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Ecosystem science for a changing world

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Executive summary

- A substantial fraction of all carbon dioxide (CO_2) emitted by fossil-fuel burning and deforestation will remain in the atmosphere and continue to influence climate for thousands of years. The potential consequences of a long-term failure to decarbonize the global economy are extremely serious. Given the importance of climate change, it is paramount that impacts and adaptation requirements be assessed accurately and dispassionately.
- The potential effects of climate change on ecosystems and ecosystem services remain surprisingly poorly understood, despite their high profile as ‘reasons for concern’. Better understanding could be achieved by a more ecumenical approach to ecosystem science and a more transparent approach to ecosystem modelling, informed by the fast-expanding base of systematic observations on organisms, ecosystems and the atmosphere.
- State-of-the-art models of carbon cycling by land ecosystems – the focus of this discussion—give widely divergent predictions and therefore, evidently, need further improvement. Some include incorrect representations of key processes, and many neglect important observational constraints. These problems could be addressed with the help of existing observations and knowledge.
- Even at its present elevated concentration of around 400 parts per million, CO_2 is one of the limiting factors for plant growth. Rising CO_2 concentration can partly counteract the effects of climate change on ecosystems. These CO_2 effects should not be neglected, even though their magnitude remains controversial and in need of resolution.
- Current predictions of how climate change will affect species’ survival depend on contradictory assumptions. Extinctions due to rapid climate changes in the geologically recent past have been few, thanks to rapid migration in most groups. The ability of most species to adapt naturally to climate change may have been underestimated. Large mammals are a notable exception. Species of cold environments generally are threatened by unprecedented warmth. Land use may inhibit unaided species migration to an unknown extent.

Contents

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- Large changes in the potential geographic ranges of both wild and cultivated species are to be expected due to climate change in the near future and agriculture, forestry and conservation will all have to adapt to this situation. Better information on these impacts of climate change is an urgent priority.
- All science relies on models. But the continuing pursuit of ecosystem modelling and the underpinning empirical science in isolation from one another limits the progress of ecosystem science, while undermining the credibility of models.
- Principles suggested here for ecosystem modelling imply a significant break with past practice. Next-generation models should be construed primarily as tools for understanding observed phenomena. They should be transparent and easily reproducible, and no more complex than required.
- A way towards better predictive understanding in ecosystem science involves (a) recognizing well-founded generalizations (even if approximate) and working towards a 'standard model', (b) full use of diverse observational data sets while developing models, (c) a culture of sharing of data, model outputs and model codes, and (d) integration of information about climate changes in the recent and more distant past.
- Science does not automatically promote the new approaches needed to solve urgent practical problems, such as those linked to climate change. The communication barriers between narrow research communities are an impediment to scientific innovation. Limits to the role of science in supporting policy making are not always well articulated or appreciated.
- Currently available depictions of the 'severity' of different impacts are greatly oversimplified, and inevitably embody value judgements. A stronger evidence base is needed, including a more coherent analysis of biospheric impacts.

Introduction

The global land surface is changing because of the increasing demands on the land for food, fibre and fuel production in a world undergoing continuing economic development. Climate change is an additional factor superimposed on these major changes that are happening in any case. Its effects can only increase; their eventual magnitude will depend on how rapidly the causes of climate change can be mitigated.

The reasons for concern about climate change in the future are not limited to the direct effects of temperature and precipitation changes on human activities, such as the consequences of heatwaves and reduced water supplies or floods. Effects of sea-level rise loom large because of the potentially major consequences for industrial, transport and residential infrastructure, and agricultural land. Other reasons for concern involve projected effects on the services provided by crops, pastures, forestry and natural ecosystems, and the survival of wild species that we care about (for practical or other reasons). Though recent climate change has been modest, its effects on ecosystems and species are already extensively documented[1]. Knowledge of these effects is important for adaptation (what crop traits to breed for, what trees to plant, how best to conserve species and habitats) and mitigation (knowing which ecosystems to protect or enhance in order to keep carbon on or in the ground). There is a clear practical need for this knowledge. It's not about 'telling scary stories' to promote action on climate change. It's about quantification and awareness of the nature and scale of the challenges.

I will argue that the current state of knowledge about climate change impacts on ecosystems and species is inadequate, and that this situation is to some extent self-imposed by the research system. The good news is that it should be possible to do much better, given awareness of the difficulties, and willingness by people with different skills and knowledge to work together. It's important to do better, because without well-founded and defensible knowledge, myths and ideology tend to fill the gap. It's not that scientific knowledge is always accepted by everyone – obviously not. But if the science is weak, it certainly doesn't help. As for myths and ideology, there are plenty to choose from. You could favour the idea (promoted at one time by some fossil-fuel lobby groups) that a world with a very much higher concentration of carbon dioxide (CO_2) will be hugely verdant, and the burning of fossil fuels thus a great boon to people in the future. Or you could accept James Lovelock's bleak picture of a warmer world in which, for some reason, most of the land surface has been taken over by uninhabitable deserts[2]. Neither of these is consistent with what we know about ecosystems and climate.

When 'global change' first surfaced as a research issue in the 1980s, the science of ecology was notably ill-equipped to answer big questions about how ecosystems and species could be expected to react to changes in the environment. To some extent it still is. Some ecologists continue to maintain a principled objection to seeking universal rules in nature. Some are still uncomfortable about sharing their data with other scientists or the public. These are probably transient problems. Meanwhile there have been huge advances in the availability of relevant observational data on different scales, from high-resolution remote sensing of the land surface to precise measurements of the composition of the global atmosphere (not traditional concerns of ecologists), as well as compilations of key measurements on tens of thousands of plant and animal species worldwide. These advances have been quite specifically motivated by the need to develop a predictive understanding of global change in relation to ecosystems. So there is now an opportunity – and I would argue, an obligation – to capitalize on a wealth of data that simply didn't exist 20-30 years ago. There has been enormous progress, starting in the 1990s, in the development of large scale models of ecosystem processes and biogeochemical cycles. The great opportunity now is to exploit the burgeoning observational base, in order to develop more rigorous basic ecosystem science and more reliable models.

The significance of climate change for decisions to be made – by both public and private sector actors – means that it is in the spotlight, all the time. The situation poses challenges that will be familiar to researchers in public health or clinical medicine, but they are relatively new for many of the scientists who now study global environmental change. Policy relevance, in my view, brings an additional responsibility: to try seriously to answer large and difficult questions, which may often cut across disciplines and straddle major knowledge gaps. Unfortunately the system of rewards in scientific research, publication and funding does not always particularly promote or reward such diligence. This is the background to the following sections, which document a certain lack of ‘joined-up thinking’ in science together with some ideas about how the scientific community might try to do better.

The global carbon cycle

A (very) brief history of carbon

The global carbon cycle involves movements of carbon between different compartments of the Earth system. On long geological time scales, tens to hundreds of millions of years, the atmospheric concentration of CO_2 has varied greatly because of changes in the long-term balance of slow processes that transfer carbon from the atmosphere to the lithosphere, the solid outer layer of the planet – principally the weathering of silicate rocks, but also the laying down of fossil carbon in coal deposits – and volcanic outgassing, which transfers CO_2 back to the atmosphere[3] (Fig. 1). These fluxes are vanishingly small on an annual basis, but large imbalances can build up over aeons. Along with other major long-term ‘drivers’, including the slowly changing geography of land and oceans, these changes in the concentration of CO_2 and other greenhouse gases have made a huge difference to the Earth’s climate.

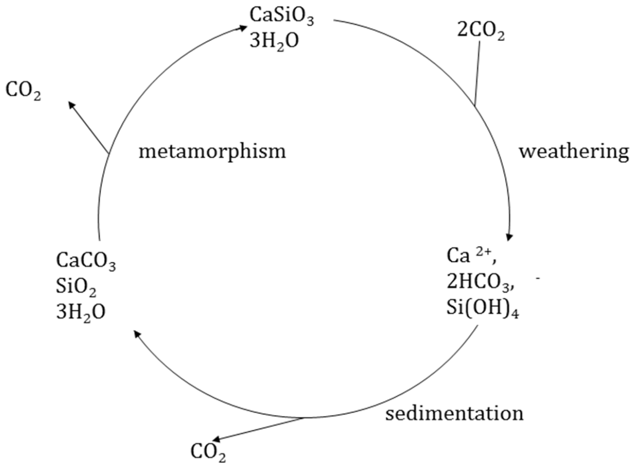

Figure 1: The carbon cycle on a long geological timescale. From a sketch by Harry Elderfield.

On Quaternary ice-age/interglacial time scales, tens to hundreds of *thousands* of years, there have been more constrained variations in the atmospheric CO_2 concentration (between about 170 and 300 parts per million, ppm: Fig. 2) reflecting transfers of carbon among the atmosphere, ocean and land. Low CO_2 concentrations were not the cause of the ice ages. They were a consequence of climate changes caused ultimately by the natural variations in the Earth’s orbit, which are the predominant driver of climate variations on these time scales. But low CO_2 concentrations helped to keep the world in a relatively cold state during ice ages, especially in regions remote from the expanded ice sheets[4].

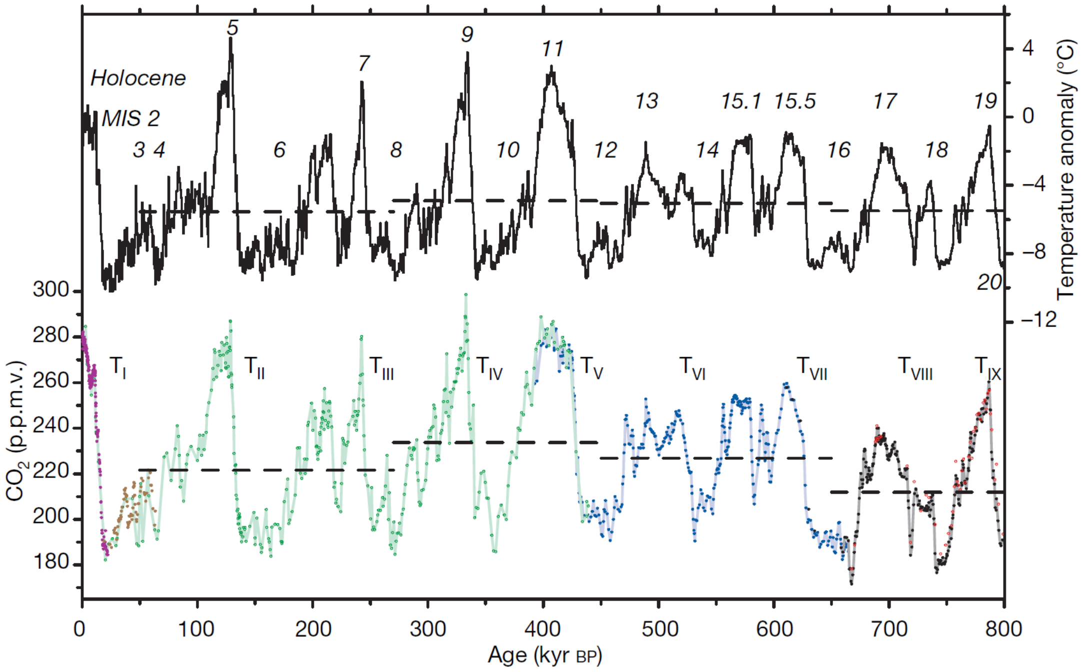

Figure 2: Variations in atmospheric carbon dioxide (CO_2) concentration during the ice ages and interglacials of the past 800,000 years. Reconstructed Antarctic temperature anomalies are also shown. Reproduced from ref. [30].

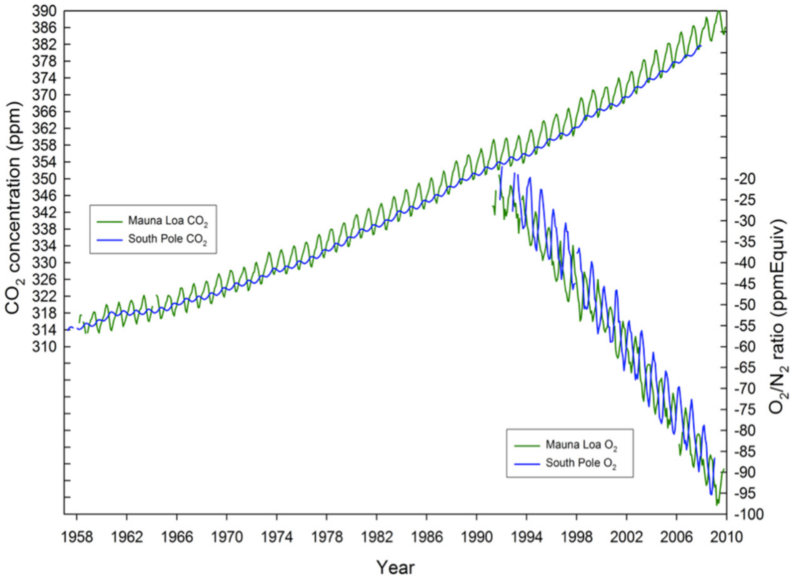

Figure 3: Atmospheric carbon dioxide (CO_2) and oxygen (O_2) changes during recent years. Diagam by Andrew Manning, reproduced from ref. [4].

The present interglacial began about 11,700 years ago and during most of this period – approximately the past 8000 years – atmospheric CO_2 concentration has been nearly constant. There was a small increasing trend, whose causes are disputed, amounting in any case to only about 20 ppm in total over the whole period. But from the Industrial Revolution onwards, CO_2 in the atmosphere has increased much more rapidly than it did during the previous 8000 years. It is now rising at about 20 ppm per decade and recently reached 400 ppm. The principal reason for this accelerated rise is that CO_2 is now being added back to the system containing the atmosphere, ocean, and land by transfers of carbon from the lithosphere, via the burning of fossil fuel.

The 'signature' of this transfer of carbon from the lithosphere to the atmosphere can be measured in the atmosphere, as changes in the isotopic composition of atmospheric CO_2. Fossil fuel lacks the radioactive isotope 14C, and is depleted in the rare stable isotope 13C relative to the common isotope 12C. As a result, the abundances of both 'heavy' isotopes have been declining during the industrial period. For 14C this trend was interrupted by fall-out from atmospheric nuclear bomb tests in the 1960s, but it can be measured in tree rings laid down in earlier years.

The signature of global change in recent decades also includes a decline in the atmospheric content of oxygen (O_2). This is not dangerous, because there is a far larger amount of O_2 in the atmosphere than there is CO_2. It is a useful measurement nonetheless (Fig. 3). Among other things, the decline in O_2 shows that the increase in CO_2 is due to a process that consumes O_2, as burning does.

CO_2 uptake and climate feedback

Not all of the additional CO_2 contributed by fossil-fuel burning ends up in the atmosphere. About half, on average, ends up either in the ocean, where it contributes to acidification, or on land, where it adds to the stock of biomass and soil carbon. We can use the O_2 measurements to help quantify the separation between land and ocean uptake. This is because ocean uptake doesn't release oxygen, whereas land uptake releases oxygen because it involves the conversion of CO_2 to organic form of carbon, which contain less oxygen than CO_2.

Measurements also show that the land uptake is highly variable from year to year, because it is sensitive to climate variability. Notable variations are linked to the El Niño-Southern Oscillation, and the after-effects of larger volcanic eruptions such as those of Pinatubo and El Chichon[5] (Fig. 4).

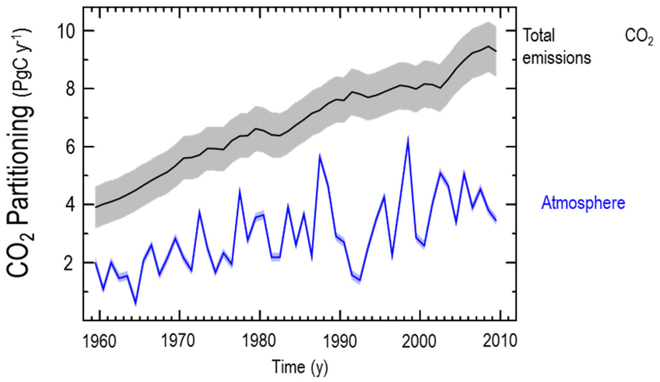

Figure 4: Interannual variability of the CO_2 growth rate. From http://www.globalcarbonproject.org/, updated from ref. [31].

These net uptakes of emitted CO_2 must not be confused with the gross fluxes that are exchanged every year between the ocean and atmosphere, and the land and atmosphere.

These exchange fluxes are more than an order of magnitude larger than fossil-fuel emissions. This is why the land uptake, especially, can vary so much from year to year. Relatively small perturbations in the gross flux, due to climate variability, cause relatively large variations in net uptake. The gross fluxes can be ignored for some purposes, but not others – it's important to take account of them, for example, when calculating the expected change in isotopic composition of atmospheric CO_2 due to fossil-fuel burning.

One carbon-cycle question has attracted particular scientific attention recently. As global temperature increases, how much *additional* CO_2 will be put into the atmosphere as a result of faster decomposition of soil organic matter, and other modelled effects of global warming – such as a projected die-back of the Amazon rainforest? This is a positive feedback (in the technical sense, i.e. an amplification of the original forcing), known as the climate-carbon cycle feedback.

It has recently been shown[6], using a simple observational constraint, that this feedback amounts to about a 25 ppm CO_2 increase for each degree of global warming. This is small compared to the increase in CO_2 concentration projected in most scenarios for the 21st century. It has also been shown that Amazon forest die-back during the 21st century is improbable[7]. These findings suggest that the climate-carbon cycle feedback is significant quantitatively, but not necessarily a game-changer. I will return to this topic after a discussion of carbon-cycle models.

Problems with carbon models

There are now dozens of models, based on a substantially overlapping set of physiological and ecological principles, which are supposed to represent how carbon exchanges between land ecosystems and the atmosphere are affected by variations in CO_2 concentration and climate. But when 11 such models – all coupled to climate models – were asked to predict the size of the climate-carbon cycle feedback, they came up with answers differing by a factor of more than seven[8]. And when the response of the models was broken down into components, the responses of individual components varied greatly[9]. For example, global net primary production (NPP, the annual rate at which carbon is incorporated into the tissues of growing plants) was predicted by some models to increase, and by others to decrease (Fig. 5), in response to the same scenario in which CO_2 emissions increased at a prescribed rate.

This large variation among carbon-cycle models shown in ref. [8] has been called 'uncertainty'. I prefer to call it 'ignorance'. The carbon-cycle models had not been subjected to basic quality control checks ('benchmarks') even though benchmarking protocols already existed. For example, the network of high-precision CO_2 concentration measurements around the globe provides valuable constraints on carbon cycle models[10]. If anything, the variation among models has widened since 2006 due to the inclusion of explicit nitrogen-carbon cycle coupling in many models. This stalemate has prompted a recent surge of interest in the idea of a universal set of benchmarks for terrestrial carbon cycle modelling. Routine benchmarking of models would at least help prompt re-examination and reduce avoidable divergences among models.

Benchmarking is not a panacea, however. The discrepancies among models seem to be symptomatic of a more fundamental lack of consensus about several aspects of the science that underpins them. Net primary production, the basis for all green vegetation and crop production, provides a good example. It was established in agricultural science as long ago as 1972 that the NPP of a crop over a given interval is proportional to the light it absorbs during that interval[11]. That is, NPP is proportional to the product of the incident light flux (which depends on sun angles, cloud cover and time) and the fraction of incident light absorbed by the leaves. This empirical fact can also be explained physiologically as a consequence of the acclimation of photosynthetic capacity to light. But new models continue to be published in the ecological literature where NPP depends only on temperature and rainfall, and not at all on light. These may work well enough for many practical purposes but they should not be used, for example, to project the consequences of geo-engineering schemes that rely on reducing solar radiation.

There seems to be continuing confusion about the controls of NPP. One recent paper claimed that the NPP of land ecosystems (by a flawed analogy with marine ecosystems) depends mainly on the availability of nutrients[12]. Another reported that global NPP was declining[13] (Fig. 6); the paper's summary hinted that this trend might continue and could adversely affect agriculture. The result was based on a remote-sensing product using satellite data as input. The journal later published two technical critiques of the paper, but it probably wasn't clear for the general reader that

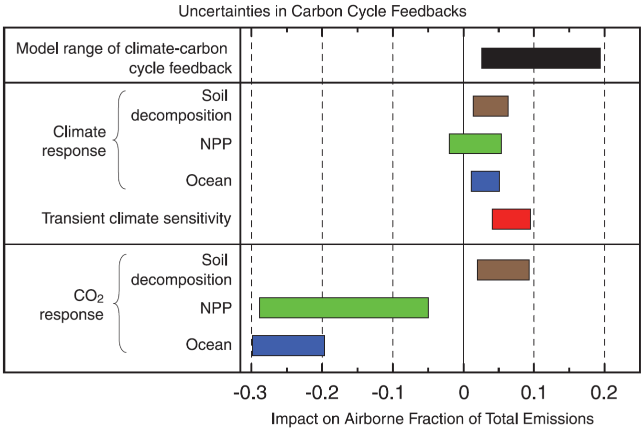

Figure 5: The range of responses of different processes in the carbon cycle to global carbon dioxide (CO_2) increase and associated warming, as simulated by different models. The 'airborne fraction' is the fraction of emitted CO_2 that remains in the atmosphere. Positive values (to the right) refer to processes that increase atmospheric CO_2, negative values (to the left) to processes that reduce atmospheric CO_2. Reproduced from ref. [9].

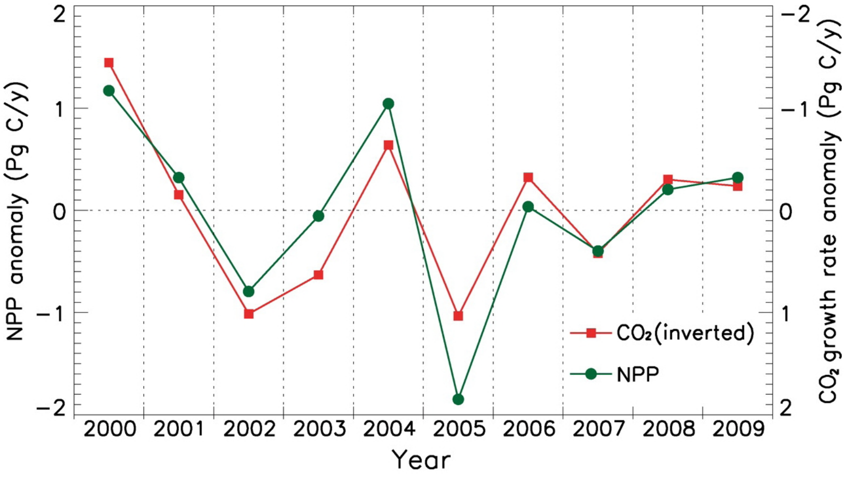

Figure 6: Comparison of interannual variability in the rate of increase of atmospheric carbon dioxide (CO_2) with net primary production (NPP) from a satellite-based model. Years with lower than usual NPP coincide with years when the growth rate of CO_2 in the atmosphere is higher than usual. On this time scale, as in Fig. 4, the biosphere is 'driving' and the CO_2 growth rate is responding. But in this particular model the response is entirely via reduced NPP – and therefore not at all by increased soil organic matter decomposition, which is also thought to play an important role. Reproduced from ref. [13].

the so-called declining trend (a) was not statistically significant over much of the world, and (b) was a model result, not a measurement. These are extreme examples illustrating the need for a more open, community-based approach to the fundamentals of ecosystem science and modelling; and a concerted attempt to establish what is actually known, and therefore should be common to all models.

Another feature of the model employed in ref. [13], often referred to simply as 'MODIS NPP' (MODIS is the satellite instrument that provides the 'greenness' measurements as input to the NPP model), is that it appears to disregard the effect of increasing CO_2 in increasing NPP. If all of this effect were manifested as increases in greenness, then it would be implicitly included. But increasing CO_2 increases photosynthesis per unit leaf area, and this effect – likely to be more important than any greenness effect in forests, for example – is not included. The so-called 'CO_2 fertilization' effect is well known from experiments at scales ranging from single leaves to whole forests. It is the principal contender as the cause of the measured net global CO_2 uptake by land ecosystems[4]. The causal connection is hard to prove or disprove empirically, because the uptake is small compared with the existing stocks of carbon in the biosphere. But computations show that CO_2 fertilization estimated from first principles is in the right magnitude to explain the measured uptake of CO_2 by ecosystems on land.

The effect of CO_2 in increasing plant productivity might be referred to as a different kind of 'inconvenient truth'. It is true regardless of who promotes it, or their motives in doing so! There is still controversy among ecosystem scientists about its magnitude, and especially the extent to which this will be constrained by other factors (such as nitrogen supply) in the long term. But it exists, and to pretend otherwise is unhelpful. A re-appraisal of the various lines of evidence for the magnitude of the CO_2 fertilization effect is overdue.

It's the emissions, stupid!

Fortunately, our understanding of the global carbon cycle is sufficient to make some robust, non-controversial statements about the efficacy (or otherwise) of mitigation measures, which apply regardless of any particular carbon cycle model.

The central point is that in the absence of technology to strip CO_2 out of the atmosphere on a massive scale, the climate impact of CO_2 emissions is effectively irreversible[5,14]. Although about half of the emitted CO_2 is taken up by land and oceans, the remainder stays in the atmosphere for *thousands of years*. There is no 'safe' level of CO_2 emission that is low enough that all of it would be taken up by natural 'sinks'. The reason is that the current 'sinks' (i.e. the uptake of CO_2 by the land and oceans) are caused by the increase of CO_2 concentration, and their magnitude is proportional to the rate of increase. If CO_2 concentration were stabilized, CO_2 uptake would decline, eventually to a very low background level determined by the growth of peat bogs, the accumulation of charcoal, and the formation of deep-ocean sediments[5].

Scenarios that achieve rapid drawdown of CO_2 concentration during the 21st century seem to avoid this problem, but they rely heavily on a hypothetical transformation of ecosystems into sources of biomass energy coupled with geological sequestration of the CO_2 produced during combustion. In principle this system, known as Biomass with Carbon Capture and Storage (BCCS), can create negative net emissions. But there are good reasons to doubt its practicality (or desirability, in terms of other objectives such as biodiversity conservation) as a primary means of 'planetary management', on the extraordinary scale that such scenarios require.

Simple calculations also show that there is spare capacity in the land biosphere to store carbon (mainly a consequence of previous deforestation) and suggest that CO_2 'fertilization' has brought about a modest increase in this capacity – that is, a little more carbon could be stored than has been released. But this capacity is grossly insufficient to allow emissions into the future to be offset by planting trees, especially when requirements for food production are taken into account[14]. There is however a much larger remaining carbon store in extant forests. Hence the current policy focus on Reducing Emissions from Deforestation and forest Degradation (REDD) as a means to avoid yet further, non-fossil-fuel emissions of CO_2.

The bottom line is that the present rate of CO_2 increase is largely sustained by fossil-fuel burning emissions and that CO_2 concentration will continue to increase until these are reduced almost to zero. The more the cumulative emissions, the higher the long-term concentration of CO_2, the warmer the climate, and the greater the impacts of climate change. One consequence is that a certain amount (depending on mitigation measures taken during the coming decades) of further climate change is inevitable, and we will have to adapt to it.

Biodiversity and climate change

Unreliable models for species

If the global carbon cycle and the effects of increasing CO_2 concentration are controversial, the question of climate-change impacts on species is inflammatory. There is an almost complete disconnect between predictions made using 'species envelope models' on the one hand, and those made using physiologically based models, such as those used by foresters to predict forest growth and yield.

Species envelope models, also called niche models, are based on the observed correlation between the present geographic distributions of species and variables representing different aspects of climate. Many predictions made with these models are extremely pessimistic, because they predict that most species, especially in topographically flat regions, will be forced to migrate long distances in order to keep up with the displacement of their modelled climatic range[15]. The pessimism is compounded when authors of papers choose to assume that species can't migrate – in which case, partial or complete extinctions of species are the only possible outcomes.

On the other hand, forest growth and yield models generally assume that a given tree species will grow wherever it is planted, and do not attempt to account for natural range limits. I will give one example I am familiar with from Sweden. The natural western and southern limit of Norway spruce in Europe closely follows the 0°C isotherm for mean temperature of the coldest month, around numerous mountain ranges – this species avoids climates with milder winters, whether in western or southern Europe, including the southernmost counties of Sweden. It can be grown to the west of its native range, but it has not been a success in commercial forestry terms. Non-European species such as Sitka spruce from the mild Pacific Northwest of the USA are favoured in Britain, for example.

There are various anecdotal explanations for why Norway spruce is not successful in Britain, although none seems to be generally accepted. Nevertheless, all climate change projections show rapid winter warming (continuing a trend already well underway) in Sweden. And any species envelope model, based on the observed distribution of this species, must predict the *elimination* of Norway spruce from the productive southern part of the country. I suggest that if the range limit of a species today closely follows a particular isotherm, there is likely to be a reason for it; and the natural (and commercially useful) range of the species surely will move as the isotherm moves.

Conflicting scientific results can lead to conflicting policies. I have heard a report of one conservation organization seriously debating whether to give up supporting practical conservation activities, on the grounds that the effects of climate change on species will be so disastrous (according to research based on species envelope models!) that all funds should be channelled into lobbying for more effective mitigation of climate change. At the other extreme, in Sweden, although some biologists have expressed contrary views, the official advice to foresters remains: 'plant Norway spruce'.

There are many reasons to doubt the more catastrophic predictions of species envelope models: too many to list here. One key criticism of these models is that they are untestable, because all of the information on the present distribution of species is used in the construction of the model. In other words, it is *assumed* that the species' range boundary is entirely determined by some combination of climate variables. It would be more defensible to fit only limits corresponding to a mechanism *known* (or at least, defensibly hypothesized) to restrict the boundary of species of a particular group of organisms. Many groups of organisms, for example, have reasonably well-understood requirements for summer heat, and limited tolerance of drought and winter cold. Another key criticism is that because of their purely empirical nature, species envelope models do not have any way to include the physiological effects of CO_2. Increasing CO_2 not only increases photosynthesis; it also decreases stomatal conductance, and therefore water loss per unit leaf area. So there is an 'upside' for species: the physiological effects of CO_2 could counteract the effects of drought. The extent of this effect is unknown but sensitivity tests with models suggest that it could be crucial in determining species' range limits in dry climates[16].

A palaeoecological perspective

The view that species are incapable of rapid migration can be challenged on the basis of evidence to the contrary. A palaeoecological perspective is useful here, because although there is abundant evidence that species distributions are already changing in the directions expected due to recent climate changes[1], the recent observations don't provide information needed to test the effects of larger climate changes. In the past there have been long-distance migrations of species, for example during the transition from the last ice age to the present interglacial. The magnitude and rate of this transition varied across the world but the mean temperature increase was of the order of five degrees and in the North Atlantic and surrounding continents this final warming, marking the end of the cold Younger Dryas period, took place during a period no longer than 20-30 years[17]. Remarkably, based on thousands of records of plant pollen, seeds, leaves and wood fragments, only *one* plant species in the entire world is known to have become extinct during this transition[18] – even though many species' ranges were displaced by thousands of kilometres. Insects and small mammals, which also have a rich recent fossil record, showed equally prodigious migration ability.

The abrupt end of the last ice age was not the only rapid warming event to have occurred in geologically recent times. So-called Dansgaard-Oeschger events (rapid warmings followed by slower coolings) punctuated the last and previous ice ages[17]. These appear to have been nearly global in extent. Many were of even larger amplitude than the warming at the end of the Younger Dryas, and they took place typically over 20-200 years[19]. More than twenty such events happened during the last ice age. Globally, the changes were so large as to have measurable impacts on atmospheric constituents (methane, nitrous oxide, dust) and wildfires (Fig. 7). It seems likely that natural, rapid climate changes have been a powerful selective force favouring the ability to migrate rapidly: at least in organisms with a high enough reproductive rate.

In contrast, many species of large mammals went extinct at or around the end of the last ice age. The situation is complicated by the possibility that over-hunting by prehistoric people played a role in these extinctions. This is a long-running, controversial topic, but recent genetic evidence supports climate change at least as a major contributory factor in the demise of now-extinct ice-age mammals[20]. Moreover, there is evidence for extinctions of large mammals in earlier periods of rapid warming.

Adaptive management – but how?

Although the magnitude and rate of CO_2 increase today, and projected over the 21st century, greatly exceed those of the deglaciation, at least certain regions and times appear to have experienced repeated temperature increases as large and rapid and those projected over the 21st century. It must be presumed that extant species have been selected for the ability to adapt naturally to climate changes, at least in groups where extinctions were few. The palaeorecord also points to the importance of migration, among other responses, as an adaptive mechanism. This is consistent with range shifts observed to have taken place already during the past half-century.

Should we then assume that all species will survive climate change? The answer is no. Large mammals are at risk, based on the palaeoecological evidence. Moreover, the warming today is relative to an already warm (interglacial) baseline, whereas Dansgaard-Oeschger warming events were relative to a cold (ice-age) baseline. Temperatures are therefore moving towards values not experienced during at least the past 800,000 years (the period covered by ice-core records) and probably much longer. As a result, habitat for polar and montane species in particular is shrinking. Finally, land use has fragmented habitats over much of the globe. Observations of range shifts in many groups indicate that land use is not necessarily an obstacle, but the extent to which intensively farmed areas constitute migration barriers, or the implications of habitat fragmentation for different groups of organisms, are essentially unknown. Conservation practitioners are considering a range of options that differ sharply from the

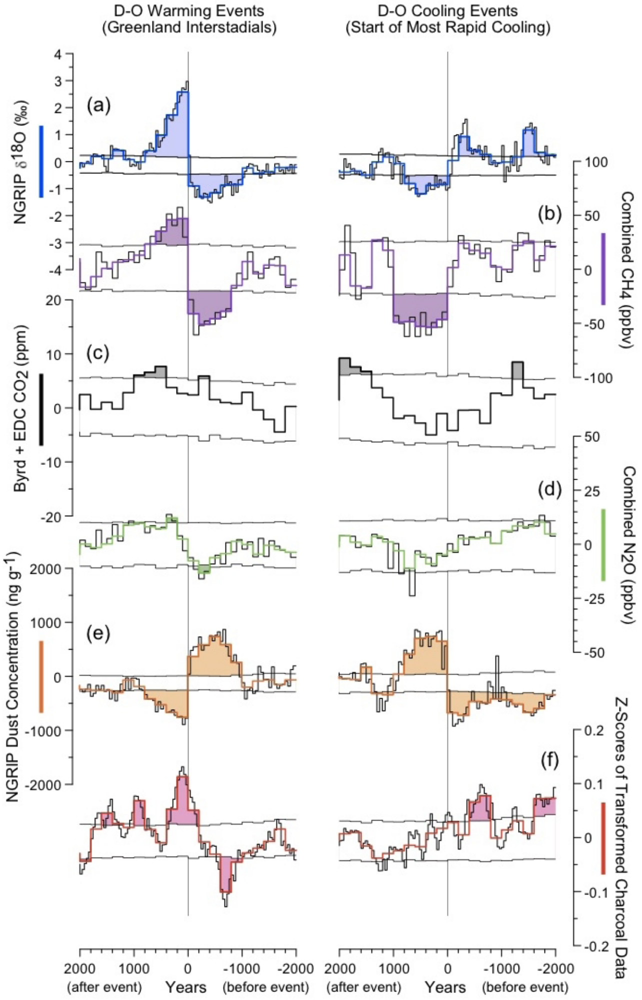

Figure 7: Superimposition of global changes associated with each of the Dansgaard-Oeschger (D-O) warming and cooling events. Note that time goes from right to left. The variables plotted are: **NGRIP δ18O**, a stable-isotope indicator of Greenland temperature; **Combined CH_4**, a composite ice-core record of atmospheric methane (CH_4) content; **Byrd + EDC CO_2**, a composite ice-core record of atmospheric carbon dioxide (CO_2) content; Comined N_2O, a composite ice-core record of atmospheric nitrous oxide (N_2O) content; **NGRIP Dust Concentration**, a mesaure of the amount of dust deposited on the Greenland ice sheet; and **Z-scores of Transformed Charcoal Data**, a measure of biomass burning based on a global compilation of sedimentary charcoal deposition rates. Reproduced from ref. [17].

traditional *in situ* approach to species conservation, judging that the future is likely to require a mix of corridors (to facilitate natural migration), *ex situ* conservation (for especially vulnerable species) and assisted migration – for example, moving upper montane species to higher mountain ranges.

In conclusion, we still don't know how to predict the fate of species in a changing world. It is very difficult to know how to design climate-proof conservation strategies, especially in the complex, fragmented landscape that human activity has created. It would be useful to have credible models to inform conservation policy. They should, at least, be able to predict responses known from rapid climate change situations in the past.

Adaptation needs in agriculture and forestry

The potential impacts of climate change on crops, grazing systems and forest trees loom large among the areas where more specific, quantitative knowledge is urgently required. There is no doubt that crops and grazing systems in some regions will suffer from climate change; effects are already being seen in many regions, and will no doubt intensify. Climate change will also bring new farming opportunities to some regions. Intensive efforts to breed heat- and drought-resistant crops will certainly help, but are unlikely to fully counter the necessity of geographic shifts in farming systems. Global data needed to analyse such shifts have been assembled[21], and could be used in model development.

The role of models

Modellers versus other scientists: an unhealthy separation

All science relies on models: conceptual, mathematical and numerical. But a curious situation has arisen in the science of climate change, including ecosystem impacts. An artificial separation has developed between the practice of model development (increasingly the preserve of relatively few specialists) and the wider field of science that should underpin modelling. In ecosystem science this separation is so complete that it is considered normal for a 'modeller' of ecosystem processes never to read ecophysiology journals, for example, and therefore to be unaware of recent developments in that field, or even for an experimentalist to claim 'not to believe in models'. Such polarization would be considered untenable in most fields of science. In any case the separation is counterproductive. It has led to models being developed without reference to relevant observations and experiments. It has also led to experimentalists failing to use powerful tools that could help to frame and analyse experiments, and (too often) making misleading claims about what models do and don't assume about the processes they study.

The sheer complexity of plant and ecosystem processes in their global environmental context is a challenge, equally for modellers and other kinds of scientists. The Earth system, composed of atmosphere, ocean, and land ecosystems, cannot usefully be reduced to a small set of equations. The consequence for models is that the complex system needs to be represented by a suitably complex model structure. But equally, experimental results need to be interpreted in a whole-system context, and experiments on plants carried out in controlled environments need to be complemented by experiments carried out on a larger scale. This is the rationale behind the movement in ecosystem science towards field-based experiments, including Free Air Carbon Dioxide Enrichment – FACE – a technology that has provided great insights on CO_2 effects on temperate ecosystems and crops. FACE needs to be extended to include a wider range of ecosystems and crops that are expected to respond in different ways[22]. There are also strong arguments for a wider range of experiments in controlled environments, linking large scale field manipulations to leaf-level physiology.

New principles for modelling?

Complex model structure has brought one particularly dangerous side-effect: the accumulation of ever greater opacity in models. At best, legacy codes with a 20-year or longer history (I admit to having developed one such 'Frankenmodel' myself!) are very hard for outsiders to understand. At worst, the complexity of these model codes provides effective protection from scrutiny by a wider community. But this approach to modelling is still the norm.

Just as in climate modelling, where there is the same problem, most ecosystem models have names that refer to a particular modelling centre or group of collaborators. In other words, a 'model' is a construct developed over time by a series of people connected with a particular institution or group of collaborators. It is not an identifiable or coherent theory of how the system works. Comparison of models accordingly focuses on Model Intercomparison Projects (MIPs) in which the differently named models participate. MIPs have value in showing how differently named models perform (against observational benchmarks, at least in the more recent MIPs). But they rarely provide much insight into why the models produce the different results they do, or how they might perform better against the benchmarks. It is possible to analyse MIP results more deeply to reveal causes of differences among models, and in doing so, to uncover specific deficiencies in particular models. But to do requires a sound theoretical framework, and to jettison the presumption that 'all models are equal'.

Under the auspices of the Australian Centre for Ecological Analysis and Synthesis (ACEAS) a Working Group of scientists involved in large scale ecological and hydrological modelling recently met to develop a series of modelling principles, representing potentially a significant break with past practice. The following is a selection of the principles proposed by the Working Group:

- The main purpose of models is to assist understanding of observed phenomena. The application of models for future projection is a valuable outcome, but should not take priority.
- Examine the model you are using. Does it represent processes in the way you intended? Does it do what you expect?

- Aim for a pedagogical representation of model structure and functional relationships, to help others understand its assumptions.
- When an effect is seen in a model, diagnose why. This can't always be done in the real world. It can *always* be done in the model world.
- Use a much simpler model as a baseline, i.e. as a tool to help diagnosis.
- Consider whether every process or function is needed in the model, and consider removing processes and functions that are not needed.

Some of these principles are beginning to be seen in the practice of many modelling groups. Their systematic adoption would be an important step.

A way forward for ecosystem science?

Critical collaboration

Breakthroughs in science will always require clear thinking by individuals. But no one individual is likely to have all of the skills and knowledge needed to make rapid progress on questions about ecosystems and the environment that the disciplines in their current state have failed to answer. Collaboration is essential.

Collaboration will not happen, or not be effective, however, unless scientists spend more time and effort 'looking over the fence' at what's happening in related fields, and doing so with an open mind. Every scientific community probably does some things well and some badly. So it's important to be critical, as well as being open to new ideas from other communities.

Four ways to do it better

For ecosystem science, and the development of predictive models of ecosystems, I suggest four key points that could transform practice. Much of what I'm suggesting is not specifically encouraged by the current ways in which scientists and scientific institutions are assessed. But real progress generally is encouraged once it has gained momentum. Nothing that I'm suggesting is impossible, or illegal! I'm proposing, in a nutshell, that we have the data, and at least part of the knowledge, that's required in order to make rapid progress.

I'm arguing that progress has been limited mainly by lack of imagination, and a failure to 'look over the fence'.

- Recognize that there is a growing body of quantitative understanding of the function of ecosystems, including carbon, water and nutrient cycles, and codify this knowledge in the form of models that are no more complex than they need to be for the purpose. Ecosystem science does not yet have a 'standard model', and yet there are many common components of current model which could usefully be identified, and sets of observations that could help to constrain model parameters. Codifying *what is known* would also help greatly in defining *what is not known*, and encourage redoubled efforts to fill the knowledge gaps.
- Engage all relevant observations as a test of and to place constraints on models. For example, complex models that claim to represent carbon cycling on land at a minimum must be tested against patterns of CO_2 uptake and release shown by regional CO_2 concentration measurements, as well as local CO_2 flux measurements, and other benchmarks such as patterns of NPP and vegetation and soil carbon storage. Better still, these observations should be used directly to estimate parameters of the model.
- Embrace sharing of and unrestricted access to all relevant observations, model outputs and source codes. Current systems that restrict access to certain types of data should be reformed, while maintaining the incentives for researchers to collect the data in the first place. New model codes should be written in a transparent, modular fashion and made publicly available, so that reproducibility can be established.
- Adopt an appropriate time scale for the choice of observations to promote understanding of a particular process or phenomenon. For climate change impacts this means taking seriously the information from 'palaeo' time scales, because it is only by using information from prehistory that we can gain observational insight into climate changes (and their effects) of similar magnitude to those projected for the 21st century and beyond. This development is beginning to happen. For example, data from the last glacial maximum have been used to provide a data-based constraint on climate sensitivity – one of the key properties of the climate system about which climate models still show substantial disagreement[23]. Climate sensitivity is notoriously difficult to estimate from recent observations. Other fields where palaeodata could help resolve controversies are CO_2 effects on NPP, climate-carbon cycle feedback, and the consequences of rapid climate change for ecosystems and species.

A reply to possible critics

I'm aware of many possible objections to these prescriptions, but I'm convinced that whereas there will no doubt be plenty of problems, they will not be fatal to the enterprise.

To the first idea, it can be countered that all species are different and natural selection does not achieve complete convergence of ecosystem function. This is probably true, but I suspect that convergence of function in the real world is much closer than the convergence of current *models* of ecosystem function. This at least is a testable hypothesis. Furthermore, considerable progress has been made in developing universal descriptions of ecosystem function with the help of optimality hypotheses, which explicitly propose convergence of function by natural selection. The 'laws' of ecology may be 'fuzzy' compared to those of physics: this does not invalidate the search for such laws[24, 25].

To the second idea, it has often been objected that ecosystem measurements, including flux measurements which typically record CO_2 and energy exchanges over about 1 km2, describe a very particular piece of the landscape that can't be compared with the large scale averages represented in global models. The heterogeneity of the landscape (both in terms of species occurrence and in terms of soil conditions) is great, and it's certainly a potential obstacle. I regard this as a problem of quantifying uncertainty in the appropriate way. Trying to get a model to match individual flux-tower measurements precisely is probably not useful. But the justification for measuring fluxes is that they are characteristic of the landscape to some degree. CO_2 concentration measurements can also be used. They integrate more effectively across large regions. Their particular difficulty is that to compare them with model results requires the intervention of another kind of model (for atmospheric transport) which brings additional uncertainty. However, atmospheric transport models are well-studied, and their uncertainties quantified. I suggest that there is no excuse for neglecting one of the most powerful techniques for testing the large scale performance of ecosystem models.

I cannot think of any legitimate objection to the third idea. Just as science funding bodies worldwide are moving rapidly towards open-access policies for publication, they could introduce a strong mandate (as already exists in the USA) for publicly funded data, at least, to be made available to the public that funded its collection. One excuse I have heard for not sharing (ecological) data can be stated as follows: 'I don't want to make my data available because other people may misinterpret them'. This is as counterproductive as it is arrogant. Individual scientists have no basis for claiming that their own interpretation of a given set of observations is necessarily the correct one. As regards models, the climate modeling community has made a big step towards open access to the *outputs* of models. At one time, climate model projections – carried out with a view to consideration by the Intergovernmental Panel on Climate Change (IPCC) – were made accessible only after a committee had approved a proposal to use the results. This allowed representatives of the climate modelling community to act as gatekeepers. The system was abandoned as being unworkable, as well as undesirable. Today, the climate modelling community leads the way by making the very large CMIP5 archive (the central repository for state-of-the-art climate modelling results) available to the public. Proposal-based access to data is still practised by some ecosystem science communities but it is to be hoped that this outmoded practice will soon be abandoned.

To some extent the trend to open access has been driven by technology: data storage capacity and internet bandwidth have increased so greatly, and so rapidly, that what might have been seen as hopelessly idealistic ten years ago is now everyday reality. The same development now needs to be extended to model codes, taking advantage of the same technological developments but also major advances in software which are facilitating transparent algorithm specification, 'plug and play' modularity with modules written in different languages, and sub-versioning software that makes it possible to track workflows and ensure replicability of model results. The extraordinary success of open-source programming languages, including the near-universal adoption of the computer language 'R' for statistical analysis, could inspire parallel developments in process-based modelling of ecosystems.

The final idea, concerning data from longer time scales, is a 'textbook' example of the failure of one community to take seriously (and critically) the work of another community. The disconnects between palaeoclimatology and contemporary climate science, and between palaeoecology and contemporary ecosystem science, have been almost complete until very recently. A critical view of 'palaeo' science is certainly in order. There are long-standing problems with traditional approaches, including a sometimes less-than-rigorous approach to the interpretation of past changes in ecosystems and some degree of residual prejudice (especially outside North America) against the sharing and reuse of data. But this situation is changing rapidly, thanks to the efforts of a few pioneers. There should no longer be any excuse to ignore the past.

Moreover, the past (on many time scales) is a topic of abiding public interest. When I've heard non-scientists questioning the causes and consequences of climate change today, often the questioner's starting point is the common knowledge that there have been warmer and colder periods in modern history; there have been ice ages, and warm interglacials; there have been long periods in Earth's history when there were no ice sheets, and CO_2 concentrations many times higher than they are now. All these things are true, and are reasonably well understood by palaeoclimate scientists. Yet it was only in the fourth report of the IPCC, in 2007, that palaeoclimate science first rated a chapter of its own. The grand history of the Earth and its inhabitants, and our understanding of the huge changes in climate that the Earth has seen even in the very recent (geological) past, don't seem to figure much in the official narrative about climate change. No wonder people are confused!

The tyranny of disciplines

Fragmentation in science

Many of the criticisms I have levelled above at the current state of ecosystem science and modelling relate to problems regarding the transfer of information between different disciplines and communities of practice. The degree of fragmentation – the number of these different communities that operate separately – is extraordinary, and yet it is so built into the current system of assessment (of papers, proposals and reputation) that it is rarely remarked on.

Take first the term 'ecosystem science – isn't this the same as 'ecology'? No it isn't. The US National Science Foundation has separate panels for ecology and ecosystem science. Carbon and nutrient cycles are ecosystem science. Species distributions are ecology. Other specialisms include remote sensing (a world with completely different norms and funding systems, and a famously impenetrable jargon), palaeoecology (divided into two largely non-communicating fields working on different time scales: the Quaternary and 'deep time'), ecophysiology, biogeography, biogeochemistry... It can take decades for information to pass from one of these communities to another. This is why it is routine to publish results in the literature of one community that ignore key data or relevant research findings from another. The barriers to communication across the boundaries of conventionally defined disciplines, e.g. between biology and chemistry, are probably no higher than the barriers that exist within them.

Why does this matter? It matters for the progress of science as much as for the ability of science to provide useful advice in a wider context. It matters because fragmentation promotes intellectual laziness (it's always easiest to publish results that conform to currently dominant views in your community, and you don't have to read widely or think 'outside the box') and works against scientific innovation and problem solving.

Limits to the role of science

It is important also, in a policy-relevant field, to be aware of the limits to the role of science. Impacts and adaptation have enormously important social and economic dimensions. Policies, by definition, have a political dimension.

Policy relevance brings an obligation to communicate findings clearly without exaggeration or bias. This is apparently not easy. Roger Pielke Jr's book *The Honest Broker*[26] is an attempt to clarify the different roles that can be played by scientists in the public sphere. He notes that scientists can legitimately make different choices: for example, to entirely avoid considering the policy implications of their research, or to advocate particular policies consistent with their worldview. But neither of these options are helpful to policy makers. In particular, Pielke touches on the dangers when advocacy and science are not clearly distinguished. These dangers tend to loom especially large when quantitative knowledge is lacking.

Recognizing that the business-as-usual approach in science can be blind to the social and political dimensions of policy, funders have for some years been encouraging the idea that natural scientists should 'work with social scientists' on climate change. This is now a pervasive idea, but there are some problems lurking here as well. First, social researchers tend to be (rightly!) unhappy about being perceived as a service industry to help answer questions framed by natural scientists. These are often seen as being the wrong questions to ask. On the other hand, the social sciences don't necessarily have the tools to answer the questions that are posed by natural scientists. The tools that might be needed to assess societal adaptation challenges and the effectiveness of different policy options in a given country, for example, for the most part don't exist.

It is possible that a new and useful kind of interdisciplinary research could be forged through a sustained collaboration among researchers from quite different backgrounds, working on 'real-world' problems. I think it is likely that such a collaboration would lead researchers to discover promising new directions for fundamental research as well. For the time being, I suggest scientists need to focus on doing (better) what they are good at; while recognizing its limits, and being willing to engage with researchers and practitioners from other fields[27].

The communication of impacts

Hardly a week goes by without my reading or hearing, somewhere in the media, that 'scientists say' global warming must be limited to two degrees 'to avoid dangerous consequences for climate'. The ubiquity of this idea would be a remarkable communications success *if it were true*. Unfortunately, its actual scientific basis is untraceable.

Reality is surely more complex. On the one hand, some impacts of climate change are documented already (with less than 1˚C of warming). More importantly, a focus on limiting climate *change* to a certain level implicitly assumes that there is no problem with our degree of adaptation to climate as it is. This assumption doesn't bear scrutiny, even for developed countries where floods, storms, droughts and heatwaves continue to cause significant economic damage and loss of life. Still less does it apply to most developing countries. On the other hand, there is no evidence for a steep ramping-up of impact 'severity' (however defined) at levels of warming greater than 2˚C. It does seem likely that impacts of climate change on human systems will increase nonlinearly with the degree of change. But this expectation does not point to any one particular number as the natural target. Therefore, if scientists defend this number publicly, they presumably are motivated in part by a desire to send a simple and consistent message. Whether this is a good idea is open to dispute.

More information can be conveyed by presenting results (e.g. maps and summary statistics) corresponding to various different degrees of warming. This can be done using models – with all the caveats discussed above. However, caveats also apply to diagrams based on expert judgement, such as the "Burning Embers"[28]. The original publication of this diagram provided (for the very first time) a synthetic summary of the 'reasons for concern' about climate change, and a comparative assessment of the degree of concern. As a communication tool it evidently worked, because it has been widely reproduced and modified (e.g. Fig. 8). But there is a basic problem, which is that the colour scale doesn't have units. Inevitably, given the state of knowledge, the diagram relies on subjective judgements in its choice of colours. There is also an easy mis-reading of the diagram to imply that the severity of an impact is independent of the resources available to adapt to it; which is of course false. And from there, it's a short step to a the unrealistic assumption that policy should aim to keep climate change within certain bounds irrespective of the economic costs, technical challenges and benefits of doing so, or regardless of the socio-economic pathway by which the aim is achieved.

Readers who have followed the recent literature will recognize that similar criticisms could be applied to other, more recent efforts to portray more broadly the human 'footprint' on Earth system processes. The complexity of human-environment interactions will no doubt resist quantification. It may make sense to try to formulate the impacts of global environmental changes qualitatively, e.g. to focus on identifying outcomes that would be widely recognized as unacceptable. However, this cannot be

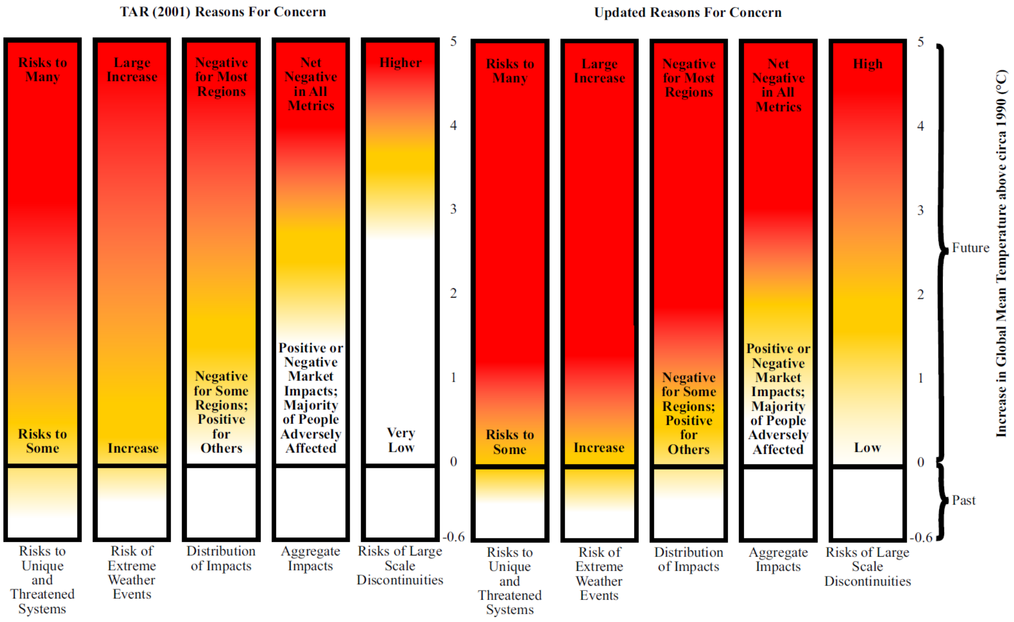

Figure 8: The right-hand graph is an update of the original 'Burning Embers' diagram, which is reproduced as the left-hand graph. The red colours have crept downwards in the right-hand graph, signifying greater danger – but the colour scale remains undefined! Reproduced from ref. [32].

achieved without evidence, and I suggest that the assessment of ecosystem impacts needs a considerably stronger evidence base than is available now. On the natural science side, this could be provided through a more rigorous, observationally constrained approach to modelling biosphere processes.

Concluding remarks

Nothing I have written should be interpreted as 'scepticism' about the reality of climate change, or the need to mitigate it in order to avoid its worst impacts. The scientific case for the reality of human-caused climate change should by now be clear. Claims to the contrary are, at best, misinformed or confused. (There are many reasons why people might be confused, just a few of which are discussed above.) Economic assessments of climate change have come to different conclusions about the optimal policies for mitigation, depending on various assumptions – particularly about the appropriate discount rate to apply to future impacts. But there is no economic case for ignoring the problem[29]. The differences among economic assessments are about such things as the optimal rate of investment in alternative energy sources, and the need for policies that actively encourage such investment.

I have focused on the land biosphere where there is incomplete understanding of many key processes, leading to inconsistent models of how climate change induced by rising atmospheric CO_2 concentration is likely to affect natural ecosystems, species, forests, crops, and atmospheric CO_2 itself. There are large uncertainties in other aspects of climate-change impacts too, including the likely rate of sea-level increase under different warming scenarios, and the impacts of ocean acidification on marine ecosystems and fisheries. These aspects are beyond the scope of this paper, but certain points are unambiguous. The availability of fossil fuels – given ingenuity, and potential economic incentives for the extraction of unconventional sources such as methane hydrates – is unlikely to limit climate change[29]. It may well be technologically and economically feasible to set the world on a course towards a complete melting of the Greenland and Antarctic ice sheets, resulting in the drowning of the coasts and coastal cities. It's only necessary to go back to the Eocene (about 34 to 56 million years ago) – a relatively recent period in geological terms – to encounter a state of the Earth with very high CO_2 concentration, and no ice sheets at all. I think everyone can agree that we don't want to go back to the Eocene climate, or to anything remotely like it. Adapting to projected sea-level changes over the 21st century is already a major challenge for cities worldwide. The economic and social costs of abandoning and rebuilding cities are almost unimaginable.

The overarching policy questions then are (a) how much should be invested, and when, in rapid decarbonisation of the global economy, implying a ramp-up in the production of energy in ways that don't cause a net emission of CO_2, and (b) what changes will be needed to existing systems of food and fibre production, water supply, and conservation in order to adapt to the substantial climate changes that cannot be avoided under any realistic energy future? Questions of type (a) require continued interdisciplinary assessment of the risks. It's important to recognize that economics and politics are involved as well as science. Questions of type (b) need interdisciplinary research as well. We need this research to be carried out with greater quantitative rigour, and communicated greater clarity about what we know and what we don't.

About the author

Professor Colin Prentice is an ecologist and palaeoecologist by training, who has developed broad research interests in climate change (both natural and anthropogenic) and its consequences for plants, ecosystems and the biosphere. He has led the international development of global-scale models for land ecosystem processes and feedbacks in a changing environment, and he is an expert on the global carbon cycle and its connections to the hydrological cycle via plants.

Colin Prentice obtained his Ph.D. in Botany from Cambridge and has held research positions in the Universities of Bergen (Norway), Newcastle-upon-Tyne, Southampton, Utrecht (The Netherlands), Uppsala (Sweden) and Lund (Sweden). He was founding Director of the Max Planck Institute for Biogeochemistry in Jena (Germany) in 1997. He returned to the UK in 2003 to become Professor of Earth System Science at the University of Bristol and to lead NERC's research programme Quantifying and Understanding the Earth System (QUEST). In 2010 he moved to Sydney (Australia), as a Professor of Ecology and Evolution at Macquarie University, while also taking on a part-time commitment as Professor of Climate and Biosphere Interactions at Imperial College. His new role at Imperial (since March 2013) is as the AXA Chair in Biosphere and Climate Impacts, at the Department of Life Sciences and the Grantham Institute, while continuing to maintain a connection with Macquarie.

Among many national and international roles, he has been co-ordinating Lead Author for carbon cycle science in the IPCC's Third Assessment Report (2001), co-chair and chair of the International Geosphere-Biosphere Programme (IGBP's) Global Analysis, Integration and Modelling (GAIM) task force, and co-chair of the IGBP's Analysis, Integration and Modelling of the Earth System (AIMES) project. He shared in the award of the Nobel Peace Prize to the IPCC in 2007.

As leader of QUEST, he contributed to building an Earth System Science community in the UK. Core activities of QUEST were marked by a strong focus on the interaction between policy questions and fundamental science – a field of interest to which he now returns through the AXA Chair, and the research programme he has planned. The programme combines the synthesis and analysis of ecological and biophysical data with the assessment of climate change impacts. Assessment will be informed by state-of-the-art models of primary production (by natural and managed ecosystems, forests and crops) and climate.

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