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LETTERS

Old-growth forests as global carbon sinks

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Old-growth forests remove carbon dioxide from the atmosphere[1,2] at rates that vary with climate and nitrogen deposition[3]. The sequestered carbon dioxide is stored in live woody tissues and slowly decomposing organic matter in litter and soil[4]. Old-growth forests therefore serve as a global carbon dioxide sink, but they are not protected by international treaties, because it is generally thought that ageing forests cease to accumulate carbon[5,6]. Here we report a search of literature and databases for forest carbon-flux estimates. We find that in forests between 15 and 800 years of age, net ecosystem productivity (the net carbon balance of the forest including soils) is usually positive. Our results demonstrate that old-growth forests can continue to accumulate carbon, contrary to the long-standing view that they are carbon neutral. Over 30 per cent of the global forest area is unmanaged primary forest, and this area contains the remaining old-growth forests[7]. Half of the primary forests (6×10^8 hectares) are located in the boreal and temperate regions of the Northern Hemisphere. On the basis of our analysis, these forests alone sequester about 1.3 ± 0.5 gigatonnes of carbon per year. Thus, our findings suggest that 15 per cent of the global forest area, which is currently not considered when offsetting increasing atmospheric carbon dioxide concentrations, provides at least 10 per cent of the global net ecosystem productivity[8]. Old-growth forests accumulate carbon for centuries and contain large quantities of it. We expect, however, that much of this carbon, even soil carbon[9], will move back to the atmosphere if these forests are disturbed.

We conducted a literature search to test the hypothesis that old-growth forests continue to accumulate atmospheric carbon dioxide (CO_2). Site-level estimates of the annual sums of carbon-cycle components were compiled, including those of biometry-based net primary production (NPP), eddy-covariance or biometry-based net ecosystem production (NEP) and chamber-based heterotrophic respiration. The data set was completed with site information related to stand characteristics, standing biomass and stand age. Data were compiled from 519 plot studies that reported one or more components of the carbon cycle. The studies involved boreal (~30%) and temperate (~70%) forests and represented the full range of conditions of such forests, excluding those subjected to experimental treatments such as fertilization and irrigation (Supplementary Information, section 1.1). Tropical forests were excluded from the analysis because only 12 sites were found for which NEP and age estimates are available.

The NEP is the net carbon balance of the forest as a whole, and is the difference between CO_2 uptake by assimilation and losses through plant and soil respiration. On the basis of our global data set we find that in forests between 15 and 800 years old, the NEP is usually positive; that is, the forests are CO_2 sinks (Fig. 1a). The maximum probabilities of finding a single forest to be a source of carbon at 60, 180 and 300 years of age are 0.20, 0.25 and 0.35, respectively. However, the probability of finding an ensemble of ten old-growth forests that are carbon neutral is negligible (Supplementary Fig. 1). In the small number of case studies on the effect of age on the carbon balance of forests, several have demonstrated some age-related decline in NEP but very few have shown old forests to be sources[1,2,10–13]. Our NEP estimates suggest that forests 200 years old and above sequester on average 2.4 ± 0.8 tC ha^{-1} yr^{-1} (tC, tonnes of carbon; Fig. 1a). In our model (Supplementary Information, section 1.3), we find that old-growth forests accumulate 0.4 ± 0.1 tC ha^{-1} yr^{-1} in their stem biomass and 0.7 ± 0.2 tC ha^{-1} yr^{-1} in coarse woody debris, which implies that about 1.3 ± 0.8 tC ha^{-1} yr^{-1} of the sequestered carbon is contained in roots and soil organic matter.

The commonly accepted and long-standing view that old-growth forests are carbon neutral (that is, that photosynthesis is balanced by respiration) was advanced in ref. 6 and was originally based on ten years' worth of data from a single site[5]. It is supported by the observed decline of stand-level NPP with age in plantations[14,15], but is not apparent in some ecoregions[16]. Yet a decline in NPP is commonly assumed in ecosystem models (Supplementary Information, section 1.4). Moreover, it has led to the view that old-growth forests are redundant in the global carbon cycle.

If, however, the hypothesis of carbon neutrality[6] were correct, the expected probabilities of observing a sink or source would be equal and around one-half, the average sink strength for a random ensemble of forests 200 years old and above would be zero and the mean CO_2 release from heterotrophic respiration would equal the mean CO_2 sequestration through NPP (thus, the ratio of heterotrophic respiration to NPP would be approximately one). However, we observe this ratio to be well below one on average (Fig. 1b) and not to increase with age. Hence, all three quantitative tests fail to support the hypothesis of carbon neutrality. The currently available data consistently indicate that carbon accumulation continues in forests that are centuries old.

In fact, young forests rather than old-growth forests are very often conspicuous sources of CO_2 (Fig. 1a) because the creation of new forests (whether naturally or by humans) frequently follows disturbance to soil and the previous vegetation, resulting in a decomposition rate of coarse woody debris, litter and soil organic matter (measured as heterotrophic respiration) that exceeds the NPP of the regrowth[2,17–22] (Fig. 1b).

The scatter in the relationship between NPP and age is considerable, but given the climatic, edaphic and biological diversity of the observations in combination with differences in disturbance histories, this is to be expected. There is some degree of age-related decline in NPP beyond 80 years of age (Fig. 1c), and temperate and boreal forests both show a consistent pattern of declining NPP beyond an early maximum (Supplementary Fig. 2a) when analysed separately. The decline in NPP could be partly attributed to the presence or absence of management (Supplementary Fig. 2b). However, we expect that this decline is not strictly a management effect, but a

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reflection of differences in disturbance history between managed and unmanaged forests.

Consistent with earlier studies[2], biomass continues to increase for centuries irrespective of whether forests are boreal or temperate (Supplementary Fig. 3). In the course of succession, plants compete for resources and self-thinning[23] (or thinning by humans in the case of managed forests) occurs (Fig. 2), so the older stands contain a relatively small number of individuals, although of course these trees tend to be large. Obviously biomass cannot accumulate forever. Our data (Supplementary Fig. 3) suggest a possible upper limit somewhere between 500 and 700 tC ha^{-1} (equivalent to 1,400 to 1,800 cubic metres of wood per hectare); these high-biomass forests were located in the Pacific Northwest USA[16].

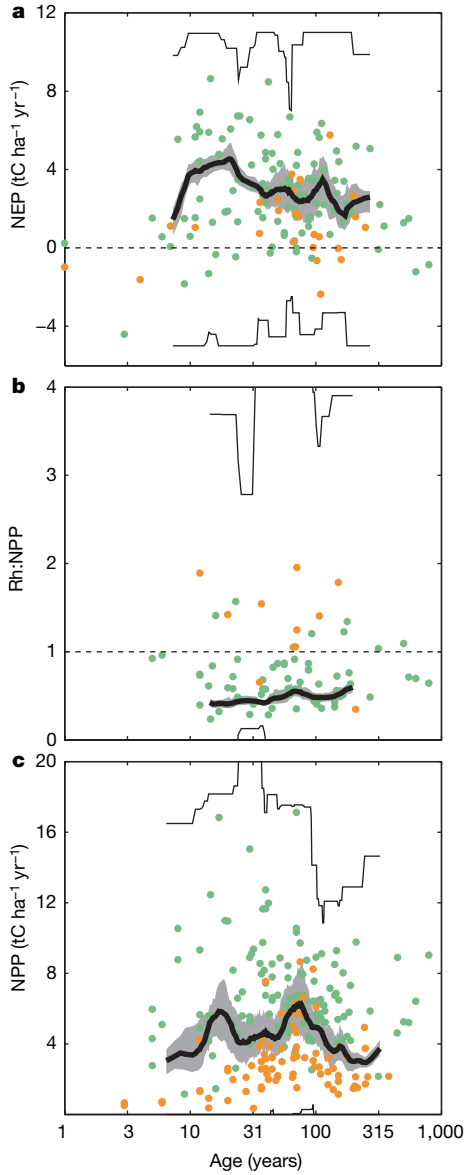


Figure 1 | Changes in carbon fluxes as a function of age. **a**, Observed NEP versus age; positive values indicate carbon sinks and negative values indicate carbon sources. **b**, Observed ratio of heterotrophic respiration (Rh) to NPP versus age; Rh:NPP < 1 indicates a carbon sink. **c**, Observed NPP versus age. It appears that temperate and boreal forests both show a pattern of declining NPP. Most probably, the late-successional increase in NPP is caused by the combination of data from different climate regions or the combination of disturbance regimes (Supplementary Fig. 2a, b). In each panel, the green dots show observations of temperate forests, the orange dots show observations of boreal forests, the thick black line shows the weighted mean within a moving window of 15 observations, the grey area around this line shows the 95% confidence interval of the weighted mean and the thin black lines delineate the 95% confidence interval (where visible) of the individual flux observations.

We speculate that when high above-ground biomass is reached, individual trees are lost because of lightning, insects, fungal attacks of the heartwood by wood-decomposers, or trees becoming unstable in strong wind because the roots can no longer anchor them. If old-growth forests reach high above-ground biomass and lose individuals owing to competition or small-scale disturbances, there is generally new recruitment or an abundant second canopy layer waiting in the shade of the upper canopy to take over and maintain productivity.

Although tree mortality is a relatively rapid event (instantaneous to several years long), decomposition of tree stems can take decades. Therefore, the CO_2 release from the decomposition of dead wood adds to the atmospheric carbon pool over decades, whereas natural regeneration or in-growth occurs on a much shorter timescale. Thus, old-growth forest stands with tree losses do not necessarily become carbon sources, as has been observed in even-aged plantations (that is, where trees are all of the same age). We recognize that self-thinning theory was originally developed and validated for even-aged single-species stands; however, it has been shown to hold for uneven-aged multi-species plant communities (Supplementary Information, section 1.3). In reasonable agreement with our observations (Fig. 1b), self-thinning theory predicts that the ratio between heterotrophic respiration and NPP is constant and around 0.65 ± 0.02 (indicating a carbon sink; Supplementary Fig. 4), as long as stand density is driven by small-scale, rather than stand-replacing, disturbances. Old stands, with sufficiently high densities (that is, through development of a multilayer canopy structure) are thus expected to maintain biomass accumulation for centuries. Hence, we postulate that biomass accumulation and decline are largely driven by stand structure.

A stand must be spared for centuries from stand-replacing disturbances (such as fires, insect outbreaks, wind-throw and avalanches) in order to accumulate sufficient aboveground biomass to become old growth. Because the cumulative probability of disturbances is higher in stands with high above-ground biomass, old stands are rarer than young stands, even in unmanaged landscapes. At the landscape level, we expect a mosaic of forests characterized by different times since the last stand-replacing disturbance[24]. Despite differences in age and density, these forests are, however, expected to follow the same relationship between biomass and density (Fig. 2).

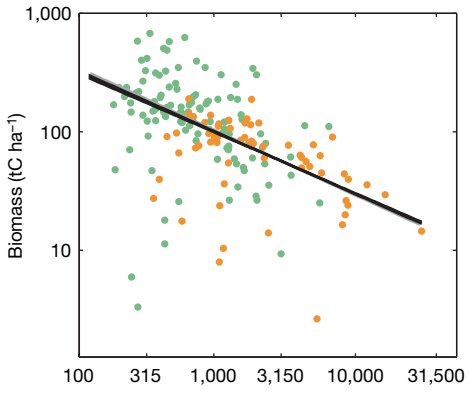


Figure 2 | Biomass accumulation as a function of stand density. Each data point represents a different forest, many of which have different growing conditions and tree species. Not all growing conditions and species compositions allow for the accumulation of the global maximum observed biomass. Self-thinning, the process of density-dependent mortality, is shown (solid line, of slope γ) as the relationship between the logarithm of above-ground biomass and the logarithm of stand density according to ref. 23 ($\gamma = -0.51 \pm 0.08$, $r^2 = 0.25$, $P < 0.01$). The green dots show observations of temperate forests, the orange dots show observations of boreal forests and the grey area (which is barely wider than the solid line) shows the 95% confidence interval of the median.

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Under the Kyoto Protocol (http://unfccc.int/resource/docs/convkp/kpeng.pdf) only anthropogenic effects on ecosystems are considered (Article 2 of the Framework Convention on Climate Change (http://unfccc.int/resource/docs/convkp/conveng.pdf); Supplementary Fig. 5) and the accounting for changes in carbon stock by afforestation, reforestation and deforestations is mandatory (Article 3.3), operating from a base line of 1990. Leaving forests intact was not perceived as an anthropogenic activity. In addition, the potential consequences of excluding old-growth forests from national carbon budgets and from the Kyoto Protocol were downplayed in the carbon-neutrality hypothesis[6]. However, over 30% (1.3×10^9 ha) of the global forest area is classified[7] by the Food and Agriculture Organization of the United Nations as primary forest, and this area contains the world's remaining old-growth forests. Half (0.6×10^9 ha) of the primary forests are located in the boreal and temperate regions of the Northern Hemisphere. On the basis of our analysis, we expect that these forests alone sequester at least $1.3 \pm 0.5\,\mathrm{GtC\,yr^{-1}}$. Hence, 15% of the global forest surface, which is currently not being considered for offsetting increasing atmospheric CO_2 concentrations, is responsible for at least 10% of the global NEP[8]. Sporadic disturbances will interrupt carbon accumulation, implying that net biome productivity[25] will be lower, but it will remain positive as demonstrated by the accumulation of carbon in soils[4,26], coarse woody debris and charcoal[27,28].

The present paper shows that old-growth forests are usually carbon sinks. Because old-growth forests steadily accumulate carbon for centuries, they contain vast quantities of it. They will lose much of this carbon to the atmosphere if they are disturbed, so carbon-accounting rules for forests should give credit for leaving old-growth forest intact.

METHODS SUMMARY

We conducted a literature and database search to determine the fate of the carbon sequestered in forests. Observation-based estimates were compiled for carbon-cycle components, including biometry-based NPP, eddy-covariance or biometry-based NEP and chamber-based heterotrophic respiration[29]. The data set was extended with site information related to stand characteristics, standing biomass and stand age. In general, uncertainties in flux estimates were not reported in the literature. Therefore, we estimated the total uncertainty for every component flux contained in the data set using a consistent framework based on expert judgment (Supplementary Information, section 1.2). The uncertainty framework in our database was designed to account for differences in data quality between sites due to length of time series, methodology and conceptual difficulties (that is, gap filling and dark respiration). Also, an uncertainty of 20% was assigned to the biomass, age and density estimates. These uncertainties were propagated through the statistical analyses by means of random realizations based on Monte Carlo principles. Within each of the 1,000 random realizations, normally distributed random errors, based on the uncertainty framework of our database, were added to the observed fluxes. Therefore, all results that are based on flux data are reported as the weighted mean and the 95% confidence interval of the probability distribution.

Despite the climatic, edaphic and biological diversity of our observations, above-ground biomass was observed to be related to stand density in the way described by self-thinning theory[23]. Although, this theory was initially developed for even-aged single-species plant communities, we applied it to our data (Supplementary Information, section 1.3) to determine the components of the flux-computed NEP, specifically the above-ground biomass, woody debris and soil sequestration. Furthermore, self-thinning theory was used to calculate the theoretical ratio of heterotrophic respiration to NPP and compare it with the observed ratio in support of the hypothesis that biomass accumulation and decline are largely driven by stand structure.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions S.L., B.E.L., A.K. and P.C. compiled the data set. S.L., A.B. and D.H wrote code and analysed the data. S.L., E.-D.S., A.K., B.E.L., P.C. and J.G. designed the analyses and wrote the manuscript.

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