year and around 8.5 million–9.5 million tonnes of it finds its way into the oceans^{25,28}. This is estimated to be approximately eight times the natural background rate of influx.

Records of Earth history show that large-scale ocean anoxic events occur when critical thresholds of phosphorus inflow to the oceans are crossed. This potentially explains past mass extinctions of marine life. Modelling suggests that a sustained increase of phosphorus flowing into the oceans exceeding 20% of the natural background weathering was enough to induce past ocean anoxic events²⁹.

Our tentative modelling estimates suggest that if there is a greater than tenfold increase in phosphorus flowing into the oceans (compared with pre-industrial levels), then anoxic ocean events become more likely within 1,000 years. Despite the large uncertainties involved, the state of current science and the present observations of abrupt phosphorus-induced regional anoxic events indicate that no more than 11 million tonnes of phosphorus per year should be allowed to flow into the oceans – ten times the natural background rate. We estimate that this boundary level will allow humanity to safely steer away from the risk of ocean anoxic events for more than 1,000 years, acknowledging that current levels already exceed critical thresholds for many estuaries and freshwater systems.

Delicate balance

Although the planetary boundaries are described in terms of individual quantities and separate processes, the boundaries are tightly coupled. We do not have the luxury of concentrating our efforts on anyone of them in isolation from the others. If one boundary is transgressed, then other boundaries are also under serious risk. For instance, significant land-use changes in the Amazon could influence water resources as far away as Tibet³⁰. The climate-change boundary depends on staying on the safe side of the freshwater, land, aerosol, nitrogen-phosphorus, ocean and stratospheric boundaries. Transgressing the nitrogen-phosphorus boundary can erode the resilience of some marine ecosystems, potentially reducing their capacity to absorb CO₂ and thus affecting the climate boundary.

The boundaries we propose represent a new approach to defining biophysical preconditions for human development. For the first time, we are trying to quantify the safe limits outside of which the Earth system cannot continue to function in a stable, Holocene-like state.

The approach rests on three branches of scientific enquiry. The first addresses the scale of human action in relation to the capacity of Earth to sustain it. This is a significant feature of the ecological economics research agenda³¹, drawing on knowledge of the essential role of the life-support properties of the

environment for human wellbeing^{32,33} and the biophysical constraints for the growth of the economy^{34,35}. The second is the work on understanding essential Earth processes^{6,36,37} including human actions^{23,28}, brought together in the fields of global change research and sustainability science³⁹. The third field of enquiry is research into resilience^{40,42} and its links to complex dynamics^{43,44} and self-regulation of living systems^{45,46}, emphasizing thresholds and shifts between states⁸.

Although we present evidence that three boundaries have been overstepped, there remain many gaps in our knowledge. We have tentatively quantified seven boundaries, but some of the figures are merely our first best guesses. Furthermore, because many of the boundaries are linked, exceeding one will have implications for others in ways that we do not as yet completely understand. There is also significant uncertainty over how long it takes to cause dangerous environmental change or to trigger other feedbacks that drastically reduce the ability of the Earth system, or important subsystems, to return to safe levels.

The evidence so far suggests that, as long as the thresholds are not crossed, humanity has the freedom to pursue long-term social and economic development.

- Dansgaard, W. *et al.* *Nature* 364, 218–220 (1993).
- Petit, J. R. *et al.* *Nature* 399, 429–436 (1999).
- Rioual, P. *et al.* *Nature* 413, 293–296 (2001).
- Crutzen, P. J. *Nature* 415, 23 (2002).
- Steffen, W., Crutzen, P. J. & McNeill, J. R. *Ambio* 36, 614–621 (2007).
- Steffen, W. *et al.* *Global Change and the Earth System: A Planet Under Pressure* (Springer Verlag, 2004).
- Berger, A. & Loutre, M. F. *Science* 297, 1287–1288 (2002).
- Scheffer, M., Carpenter, S. R., Foley, J. A., Folke, C. & Walker, B. H. *Nature* 413, 591–596 (2001).

- Lenton, T. *et al.* *Proc. Natl. Acad. Sci. USA* 105, 1786–1793 (2008).
- Rockstrom, J. *et al.* *Ecol. Soc.* (in the press); available from http://www.stockholmresilience.org/download/18_1fe8f33123572b59ab800012568/pb_longversion_170909.pdf
- Intergovernmental Panel on Climate Change Climate Change 2007: *The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon, S. *et al.*) (Cambridge University Press, 2007).
- Hansen, J. *et al.* *Open Atmos. Sci. J.* 2, 217–231 (2008).
- Johannessen, O. M. *Atmos. Oceanic Sci. Lett.* 1, 51–56 (2008).
- Cazenave, A. *Science* 314, 1250–1252 (2006).
- Church, J. A. & White, N. J. *J. Geophys. Res. Lett.* 33, L01602 (2006).
- Mace, G. *et al.* *Biodiversity in Ecosystems and Human Wellbeing: Current State and Trends* (eds Hassan, H., Scholes, R. & Ash, N.) Ch. 4, 79–115 (Island Press, 2005).
- Sala, O. E. *et al.* *Science* 287, 1770–1776 (2000).
- Sahney, S. & Benton, M. J. *Proc. R. Soc. Lond. B* 275, 759–766 (2008).
- Diaz, S. *et al.* *Biodiversity regulation of ecosystem services in Ecosystems and Human Well-Being: Current State and Trends* (eds Hassan, H., Scholes, R. & Ash, N.) 297–329 (Island Press, 2005).
- Folke, C. *et al.* *Annu. Rev. Ecol. Syst.* 35, 557–581 (2004).
- Chapin, F. S., III *et al.* *Nature* 405, 234–242 (2000).
- Purvis, A. & Hector, A. *Nature* 405, 212–219 (2000).
- Foley, J. A. *et al.* *Science* 309, 570–574 (2005).
- Gruber, N. & Galloway, J. N. *Nature* 445, 293–296 (2008).
- Machenzie, F. T., Ver L. M. & Lerman, A. *Chem. Geol.* 190, 13–32 (2002).
- Carpenter, S. R. *Regime shifts in lake ecosystems: pattern and variation*, Vol. 15 in *Excellence in Ecology Series* (Ecology Institute, 2003).
- Zillen, L., Conley, D. J., Andren, T., Andren, E. & Björck, S. *Earth Sci. Rev.* 91 (1), 77–92 (2008).
- Bennett, E. M., Carpenter, S. R. & Caraco, N. E. *BioScience* 51, 227–234 (2001).
- Handoh, I. C. & Lenton, T. M. *Global Biogeochem. Cycles* 17, 1092 (2003).
- Snyder, P. K., Foley, J. A., Hitchman, M. H. & Delire, C. J. *Geophys. Res. Atmos.* 109, D21 (2004).
- Costanza, R. *Struct. Change Econ. Dyn.* 2(2), 335–357 (1991).
- Odum, E. P. *Ecology and Our Endangered Life-Support Systems* (Sinuauer Associates, 1989).
- Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Meilillo, J. M. *Science* 277, 494–499 (1997).

- Boulding, K. E. *The Economics of the Coming Spaceship Earth in Environmental Quality Issues in a Growing Economy* (ed. Daly, H. E.) (Johns Hopkins University Press, 1966).
- Arrow, K. *et al.* *Science* 268, 520–521 (1995).
- Bretherton, F. *Earth System Sciences: A Closer View* (Earth System Sciences Committee, NASA, 1988).
- Schellnhuber, H. J. *Nature* 402, C19–C22 (1999).
- Turner, B. L. II *et al.* (eds) *The Earth as Transformed by Human Action: Global and Regional Changes in the Biosphere over the Past 300 Years* (Cambridge University Press, 1990).
- Clark, W. C. & Dickson, N. M. *Proc. Natl. Acad. Sci. USA* 100, 8059–8061 (2003).
- Holling, C. S. *The resilience of terrestrial ecosystems: local surprise and global change in Sustainable Development of the Biosphere* (eds Clark, W. C. & Munn, R. E.) 292–317 (Cambridge University Press, 1986).
- Walker, B., Holling, C. S., Carpenter, S. R. & Kinzig, A. *Ecol. Soc.* 9, 5 (2004).
- Folke, C. *Global Environmental Change* 16, 253–267 (2006).
- Kaufmann, S. A. *Origins of Order* (Oxford University Press, 1993).
- Holland, J. *Hidden Order: How Adaptation Builds Complexity* (Basic Books, 1996).
- Lovelock, J. *Gaia: A New Look at Life on Earth* (Oxford University Press, 1979).
- Levin, S. A. *Fragile Dominion: Complexity and the Commons* (Perseus Books, 1999).

Editor's note This Feature is an edited summary of a longer paper available at the Stockholm Resilience Centre (<http://www.stockholmresilience.org/>) planetary-boundaries). To facilitate debate and discussion, we are simultaneously publishing a number of linked Commentaries from independent experts in some of the disciplines covered by the planetary boundaries concept. Please note that this Feature and the Commentaries are not peer-reviewed research. This Feature, the full paper and the expert Commentaries can all be accessed from http://tinyurl.com/planet_boundaries.

See Editorial, page 447. Join the debate. Visit <http://tinyurl.com/boundariesblog> to discuss this article. For more on the climate, see www.nature.com/climatecrunch.

Authors

Johan Rockström^{1,2}, Will Steffen^{1,3}, Kevin Noone^{1,4}, Åsa Persson^{1,2}, F. Stuart Chapin, III⁵, Eric F. Lambin⁶, Timothy M. Lenton⁷, Marten Scheffer⁸, Carl Folke^{1,9}, Hans Joachim Schellnhuber^{10,11}, Björn Nykvist^{1,2}, Cynthia A. de Wit⁴, Terry Hughes¹², Sander van der Leeuw¹³, Henning Rodhe¹⁴, Sverker Sörlin¹⁵, Peter K. Snyder¹⁶, Robert Costanza¹⁷, Uno Svedin¹, Malin Falkenmark^{1,18}, Louise Karlberg^{1,2}, Robert W. Corell¹⁹, Victoria J. Fabry²⁰, James Hansen²¹, Brian Walker^{1,22}, Diana Liverman^{23,24}, Katherine Richardson²⁵, Paul Crutzen²⁶, Jonathan A. Foley²⁷

¹Stockholm Resilience Centre, Stockholm University, Kräftriket 2B, 10691 Stockholm, Sweden. ²Stockholm Environment Institute, Kräftriket 2B, 10691 Stockholm, Sweden. ³ANU Climate Change Institute, Australian National University, Canberra ACT 0200, Australia. ⁴Department of Applied Environmental Science, Stockholm University, 10691 Stockholm, Sweden. ⁵Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA. ⁶Department of Geography, Université Catholique de Louvain, 3 place Pasteur, B-1348 Louvain-la-Neuve, Belgium. ⁷School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK. ⁸Aquatic Ecology and Water Quality Management Group, Wageningen University, PO Box 9101, 6700 HB Wageningen, the Netherlands. ⁹The Beijer Institute of Ecological Economics, Royal Swedish Academy of Sciences, PO Box 50005, 10405 Stockholm, Sweden. ¹⁰Potsdam Institute for Climate Impact Research, PO Box 60 12 03, 14412 Potsdam, Germany. ¹¹Environmental Change Institute and Tyndall Centre, Oxford University, Oxford OX1 3QY, UK. ¹²ARC Centre of Excellence for Coral Reef Studies, James Cook University, Queensland 4811, Australia. ¹³School of Human Evolution & Social Change, Arizona State University, PO Box 872402, Tempe, Arizona 85287-2402, USA. ¹⁴Department of Meteorology, Stockholm University, 10691 Stockholm, Sweden. ¹⁵Division of History of Science and Technology, Royal Institute of Technology, Teknikringen 76, 10044 Stockholm, Sweden. ¹⁶Department of Soil, Water, and Climate, University of Minnesota, 439 Borlaug Hall, 1991 Upper Buford Circle, St. Paul, MN 55108-6028, USA. ¹⁷Gund Institute for Ecological Economics, University of Vermont, Burlington, VT 05405, USA. ¹⁸Stockholm International Water Institute, Drottninggatan 33, 11151 Stockholm, Sweden. ¹⁹The H. John Heinz III Center for Science, Economics and the Environment, 900 17th Street, NW, Suite 700, Washington DC 20006, USA. ²⁰Department of Biological Sciences, California State University San Marcos, 333 S Twin Oaks Valley Rd, San Marcos, CA 92096-0001, USA. ²¹NASA Goddard Institute for Space Studies, 2880 Broadway, New York, NY 10025, USA. ²²Commonwealth Scientific and Industrial Organization, Sustainable Ecosystems, Canberra, ACT 2601, Australia. ²³Environmental Change Institute, University of Oxford, Oxford OX1 3QY, UK. ²⁴Institute of the Environment, University of Arizona, Tucson AZ 85721, USA. ²⁵The Faculty for Natural Sciences, Tagensvej 16, 2200 Copenhagen N, Denmark. ²⁶Max Planck Institute for Chemistry, PO Box 30 60, 55020 Mainz, Germany. ²⁷Institute on the Environment, University of Minnesota, 325 Vo Tech Building, 1954 Buford Avenue, St Paul, MN 55108, USA.