

Old-growth forest carbon sinks overestimated

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ARISING FROM: S. Luyssaert et al. *Nature* <https://doi.org/10.1038/nature07276> (2008)

Luyssaert et al.¹ reported that unmanaged, old-growth forests continue to sequester atmospheric carbon (C) at a rate of $2.4 \pm 0.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for stand ages exceeding 200 years. **This claim was based on an analysis of net ecosystem productivity (NEP) and other C flux data from temperate or boreal forest plots compiled from published studies and databases.** Their conclusions and quantitative estimates are widely cited and essential in the debate on the role of forests in climate mitigation. Thus, **it is important to discuss the validity of these estimates.**

Their conclusion was surprising given that such forests were thought to be C neutral². Using data from several different viewpoints (for example, global net land flux, soil C accumulation rate, N demand to sustain C accumulation) and a re-analysis of the data provided by Luyssaert et al.¹, **we find evidence that the forest NEP values reported in the paper are markedly overestimated.** Our analysis suggests that NEP is only $1.6 \pm 0.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for forests more than 200 years old, or about one-third less than the value reported by Luyssaert et al. Moreover, comparisons of net primary production (NPP) and heterotrophic respiration (Rh) suggest that **some old unmanaged forests might serve as C sources.** These inconsistencies bring into question the value of the NEP flux data given in Luyssaert et al.¹ and their conclusion that unmanaged old-growth forests are important C sinks.

Using the NEP estimate for old forests ($2.4 \pm 0.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) for all temperate and boreal forests ($1.9 \times 10^9 \text{ ha}$)³, the estimated C sink in these forests would be $4.6 \pm 1.5 \text{ Pg C yr}^{-1}$. Although this simple upscaling ignores small C losses from fire, volatile emissions, harvest and leaching (Supplementary Table 1), it is likely to be a conservative estimate because younger forests have higher NEP (Fig. 1a). Importantly, the combined estimate for temperate and boreal old-growth forests is almost twice the global net land C sink (2.6 Pg C yr^{-1}) reported by the Intergovernmental Panel on Climate Change (IPCC) based on other metrics⁴ and almost twice the global forest C sink (2.4 Pg C yr^{-1}) estimated from forest inventory data³. Given that tropical forests were recently concluded to be a minor C source of 0.4 Pg C yr^{-1} (ref.⁵), **we argue that the C sink and NEP estimates for old-growth forests by Luyssaert et al. are too high and are not constrained by the global C budget.**

Temperate and boreal forests on upland soils, from where most of the flux data were derived, contain $100\text{--}150 \text{ Mg C ha}^{-1}$ down to a soil depth of 1 m (ref.⁶). Luyssaert et al.¹ estimated a C sequestration rate of $1.3 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in roots and soil organic matter, which implies that the soil organic C stock should increase 1% per year and roughly double over the next century. Given that it took over 100 centuries to reach the current level, the rate of soil C sequestration appears to be highly overestimated. Only forests on peat soils could have such high soil C sequestration rates⁷.

Carbon accumulation requires nitrogen (N) accumulation since C and N are closely linked in organic matter with characteristic tissue-specific C–N stoichiometries⁸. When the estimated C sequestration rates for biomass, coarse woody debris and soil are multiplied by their specific C-to-N ratios (Supplementary Table 2) it appears that $47 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ is needed to sustain the NEP estimates of Luyssaert et al.¹. Although an input of $50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ with N deposition was observed in smaller regions^{9–11}, about 90% of the global land cover receives less than $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (ref.¹²). Whereas young aggrading forests may acquire large amounts of N from the soil pool through mineralization of organic matter¹³ (and respiration of soil C), old forests where soil organic matter is accumulating (as suggested by the data in Luyssaert et al.¹) need N from external sources. Deposition inputs can supply the N needed for net biomass C accretion (at high C-to-N ratios), but the accumulation of C in soil organic matter (at low C-to-N ratios) estimated by Luyssaert et al.¹ requires large N inputs ($40 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), either to be taken up by plants and recycled to the soil as litter or immobilized by the soil microbes during litter decomposition and transferred to relatively inactive soil organic matter through time. As such, the estimated soil C sequestration rates are likely to be unrealistic and highly overestimated.

The authors of Luyssaert et al.¹ do not discuss the management history of the forests even though the original NEP database includes a categorical variable for forest management history (recently disturbed, managed and unmanaged categories). We calculated the average NEP for different age and management history categories (Supplementary Table 3) and explored the original database in a similar way as did Luyssaert et al.¹, but with a focus on management history of the forests (Fig. 1). We were unable to reproduce their main conclusion that forests more than 200 years old sequester, on average, $2.4 \pm 0.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. The twelve forests in the database with ages exceeding 200 years had an average NEP of $1.6 \pm 0.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ and for the ten unmanaged forests the average NEP was only $1.3 \pm 0.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (Supplementary Table 3). Although the lower average NEP for forests with ages exceeding 200 years of $1.6 \pm 0.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ fits better into the global C budget, it seems to be an overestimate from the perspective of C in soil. If we accept the partitioning of NEP into trees and woody debris suggested by Luyssaert et al.¹, it implies that $0.4 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ should be sequestered in soil organic matter (doubling soil C in 300 years) and requires external inputs of about $20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ or about twice the available N input (Supplementary Table 2).

The NEP estimates for unmanaged forests are lower than for managed forests (on average half the value), but are partly separated on the age scale (Fig. 1a). Managed forests (where interventions aim to increase wood production) had higher NPP than unmanaged and disturbed forests (Fig. 1c). Ratios of Rh to NPP are clearly different for managed

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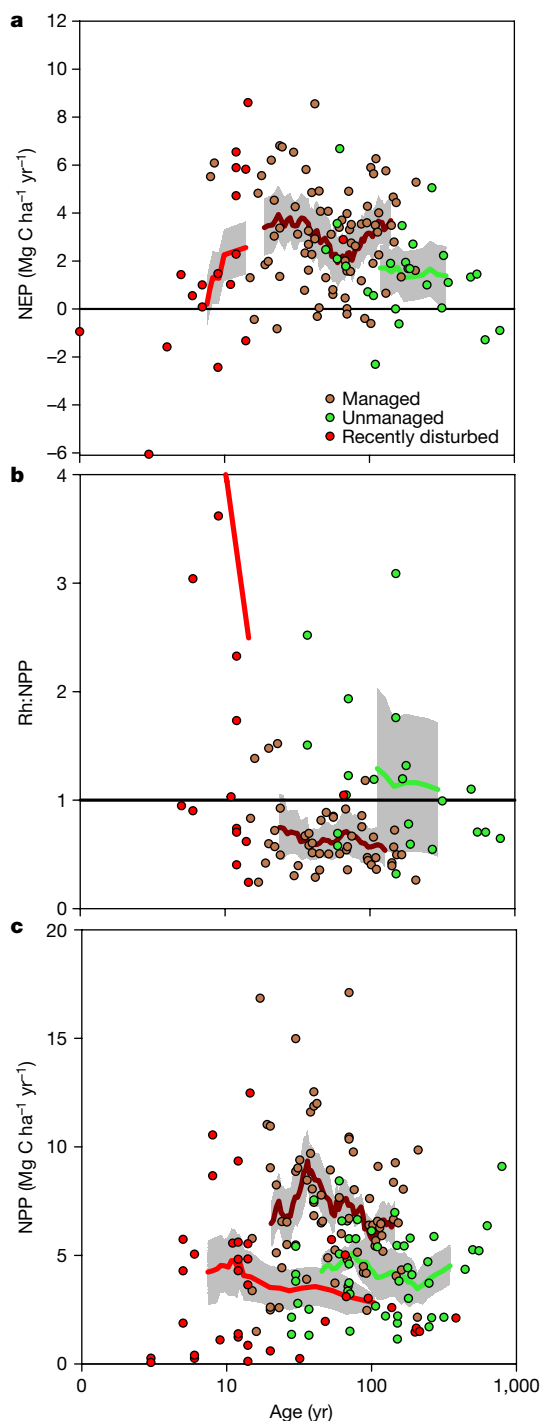


Fig. 1 | Changes in C fluxes as a function of age. **a**, Observed NEP versus age; positive values indicate C sinks and negative values indicate C sources. **b**, The observed ratio of heterotrophic respiration (Rh) to NPP versus age; Rh:NPP < 1 indicates a C sink. The large variability may be an effect of differences in disturbance history (Supplementary Table 3). **c**, Observed NPP versus age. In each panel, the red dots show recently disturbed forests, brown dots show observations of managed forests and the green dots show observations of unmanaged forests; the thick lines show the mean within a moving window of 15 observations for each forest category colour-coded as for the observations and grey areas around these lines delineate 95% confidence intervals. The analysis is based on the same dataset²² as used by Luyssaert et al.¹.

and unmanaged forests (Fig. 1b). Managed forests have Rh:NPP < 1, indicating that they are C sinks, whereas unmanaged forests have Rh:NPP > 1 on average, indicating that they are C sources (following

the interpretation of these ratios as explained by Luyssaert et al.¹). Thus, analysis of Rh:NPP ratios suggests that unmanaged forests should be expected to have negative NEP fluxes. This was, however, only the case for a few sites (Fig. 1a) and the average for unmanaged forests across all ages was $1.3 \pm 0.4 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, indicating a net C sink (Supplementary Table 2). Because Rh and NPP are estimated independently of NEP, the inconsistency again indicates that NEP estimates are too high.

Most NEP data were from studies using eddy-covariance techniques to estimate the net C flux as a difference between photosynthesis and respiration fluxes. Eddy-covariance is a well established but complex technique performed in coordinated regional networks, which are expected to produce high-quality data. However, a major limitation of the eddy-covariance technique is the requirement for turbulent atmospheric conditions during measurement, which, together with equipment failures, produce data gaps typically 20–60% of the time in annual datasets, with the majority of the gaps occurring during night-time¹⁴. The data quality and filtering procedures, the methods used for gap filling, the flux partitioning methods and site inhomogeneity all contribute to uncertainty in NEP data¹⁵. A comparison of four different gap-filling methods on a time series from an old-growth forest in Canada¹⁶ showed a methodological difference equivalent to $0.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. In that forest, the choice of gap-filling method could change the forest from being C neutral to become a C sink. Differences between gap-filling methods can be from $0.3 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ up to $0.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (ref. ¹⁴) and are obviously most important at low NEP such as in old and unmanaged forests.

During periods with low air turbulence, such as advection at night, the eddy-covariance method potentially leads to underestimation of ecosystem respiration at night¹⁷. A method comparison of eddy-covariance and biometric based NEP estimates revealed significantly higher NEP from eddy covariance than from biometric methods ($1.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in boreal forests ($n = 6$; $P < 0.02$) and $1.0 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in temperate forests ($n = 22$; $P < 0.003$))¹⁸. Although both methods are uncertain, the observed bias could explain the inconsistencies and overestimations of NEP as described above. However, recent NEP data to be used in future evaluations may have lower uncertainties and less bias owing to improvements to the eddy flux techniques since 2008^{19,20}.

A contributing reason to the overestimation may be confusion about the management history of the included forests. Old-growth forest is an ambiguous term that some use for primary forest, but others interpret to mean merely forest with old trees²¹. In their abstract, Luyssaert et al.¹ indicate that they understand old-growth forest to be unmanaged, primary forests given that they scale up their NEP estimate to the area of primary forests in the Northern Hemisphere. When referring to the database, however, it appears that the authors used both managed and unmanaged old-growth forests in their analyses.

In conclusion, the NEP data used in the analysis of Luyssaert et al.¹ appear to contain overestimates and thus the quantitative estimates of C sequestration in old-growth forests are suspect. In particular, the high soil C sequestration rate suggested by Luyssaert et al.¹ is implausible. Unmanaged forests in the dataset had lower C sequestration rates than managed forests. Therefore, the role of old-growth forests (particularly unmanaged forests) in the global C budget should be revisited.

Data availability

The data analysed in this study and in Luyssaert et al. (2008) are publicly available at https://daac.ornl.gov/VEGETATION/guides/forest_carbon_flux.html (ref. ²²). We used version 3.1 (12.06.2008).

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Reply to: Old-growth forest carbon sinks overestimated

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REPLYING TO: P. Gundersen et al. *Nature* <https://doi.org/10.1038/s41586-021-03266-z> (2021)

Following re-analysis, Gundersen and collaborators¹ found inconsistencies between the independent data they used and the flux measurements reported in our Letter². In the accompanying Comment¹, each of these inconsistencies is then used to question the quality of the flux measurements, which, if correct, would indeed call for the refutation of the main message: that at present, forests continue to take up carbon even in old age². Although most of the points raised by Gundersen et al.¹ do call for further investigation, none provides unequivocal proof of consistently low-quality flux measurements.

In a first line of reasoning, Gundersen and collaborators¹ use carbon (C) and nitrogen (N) stoichiometry to show that for most regions in the world there is not enough plant available N to sustain the C sink we reported in Luyssaert et al.². Typically, the old sites included in our analysis are relicts in a landscape dominated by young and managed forest that should, therefore, receive similar atmospheric N deposition loads. The stoichiometric approach not only suggests that the sink strength of old forests cannot be sustained but also suggests that the sink strength of young and managed forest cannot be sustained if 10 kg N ha⁻¹ yr⁻¹ of atmospheric deposition would be the only source of plant available N¹. However, a meta-analysis³ of 124 age sequences suggested that ageing forests have an intrinsic ability to accrue on average 22 kg N ha⁻¹ yr⁻¹, twice the available N estimated by Gundersen et al.¹. Rather than questioning the quality of the flux measurements and hence the overwhelming and independent evidence showing accelerated growth rates and the presence of a strong C sink in managed forests⁴, the inconsistency revealed by the stoichiometric approach could be seen as a justification to study knowledge gaps in the contribution of priming⁵, chemical weathering⁶, recycling of organic N by microbes, and biological N fixation to the N cycle.

The second line of reasoning by Gundersen and collaborators¹ suggests that our estimate is in conflict with estimates of the global net land sink. When the aim is to estimate the global net land sink, multiplying the mean net ecosystem productivity (NEP) of old unmanaged forests with the cover of temperate and boreal forests is basic and ignores the temporal evolution of the sink, that is, disturbances also affect old-growth forest everywhere and our study did not aim at quantifying the impact of disturbance on the contribution of old forest to the global net biome production⁷. Although the accounting approach by Gundersen et al.¹ (see their Supplementary Table S1) seems to be correct, it overlooks the considerable uncertainty in all of the required adjustments, which is essential to come to a fair comparison on which meaningful conclusions could be based.

Their third line of reasoning uses observed soil C pools to evaluate present-day flux measurements. The observational database

underlying the results in Luyssaert et al.² represent fluxes over an approximately 20-year period centred around the year 2000. After accounting for the biological volatile emissions and losses through dissolved (in)organic C fluxes, the adjusted fluxes should have been compared to the changes in soil C pools between 1990 and 2010 to draw conclusions on the quality of the eddy-covariance measurements. The method applied by Gundersen et al.¹ assumes that the fluxes observed around the year 2000 will persist into the next century; a claim not made by Luyssaert et al.² and that violates present-day understanding of how plant ecophysiology is driven by changes in environmental conditions⁸.

Along the same lines, Gundersen et al.¹ compares a biometric assessment of NEP based on net primary production (NPP) and heterotrophic respiration (Rh) measurements to a micrometeorological assessment based on eddy-covariance measurements. Unless C leaching and subsidies from the plant to the mycorrhizae are accounted for in the biometric estimate, it is likely to underestimate NPP by up to 30% (ref. ⁹). Using total NPP, instead of solely its biomass component, will push the ratio of Rh to NPP towards C neutrality, if not to a C sink. We note that this issue was addressed in Luyssaert et al.² by the large uncertainty interval surrounding the Rh:NPP estimates as reproduced in figure 1b of Gundersen et al.¹. We² chose not to stratify the data by the management history of the forests even though the underlying database includes this information because further stratification would have resulted in questionable sample sizes (see Supplementary Table 3 in Gundersen et al.¹). The large variation in the biometric NEP estimates for unmanaged forests points to either methodological issues or a large heterogeneity in NPP and/or Rh due to, for example, climate indices such as the El Niño/Southern Oscillation¹⁰. Data from such processes should only be averaged if their time series are long enough to represent the temporal variation in climate indices. Contrary to most biometric assessments of NEP, micrometeorological assessments were sustained for long enough to meet this criterion. They¹ conclude that a mismatch between biometric and micrometeorological NEP assessments proves that the eddy-covariance method causes overestimation, which is a misguided conclusion that ignores relevant studies¹¹, including the observation that where the data were available, eddy-covariance sites passed consistency cross-checking¹².

Gundersen et al.¹ continue to question our use of the eddy-covariance method by showing that post-processing of micrometeorological NEP estimates introduces additional uncertainties which could result in sign-switches for sites where the micrometeorological NEP estimates are close to zero. The observed sign-switch is the result of the statistical distribution of the measurements rather than a shortcoming of the eddy-covariance method. In other words, for a biometric estimate of

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a small mean NEP where the uncertainty exceeds the mean flux, small differences in data processing could also result in sign-switches of the mean flux. The poor performance of a method at individual sites—where there are too many gaps and results are sensitive to methodological choices in gap-filling—does not justify questioning the method as a whole. It may justify excluding those specific sites from the analysis although we consider it preferable to account for this uncertainty through the statistical analysis, which should prevent our jumping to conclusions.

Although the database we used in Luyssaert et al.² was state-of-the-art 12 years ago, the scaling-up was basic, despite being in line with the data availability. Going beyond Luyssaert et al.² would require both revisiting the database to include observations that have become available in the past 12 years, such as refs.^{13–16}, and making use of 12 years of progress in micrometeorological¹⁷ and biometric approaches to reprocess the observations from before publication. Much could probably be gained by refining the scaling-up approach: (1) contrary to 12 years ago, an updated database may contain sufficient observational sites to support stratifying the observations; (2) if the observed sinks could be related to widely available variables, such as stand density, scaling-up could better account for regional differences in forest structure and functioning; and (3) further refinements are to be expected from making use of over a decade worth of progress in mapping intact forests¹⁸.

Given that the Comment¹ does not make use of new data and their re-analysis confirms that forests continue to accumulate C in old age, although at a rate 30% lower ($1.6 \pm 0.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ instead of $2.4 \pm 0.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) than our estimate², the loss of additional sink capacity should still be accounted for when comparing the C budgets of different forest management systems. This being said, the drivers of this C sink^{19,20}, its size^{3,21} and its persistence²² remain topics of continuing research.

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Competing interests The authors declare no competing interests.

Additional information

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