Untangling the confusion around land carbon science and climate change mitigation policy

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Depletion of ecosystem carbon stocks is a significant source of atmospheric CO_2 and reducing land-based emissions and maintaining land carbon stocks contributes to climate change mitigation. We summarize current understanding about human perturbation of the global carbon cycle, examine three scientific issues and consider implications for the interpretation of international climate change policy decisions, concluding that considering carbon storage on land as a means to 'offset' CO_2 emissions from burning fossil fuels (an idea with wide currency) is scientifically flawed. The capacity of terrestrial ecosystems to store carbon is finite and the current sequestration potential primarily reflects depletion due to past land use. Avoiding emissions from land carbon stocks and refilling depleted stocks reduces atmospheric CO_2 concentration, but the maximum amount of this reduction is equivalent to only a small fraction of potential fossil fuel emissions.

espite the current level of mitigation effort, global CO_2 emissions continue to increase¹. In addition to reducing emissions from fossil-fuel burning, the largest CO_2 source globally, mitigation efforts now include reducing what is in aggregate the second largest net source of CO_2 to the atmosphere: namely, carbon emissions from land-use change. Land carbon emissions accounted for about 36% of the anthropogenic CO_2 emitted into the atmosphere from 1850-2000², and about 12% of annual global CO_2 emissions from 2000 to 2010¹. Avoiding and reducing land carbon emissions is therefore an integral part of any comprehensive approach to solving the climate change problem.

Globally, forests store around 300 Pg C (reported range 240-500 Pg C) in living biomass2,3, equivalent to ~140 ppm of atmospheric CO_2 (atm CO_2 ; used to denote the concentration of CO_2 in the atmosphere, and although the SI unit for atmCO₂ is µmol mol⁻¹, we have adopted the more familiar unit of ppm). Forests are distributed in both developed and developing countries (Table 1). About half of the world's forests have already been cleared, with 40 million km² remaining and around 0.16 million km² of forest cleared annually³. Only 36% (~14.4 million km²) of the world's forest is now primary forest³. In addition to deforestation, forests have been degraded by land-use activities such as logging and soil disturbance that deplete their organic carbon stocks and emit CO₂. Emissions from forest degradation are poorly quantified globally, but estimates indicate that they increase regional carbon emissions by nearly 50% over deforestation alone⁴. Conserving the world's remaining primary forests would avoid substantial emissions of CO2. Afforestation and reforestation, moreover, can directly remove CO₂ from the atmosphere — but only up to a point, as we discuss later.

Nations are engaged in negotiations to reduce emissions of CO_2 and other greenhouse gases (GHGs) under the United Nations Framework Convention on Climate Change (UNFCCC). Developed countries that are signatories to the Kyoto Protocol (ratified by 37 countries and the European Union) committed themselves to a target of reducing their emissions of GHGs from 2008–2012, relative to 1990 levels. The target reduction was based on emissions from fossil fuels and industry, but removals by the land sector could be counted towards meeting the target. The Clean Development Mechanism under the Kyoto Protocol allowed for developed countries to offset fossil fuel emissions through, among other things, planting trees in developing countries. Similar kinds of offset project are allowed through the Joint Implementation mechanisms between developed countries. The extension or successor to the Kyoto Protocol is now being negotiated. There are parallel negotiations underway on the development of policies for Reducing Emissions from Deforestation and Degradation (REDD) — a voluntary scheme to mitigate land carbon emissions from developing countries.

Negotiated policy decisions involve political compromises to accommodate national interests. So far these decisions have fallen short of what will be necessary if $atmCO_2$ is to be stabilized at a level that avoids major climate change⁵. Furthermore, there is the potential for perverse outcomes whereby mitigation efforts not only fail to reduce $atmCO_2$, but even have negative impacts — either causing $atmCO_2$ to increase or adversely affecting other landscape values, such as biodiversity. Perverse outcomes can result from a gap between land carbon policy decisions and scientific understanding of what is required for successful mitigation: that is, from confusion around land carbon science.

In this Perspective we clarify some well-established fundamentals of the global carbon cycle that are frequently either misunderstood, or seemingly overlooked. This information provides the scientific context for considering the potential of land-based mitigation and to what extent it can be legitimately considered an 'offset' for fossil fuel CO_2 emissions. We do not advocate any particular policy, but we do draw attention to some proposed approaches that are likely to be ineffective, or worse.

Human perturbation of the global carbon cycle

The global carbon cycle is the subject of considerable confusion among non-specialists. A clear understanding of how humans have

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perturbed the cycle's natural stocks and flows of carbon is essential background to clarifying key scientific issues and ensuring effective policies.

Figure 1 illustrates changes in the primary stocks of the global carbon cycle as the result of human activity in three stylized time periods: the pre-agricultural era (>8 000 yr BP; Fig. 1a); the pre-industrial era (8 000 yr BP–1850, Fig. 1b); and the contemporary era (>1850–present day; Fig. 1c). These correspond with major phase shifts in the magnitude of the human environmental footprint in terms of land clearing and use of fossil fuels. Figure 1a shows that in the pre-agricultural era there was no human use of fossil fuel and relatively minimal depletion of land carbon due to human land use. Figure 1b and 1c show the impact of human activity on the primary stocks. The sources and calculations for the values in Fig. 1 are provided in Table 2.

During the pre-industrial era, land carbon began to be depleted (white segment of land carbon stocks) leading to an increase in the atmospheric carbon stock, with some of this carbon dissolving into the ocean stock (as indicated by the green segments). In the contemporary era humans began mining fossil fuel and burning it as a source of energy, as well as engaging in accelerated land clearance. Both activities have resulted in CO_2 emissions and a rapid and significant increase in the atmospheric carbon stock. A portion of the anthropogenic emissions added to the atmosphere is concurrently taken up by plants, and a fraction is dissolved into the ocean stock. This effect is illustrated in Fig. 1c by the segments of black carbon in the land and ocean stocks.

Figure 1d illustrates the hypothetical case of cleared land being largely returned to its pre-agricultural carbon stock levels. The amount of atmospheric carbon that potentially can be stored in the land buffer is, to first order, limited to the amount of carbon that was depleted from previous land use. The black segment signifies that an extra, modest amount of fossil fuel emissions could be stored as the result of the so-called CO_2 fertilization effect discussed below.

The lifetime of CO₂ in the atmosphere

A recurrent, serious misunderstanding is that the residence time in the atmosphere of a unit of CO₂ emitted from fossil fuel burning is quite short, on the order of a century. The First Assessment Report⁶ of the Intergovernmental Panel on Climate Change (IPCC) incorrectly stated the 'lifetime' of CO₂ to be ~120 years. Many commentators since have assumed it to be about 100 years. They have probably been encouraged in this view by the use of a 100-year timeframe for the calculation of 'global warming potentials' (GWP, expressed relative to CO₂) for greenhouse gases with different lifetimes. However, it has long been recognized that any single number for the CO₂ lifetime conceals more than it reveals. CO₂ is taken up from the atmosphere by several distinct processes that have hugely different time constants^{7,8}. Part of it is taken up by the land, and part dissolves in the ocean surface and mixes to the deep ocean. About 60% is removed from the atmosphere on a time scale of 100 years but it takes a very long time to remove the remaining fraction. A 'pulse' or unit of CO₂ emitted to the atmosphere is only fully removed from the atmosphere so that it no longer interacts with the climate system when it has completely dissolved in the deep ocean - a process requiring the concurrent dissolution of carbonate from ocean sediments (about 5,000 to 10,000 years) and enhanced weathering of silicate rocks (around 100,000 years). Modelling by Archer and colleagues indicated that 20-35% of the CO₂ emitted will still be in the atmosphere after 2-20 millennia. Tracing the history of the misunderstanding of CO₂ lifetimes, they commented that "...the result has been an erroneous conclusion, throughout much of the popular treatment of the issue of climate change, that global warming will be a century-timescale phenomenon"9.

The reality is that for all practical purposes, fossil fuel CO_2 emission is irreversible¹⁰. Any eventual stable atm CO_2 will be dictated

 Table 1 | Top 10 countries for total area of forest and other

 wooded land (see Annex Table 3, ref. 3).

Rank	Country	Forest (1,000ha)	Country	Other wooded land (1,000ha)
1	Russian Federation	809,090	Australia	135,367
2	Brazil	519,522	China	102,012
3	Canada	310,134	Canada	91,951
4	USA	304,022	Russian Federation	73,220
5	China	206,861	Argentina	61,471
6	DRC	154,135	Sudan	50,224
7	Australia	149,300	Ethiopia	44,650
8	Indonesia	94,432	Brazil	43,772
9 10	Sudan India	69,949 68,434	Botswana Afghanistan	34,791 29,471

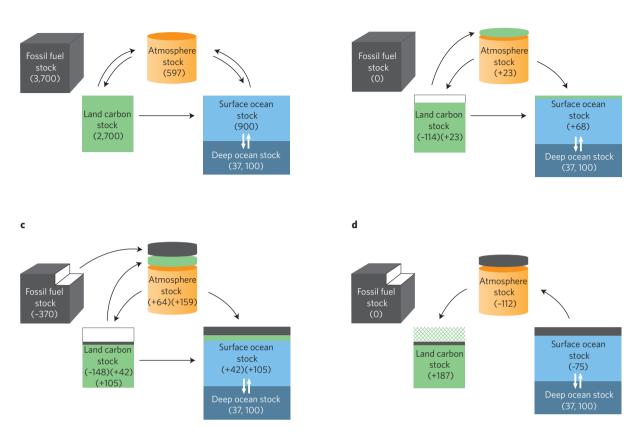
by total accumulated emissions over the preceding centuries¹¹ and not by the contemporaneous balance of emissions and removals. In this respect CO_2 behaves quite differently from the other major so-called long-lived GHGs — methane and nitrous oxide — which have atmospheric lifetimes in the order of 10 years and 100 years, respectively. This difference implies an important caveat for the use of GWP. Reduced emissions of nitrous oxide or methane might be substituted for reduced emissions of an 'equivalent' amount of CO_2 . But the effects of the emitted CO_2 will continue to be felt for thousands of years, long after the effects of the reduced emissions of the other gases have disappeared.

The limited capacity of land carbon stocks

Land carbon plays an important role in the stocks and flows of the global carbon cycle, but the magnitude is limited and it has particular characteristics which contrast with the different qualities of the other main categories of carbon stocks (fossil fuel, atmosphere and ocean). The fossil fuel carbon stock was built up very slowly over millions of years and does not de-gas into the atmosphere at any significant rate. Emissions from this stock in the contemporary era constitute a one-way flow, which is a direct result of human activity. Carbon is stored in the other three major categories of stocks in different forms (on land as biomass and soil organic carbon, in the atmosphere as CO_2 gas and in the ocean primarily as dissolved inorganic carbon) and both the land and ocean carbon stocks naturally exchange with the atmospheric stock.

The potential size of the land carbon stock is determined chiefly by climate, and modified locally by substrate and topography, and the effects these have on plant growth¹². The capacity of the land to remove atmospheric carbon and store it in vegetation and soil is limited to the amount previously depleted by land use. It has been estimated that if all the carbon so far released by land-use changes (mainly deforestation) could be restored through reforestation this would reduce atmCO₂ at the end of the century by 40-70 ppm. Conversely, complete global deforestation over the same time frame would increase atmospheric concentrations by about 130–290 ppm¹³. In comparison, the projected range of $atmCO_2$ in 2100, under a range of fossil fuel emissions scenarios developed for the IPCC, is 170-600 ppm above 2000 levels¹⁴. These estimates highlight the very modest scope for reforestation to reduce atmCO₂ compared with both the magnitude of fossil fuel CO₂ emissions and emissions from derorestation and degradation. Moreover, complete reforestation of previously cleared land is an implausible scenario due to competing land uses - especially from food production

а



b

Figure 1 | Changes in the primary stocks of the global carbon cycle. a-c, A stylized illustration of the impact of human activity on the primary stocks over three time periods: the pre-agricultural era (>8,000 yr BP; a); pre-industrial era (8,000 yr BP to 1850; b); and contemporary era (1850 to the present day; c). The objects (cylinders and rectangles) represent the primary stocks of carbon in the major reservoirs of the global carbon cycle (fossil fuel, atmosphere, land, surface ocean and deep ocean) but are not drawn to scale. d, The hypothetical and unachievable case of "refilling" the land stock, that is, if all previously cleared land being returned to its pre-agricultural carbon stock with zero continuing fossil fuel emissions. Numbers in parentheses (Pg C) are indicative estimates of the carbon stocks (a) and changes in carbon stocks (b-d). The arrows represent the direction of carbon flows (fluxes) between stocks over the era, with arrows in panel a representing the natural background carbon cycle, and arrows in the other panels indicating the impact of anthropogenic change. Natural processes (as shown in panel a) involve two-way exchanges of carbon between the atmosphere-ocean (on the order of 70 Pg C yr⁻¹) and atmosphere-land (around 120 Pg C yr⁻¹) with a small natural hydrological flux of carbon discharged from rivers into oceans of 0.8 Pg C yr⁻¹ (not shown are the very small sources due to volcanic activity and sinks due to weathering)⁴². The anthropogenic changes due to land use change and burning fossil fuels are also illustrated using colour coded slices (also not drawn to scale). These changes reflect processes that can be considered in general terms as operating over two timescales: on the order of a one to a few 1.000 years about 20% of the emitted CO₂ stavs in the atmosphere^{44,9}. 60% is taken up by the ocean and 20% by land⁴⁴; on the time scale of 100 years 43% of emissions remain in the atmosphere^{45,46} with the rest taken up roughly equally between the land and ocean⁴⁶. We use the simplified assumption that as atmospheric CO₂ is reduced, the ocean would 'outgas' CO₂, and the land would also outgas the carbon uptake due to the CO₂ fertilization effect, based on processes operating over the 100-yr timescale. The land retains the C uptake from fossil fuel emissions. Even if the unachievable was accomplished, after 100 years, there would still be an extra 134 Pg C in the atmosphere compared with the pre-agricultural era due to fossil fuel emissions. The estimates are based on sources and calculations in Table 2.

and the need to feed a human population predicted to surpass nine billion by 2050^{15} — along with projected demand for land to produce transport biofuel of 0.3–0.5 million km² by 2030^{16} . And even under this impossible scenario, land degradation means that some of the land carbon stock cannot be re-filled.

The difference between stocks and sinks

Land carbon scientists are clear on the difference between land carbon stocks and sinks, however policymakers and the interested citizen can be excused for not understanding (or sometimes forgetting) the distinction. As used in carbon cycle science, the term 'sink' always implies a net removal of carbon from the atmosphere — in other words, a net flux of carbon into the ecosystem. There is a persistent risk of confusion between a stock (in units of mass, g C) and a flux (in units of mass/time, g C yr⁻¹). Both the ocean and the

land are indeed taking up part of the CO_2 that is emitted by human activities, so they do constitute sinks. But this uptake is a transient effect as discussed below.

The land carbon stock can be described as a 'buffer' by analogy with the term used in computer science to describe a device which temporarily stores data. The impact of land use activity is appropriately reported or accounted for as a change in stock over a given time period, that is, a depletion or re-filling of the buffer. When a forest is re-planted, at first it functions as a sink — with the net uptake of CO_2 due to photosynthesis being greater than respiration — and carbon is accumulating in woody biomass and soil. Over time, the net sink rate declines as the growth rate decreases relative to respiration rates. If the forest is allowed to develop into an ecologically mature state, the carbon stock approaches a dynamic equilibrium with prevailing environmental conditions, where

Table 2 | The sources and calculations for estimated changes of carbon stocks in Fig.1

(a) Pre-agricultural			
Stock	Pg C	Sources and calculations (references given in parentheses)	
Fossil fuel	3,700	Fig. 7.3 (42)	
Land	2,700	Fig. 7.3 (42)	
Atmosphere	597	Fig. 7.3 (42)	
Shallow ocean	900	Fig. 7.3 (42)	
Deep ocean	37,100	Fig. 7.3 (42)	
(b) Pre-industrial (char	nge from pre-agricultural)		
Fossil fuel	0		
Land	-114 23	Emissions from land clearance (43) 20% taken up by land due to CO_2 fertilization effect, 1,000-year timescale (44)	
Atmosphere	23	20% of emissions remain in atmosphere, 1,000-year timescale (9,44)	
Ocean	68	60% taken up by ocean, 1,000-year timescale (44)	
(c) Contemporary (cha	nge from pre-industrial)		
Fossil fuel	-370	IPCC Fossil fuel emissions (42)	
Land	-148 42 105	Emissions from land clearance (43) 28.5% of land carbon emissions taken up by land due to CO₂ fertilization effect, 100-year timescale (46) 28.5% of land carbon emissions taken up by land due to CO₂ fertilization effect, 100-year timescale (46)	
Atmosphere	64 159	43% of land carbon emissions remain in atmosphere 100-year timescale (45,46) 43% of fossil fuel carbon emissions remain in atmosphere 100-year timescale (45,46)	
Ocean	42 105	28.5% of land carbon emissions taken up by ocean, 100-year timescale (46) 28.5% of land carbon emissions taken up by ocean, 100-year timescale (46)	
(d) Hypothetical restor	ration of the land carbon b	uffer (change from contemporary)	
Fossil fuel	0		
Land	187	+262 restored to the land (114+148), minus 28.5% reduced $\rm CO_2$ fertilization effect (–75), 100-year timescale	
Atmosphere	-112	–262 removed by land restoration, +75 out-gassed from ocean, +75 reduced $\rm CO_2$ fertilization effect on land	
Ocean	-75	Response of ocean to lowered atmospheric $\rm CO_2$ is out-gassing of 28.5% of 262, 100-yr timescale	

respiration approximately balances photosynthesis. At this point, the depleted land carbon stock has been refilled and the sink function has gone. The mitigation value of the ecosystem resides in maintenance of the stored carbon stock.

At present some forests have carbon sequestration potential due to depletion of carbon stocks from past land use¹⁷. Reforestation of previously cleared or logged land (especially in Europe, the USA and China), together with deforestation and degradation (especially, but not exclusively, in tropical developing countries), are all included in the calculation of net emissions noted above from land use change.

The land and ocean are sinks, and globally they removed an estimated 56% of all CO₂ emitted from human activities during the period 1958-2010, each sink in roughly equal proportion¹⁸. Although land-use change is a source of emissions, the land as a whole is functioning as a sink at present. This land sink reflects the natural response of ecosystems to the influence of environmental change, which is now leading to a net uptake of CO₂ due to several factors. Rising atmCO₂ leads to a boost in plant productivity (the CO₂ fertilization effect), whereby the increase in net primary production outpaces the increase in respiration of soil carbon stocks^{19,20}. Experimental evidence has shown that net primary productivity of temperate forests increases by around 23% in response to a 200 ppm increase in CO₂ (that is, when grown in atmCO₂ of 550 ppm)²¹. However, the effect varies geographically²², is constrained (to an uncertain degree) by nitrogen availability²³ and depends on CO₂ continuing to increase. If CO₂ were stabilized, this effect would disappear probably after a lag of a few decades. The practical effect of an increase in atmospheric CO2 on potential ecosystem carbon stocks is a modest increase in the size of the buffer that could be refilled.

Ecologically mature (>200 years) and old-growth forests aged up to 800 years can continue to function as sinks. Old-growth tropical forests accumulate around 5 Mg C km⁻² yr⁻¹ in living biomass, which could be yielding a carbon sink of 1.3 Pg C yr⁻¹ (0.8–1.6 Pg C yr⁻¹) across all tropical forests^{24,25}. We reiterate, however, that the mitigation value of tropical forests — and old-growth forests in general — does not lie in their present, transient function as carbon sinks. In terms of carbon mitigation policy, the primary reason to conserve forests is the carbon stocks they contain. The idea that replacing primary forests by plantations will 'create sinks' and thereby be positive for climate mitigation is incorrect, as it fails to account for the loss of carbon stock from the primary forest²⁶. Furthermore, plantation forests store less carbon than the pre-existing natural primary forest, secondary (regenerating) natural forests or a primary forest under the same environmental conditions²⁷⁻³⁰.

Climate change may increase potential carbon stocks in some regions: for example, through increased rainfall and/or decreased potential evaporation where plant growth is limited by water availability, and through enhancement of the growing season in northern temperate regions due to increases in temperature. But conversely, increasing aridity in other regions is likely to reduce plant growth through drying or heat stress³¹, and to increase the likelihood that forest areas are subject to wildfire, which can reduce the long-term carbon carrying capacity of landscapes³². Hence, there are competing processes resulting in changes in the potential land carbon stock. An analysis based on 13 coupled climate–carbon cycle models pointed to future climate change reducing the efficiency of the Earth system in absorbing anthropogenic carbon emissions, leading to a larger fraction of anthropogenic CO_2 staying airborne

and therefore some amplification of global warming. Despite large uncertainties, all models simulated a relative weakening of both the land and ocean carbon sinks in the future, warmer climate³³.

Policy implications

UNFCCC negotiations are characterized by an extraordinary effort to make use of the best available science as reviewed by the IPCC. However, the negotiations are a complex political process with many interests operating, and as policies are implemented, scientific and/or unintended shortcomings in some decisions are revealed. These are inevitable given that the attempt to mitigate human-forced climate change is a new kind of problem. As inconsistencies in policies are revealed they should be seen as part of an ongoing process for scientists and negotiators to learn and make the necessary improvements.

Parties (that is, countries; including developed and developing) that are signatories to the UNFCCC report on emissions of CO₂ due to change (depletion) in carbon stock from different land cover types. For this purpose they only report on areas of forests identified as 'managed' (but in practice these may include areas considered largely 'natural' - with native species and little or no timber removals, for instance). Under the Kyoto Protocol, Annex I (developed) countries account for changes in stock between the first commitment period (2008 to 2012) and 1990. Under Article 3.3, parties have to report all afforestation, reforestation and deforestation (that is, where there is a change of land use to or from forest land to another land class, such as grassland or cropland). Under Article 3.4 parties can elect to report changes in stocks on areas identified as 'Forest Management'; that is, it is not mandatory. Some countries, Australia for example, opted not to report on these emissions.

The implementation of the Kyoto Protocol for forests is problematic³⁵ as it does not apply a distinction between natural forest ecosystems and plantations, nor between primary forest and seminatural forests logged for industrial wood production as there is technically no change in land cover³⁶. As noted above, clear-felling of natural forest for even-aged natural regeneration or plantation³⁷ results in depletion of the land buffer and significant CO₂ emissions³⁸. If forest management is elected, these emissions will be captured as change in stock in managed forests between 1990 and the commitment period. If it is not elected, the interpretation of the rules is that the land remains forest land, and no deforestation is deemed to have occurred.

The Durban accounting rules negotiated in 2010 for the second commitment period of the Kyoto Protocol (2013 to 2020) are a significant improvement and address two key concerns³⁹. Accounting for emissions from forest management will be mandatory. Accounting for conversion of natural forests to plantation forests will be required (although it is not yet clear if this will be reported under deforestation or forest management). Furthermore, Parties will have to report on how harvesting or forest disturbance that is followed by the re-establishment of a forest is distinguished from deforestation.

Although future accounting approaches thus represent an improvement, there remain concerns that need attention by governments when formulating national policies and programs, and among business and civil society in promoting voluntary and market-based mitigation schemes. If carbon is to be usefully stored (on land, in the ocean or in geological repositories), it must remain stored not just for 100 years, but for more than 10,000 years. This issue of 'permanence' is widely recognized in the UNFCCC negotiations, but not necessarily on the long timescales involved. Indeed it is accepted de facto in many policy contexts that it is sufficient to maintain stores for 100 years. For example, Article 87 of the Australian Government's Carbon Credits (Carbon Farming Initiative) Act 2011 defines the maximum potential relinquishment period for an eligible offsets project as 100 years (that is, the time period the person holding the carbon credit is responsible for the sequestered carbon stock)⁴⁰.

Voluntary carbon offset markets in operation that are used by business including airlines, industrial and energy companies⁴¹ tend to have similar misconceptions of the science. It helps to have clarity about the meaning and intention of an 'offset'. It must be recognized that forest conservation can avoid or reduce future carbon emissions, but does not in any meaningful sense offset continuing emissions from other sources. It must also be recognized that the capacity of the land buffer to remove and store CO₂ from the atmosphere is strictly limited. However vigorous the measures taken to increase land carbon stocks, their total potential for carbon storage is minuscule compared with the stock of fossil fuels that could yet be burnt.

Conclusions

On the basis of our review of key scientific issues related to the global carbon cycle, the following insights should be considered when climate change mitigation polices are being negotiated, regulatory frameworks formulated and programmes and projects implemented.

As long as the right kinds of land management responses are implemented, the land carbon buffer can provide a valuable, cost-effective, short-term service in helping to reduce $atmCO_2$, and slow the rate of anthropogenic climate change, bringing cobenefits for biodiversity and sustainable livelihoods, and giving us some time to develop a low carbon economy.

There are strict, environmentally determined limits on the maximum amount of carbon that can be restored to land carbon stocks, and good reasons why this maximum will not be achieved. Sequestering carbon into depleted ecosystem stocks removes CO_2 from the atmosphere and is thus usefully considered as partially refilling the buffer that was depleted by human activities. Avoiding emissions by protecting high-carbon ecosystems from land-use change that depletes their carbon stocks is an important part of a comprehensive approach to greenhouse gas mitigation. The mitigation value of forests lies not in their present net uptake of CO_2 , but in the longevity of their accumulated carbon stocks.

Consistent with our understanding of the lifetime of the airborne fraction of a pulse of CO_2 , the most effective form of climate change mitigation is to avoid carbon emissions from all sources. This means that there is no option but to cut fossil fuel emissions deeply, and not to continue these emissions under the erroneous assumption that they can be offset in the long term by the uptake of CO_2 in land systems.

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NATURE CLIMATE CHANGE DOI: 10.1038/NCLIMATE1804

PERSPECTIVE

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Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence should be addressed to B.M.

Competing financial interests

The authors declare no competing financial interests.