

Phosphorus supply affects long-term carbon accumulation in mid-latitude ombrotrophic peatlands

Daniel N. Schillereff ¹, Richard C. Chiverrell², Jenny K. Sjöström ^{3,4}, Malin E. Kylander^{3,4}, John F. Boyle², Jessica A. C. Davies ⁵, Hannah Toberman⁶ & Edward Tipping⁷

Ombrotrophic peatlands are a globally important carbon store and depend on atmospheric nutrient deposition to balance ecosystem productivity and microbial decomposition. Human activities have increased atmospheric nutrient fluxes, but the impacts of variability in phosphorus supply on carbon sequestration in ombrotrophic peatlands are unclear. Here, we synthesise phosphorus, nitrogen and carbon stoichiometric data in the surface and deeper layers of mid-latitude *Sphagnum*-dominated peatlands across Europe, North America and Chile. We find that long-term elevated phosphorus deposition and accumulation strongly correlate with increased organic matter decomposition and lower carbon accumulation in the catotelm. This contrasts with literature that finds short-term increases in phosphorus supply stimulates rapid carbon accumulation, suggesting phosphorus deposition imposes a threshold effect on net ecosystem productivity and carbon burial. We suggest phosphorus supply is an important, but overlooked, factor governing long-term carbon storage in ombrotrophic peatlands, raising the prospect that post-industrial phosphorus deposition may degrade this carbon sink.

¹Department of Geography, King's College London, London, UK. ²Department of Geography and Planning, University of Liverpool, Liverpool, UK.

³Department of Geological Sciences, Stockholm University, Stockholm, Sweden. ⁴Bolin Centre for Climate Research, Stockholm, Sweden. ⁵Lancaster Environment Centre, Lancaster University, Lancaster, UK. ⁶Natural Resources Wales, Bangor, UK. ⁷UK Centre for Ecology and Hydrology, Lancaster, UK.

email: daniel.schillereff@kcl.ac.uk

Peatlands have sequestered around 500 ± 100 Pg C since the Last Glacial Maximum^{1–3}, equal to a third of the global soil organic C pool⁴. This stems from biomass production exceeding microbial decomposition over millennia. Studies of Holocene peatland development usually consider hydroclimatic and botanical drivers^{5–8} because water table depth and plant structure influences peat formation and decay⁹. Nutrient supply also affects productivity and microbial activity, creating an intrinsic link between P:N:C stoichiometry and C cycling¹⁰. As ombrotrophic peatlands receive nutrients exclusively via atmospheric input^{11,12}, small changes in supply could have substantial effects. Human activities have amplified atmospheric P and N deposition during the 20th century, with profound impacts on nutrient and carbon cycling in global ecosystems^{13–15}. There has been equivalent concern surrounding the effects of elevated N deposition on the peatland carbon sink^{16–18} but much less consideration of P, despite its parallel influence over on lake trophic status¹⁹. Similarly, large databases of N and C profiles have been compiled to explore long-term bog development, which associate accumulation rates to climate drivers and plant stratigraphy^{1,20–22}. Measurements of P in deep cores, however, are restricted to a handful of individual bogs^{23–26}. These present evidence that occasional, localised injections of P-enriched dust²⁷ or tephra^{26,28} triggered short-lived increases in C accumulation during the Holocene. The extent to which spatially variable long-term P supply affects the C dynamics and functioning of mid-latitude ombrotrophic peatlands has not yet been explored.

This is in stark contrast to published experimental evidence from fertilisation plots and isotope tracers, which confirms a key role for P in balancing modern peatland productivity and decomposition. Greater P supply, in isolation and in combination with N addition, stimulates primary productivity in *Sphagnum*-dominated peatlands because mosses intercept the deposited nutrients efficiently^{29,30}. P supply also correlates positively with microbial biomass, activity and diversity in sub-surface peat^{31–33}, which accelerates subsurface respiration^{34–36} and decomposition^{37,38} and slows C sequestration. Terrestrial ecosystems also acquire N through biological N₂ fixation provided ample P is available³⁹. There is good evidence from field manipulations and metagenomics for a direct influence of P on N₂ fixation in peatlands^{40–45}, probably by modulating the nitrogenase activity of diazotrophs⁴⁶. There is also some evidence that increasing P supply can alleviate N toxicity effects^{30,46}. But field studies span hours to years^{30,37,47,48}, whereas C burial has been ongoing for thousands of years⁴⁹. Whether long-term (centuries to millennia) biogeochemical dynamics are captured by experimental plots has yet to be established, especially in light of year-to-year transience in field observations⁴⁷.

Earlier work noted a general concordance between rates of P accumulation in deep peat and directly measured aerial P deposition^{24,50} but the P deposition monitoring network across global peatlands is sparse. Local inputs, which have recently been shown to dominate mineral deposition in Swedish bogs^{51,52}, are likely to be missed. Long-distance transport of fine mineral dust is important for global biogeochemical cycling⁵³, but an imbalance between this flux and far higher directly measured rates of P deposition requires additional, presumably short-distance, aerial contributions⁵⁴. Combustion sources may represent up to 50% of the global atmospheric P budget⁵⁵, although much less prior to industrialisation. Gorham and Janssens²⁵ postulated that proximity to agricultural dust emission governs recent P content in bogs across North America, whereas biological particulates such as plant fragments, microorganism dispersal and bird strike make up a poorly constrained proportion of aerial P inputs through the Holocene⁵⁴. These represent short-range and spatially heterogeneous and temporally dynamic transfers^{54,56}. The implications of such differences in P deposition to individual bogs have not previously been evaluated.

Phosphorus input appears to be an important control on modern peatland functioning, but its long-term role remains poorly understood. Here, we compile the first database of P:N:C stoichiometry from deep mid-latitude ombrotrophic peatlands spanning continents to test the idea that, over millennia, differences in local P input to individual bogs is a key driver of the biogeochemical cascade from surface vegetation to burial in the catotelm. We hypothesise, drawing on modern field data, that *Sphagnum*-rich bogs in receipt of more P can fix more N and promote more intense microbial decomposition and C export from the bog prior to burial. Hence, a link should exist between site-specific P input and C sequestration over long (centuries to millennia) timescales.

Results and discussion

The long-term stoichiometric cascade in ombrotrophic peatlands. Data from a literature search were combined with new measurements from a bog in southern Sweden to produce a database of P, N and C concentrations, accumulation rates and stoichiometric profiles through the acrotelm and catotelm for 11 sites that stretch across northerly and southerly mid-latitudes (45–60°) (Fig. 1 and Supplementary Table 1). Most are in Europe and North America, with a single site in southern Chile. A further 12 sites across northerly mid-latitudes that report P, N and C concentrations to suitable depth but lack chronological information were also incorporated (see Supplementary Methods).

Rates of P, N and C accumulation in catotelm peat, (i.e. long-term burial), average 10.2 ± 1.6 mg m⁻² yr⁻¹, 0.53 ± 0.04 g m⁻² yr⁻¹ and 23.0 ± 2.1 g m⁻² yr⁻¹ (mean \pm standard error) (Fig. 2, Supplementary Table 2 and Supplementary Data 1). Our mean N and C burial rates are very similar to larger published syntheses (0.50 gN m⁻² yr⁻¹ and 22.9 gC m⁻² yr⁻¹)¹. Thus, our database appears representative of mid-latitude peatlands. Our value for catotelm P accumulation is the first regionally aggregated estimate for global peatlands, and is substantially lower than earlier estimates (~ 18 mg m⁻² yr⁻¹)^{50,57}. The higher values in previous studies are derived by averaging all samples through the full peat profile, so are influenced strongly by rapid apparent rates of accumulation in the acrotelm (Supplementary Fig. 3). Our full-core average is very similar: 17 mg m⁻² yr⁻¹. This highlights the importance of differentiating biogeochemical behaviour across the diplotelmic cascade.

Nutrients and C accumulate in the catotelm significantly more slowly ($p < 0.05$) than the acrotelm (Fig. 2) because of the anoxic state and that easily decomposable material has already been lost. Wide ranges of reported accumulation rates in acrotelm peats are unsurprising because of variation in biomass production, meteorology and resolution of the chronological control. The ranges of PAR (phosphorus accumulation rate), NAR (nitrogen accumulation rate) and CAR (carbon accumulation rate) are very similar in the acrotelm (relative standard deviation (RSD) = 53–55%). Catotelm NAR and CAR show lower inter-site variability (RSD = 30% and 23%), whereas catotelm PAR shows more variance between sites (RSD = 52%). P also shows the largest difference between mean acrotelm and catotelm accumulation rates (3.5 times lower).

Phosphorus follows a fundamentally different stoichiometric cascade from living biomass to buried peat from that of N (Fig. 3). Near-surface P enrichment is observed at every site, with maximum P concentrations measured in the shallowest 20 cm of peat (Supplementary Figs. 1 and 2). Nitrogen concentrations and N:C ratios show more complex behaviour, rising towards the surface at only half of our sites and declining or remaining stable at the others. This could reflect differences in the recalcitrance of surface vegetation at each site¹. Peat N:C below 100 cm depth is not significantly different (one-tailed t -test) to living biomass (Fig. 3C), whereas P:C and P:N ratios move progressively away

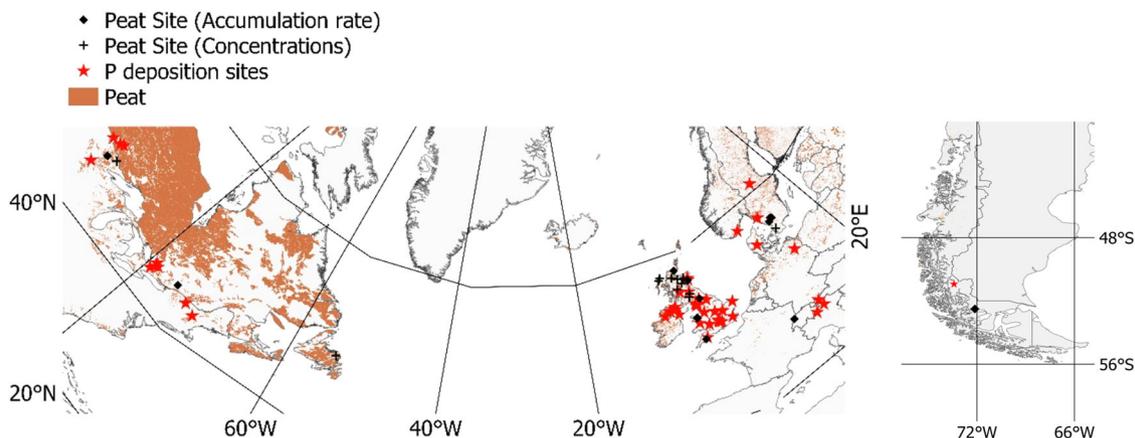


Fig. 1 Location of bog stoichiometric profiles and monitoring sites for P deposition. We collated P, N and C concentration data for 23 mid-latitude sites (crosses; Supplementary Figs. 1 and 2), of which 11 also provided accumulation rates (diamonds). Red stars represent the locations of regional monitoring stations for P deposition used in the analysis, originally reported by Tipping et al.⁵⁴ and Brahney et al.¹⁹. The distribution of peatlands is taken from the PEATMAP of Xu et al.⁹⁶.

from those of source vegetation with depth (and time). This divergent stoichiometric behaviour is in contrast to other terrestrial ecosystems in which plant biomass becomes the sink, where P:N of the material being buried approaches that of the living vegetation⁵⁸. That we do not see this trend in ombrotrophic peatlands (Fig. 2) is consistent with the idea that average plant biomass is continuously being buried in the catotelm but cycling and retention of P within the acrotelm is necessary to maintain peat growth and ecological functioning. This would also explain why catotelm peats fall below the stoichiometric threshold for P limitation^{59,60} at all sites (Fig. 2). The mechanisms by which P is recycled are not fully understood: root, frond or mycorrhizal uptake are probably involved^{11,23,24} and the gene abundance of P-mediating microbes exhibits a similar depth profile³². The release of P from mineral oxide-bound phosphates under reducing conditions in the anoxic catotelm is another mechanism by which P could be returned to the acrotelm²⁴, although the prevalence of mineral-organic matter complexes in organic, humic-rich soils such as peatlands has recently been shown to decrease P adsorption⁶¹ and Fe- and Al-phosphate behaviour under low pH remains uncertain⁶². While N, P and occasionally potassium (K) can each limit the growth of contemporary peatlands⁶³, our data indicate P supply has had an important long-term effect on productivity and peatland development over Holocene timescales.

Phosphorus supply is a spatially persistent driver of carbon cycling. The effects of spatially variable P burial on peatland functioning and C sequestration is illustrated by the striking relationship we observe between PAR and N:C ratio in the catotelm ($r^2 = 0.91$, $p < 0.001$; Fig. 4A). Down-core N:C is commonly interpreted as a decomposition proxy in *Sphagnum*-dominated peatlands because C is preferentially lost as organic matter passes through the acrotelm^{64–67} (see ‘Methods’). PAR is negatively correlated with Δ N:C (the difference between acrotelm and catotelm N:C ratios), which is likely to be more representative of relative decay intensity during peatland development (Fig. 4B). Furthermore, bogs that experience proportionally greater burial of P relative to N seem to sequester C more slowly ($r^2 = 0.64$, $p = 0.003$; Fig. 4C), showcasing a direct link between nutrient stoichiometry and long-term C cycling. The influence of P-driven processing as organic material passes through a peatland is illustrated by the positive association between PAR and CAR in the acrotelm ($r^2 = 0.53$, $p = 0.01$) that flips in deep peat

($r^2 = 0.26$, $p = 0.1$). This differs from studies of whole cores from single sites, which find strong, positive correlations between nutrient and C profiles^{23,26,68}. We propose that our finding that bogs that accumulate more P are characterised by higher N:C (lower Δ N:C) ratios, indicative of more efficient decomposition, is a widespread and largely overlooked biogeochemical characteristic of ombrotrophic peatlands.

Carbon cycling in ombrotrophic peatlands is also known to be influenced by hydroclimate, vegetation composition and N deposition. Competitive displacement of *Sphagnum* by vascular plants, which decompose more efficiently, has been widely reported under enhanced 20th-century N deposition^{37,47,69,70} but sites in our database for which botanical stratigraphies are available are dominated by *Sphagnum*. We also assessed the potential effects of pH at seven sites that reported sub-surface measurements. Mean pH was 4.1, typically for ombrotrophic bogs, and down-core pH profiles remain stable or fluctuate by 0.5 units or less. Although variability in water table depth does influence peat decomposition⁹, our analysis depends on long-term averages, which should smooth hydroclimatic effects, and we do not find evidence that mean annual precipitation and temperature affect C sequestration (regressions of MAP and MAT on CAR: $r^2 < 0.04$, $p > 0.1$) across the sites in our database, nor an association with photosynthetically active radiation²¹ (PARad; $r^2 = 0.02$, $p > 0.1$). For the sites in our database, we find no association between N deposition rates and catotelm CAR ($r^2 = 0.01$, $p > 0.1$) or the N:C ratio ($r^2 = 0.02$, $p > 0.1$). A multiple regression model incorporating climate and depositional covariates explained 42% of variance in catotelm CAR but P deposition is the only significant explanatory variable ($\beta = -0.59$, $p = 0.02$; Supplementary Table 3), and no effect from N deposition. There is little suggestion of multicollinearity (variance inflation factors ~ 1). This furthers the case for P as a spatially consistent driver of peatland functioning, although we cannot exclude the possibility that N deposition or climate may be more important at peatland sites not included in our database.

On the basis that aerial inputs are the sole source of P to ombrotrophic bogs, we compared our peat data with modern measurements of P deposition rates in the same areas (Fig. 5 and Supplementary Fig. 4). The scarcity of P deposition monitoring stations means regional median values are used (see ‘Methods’), and the few data points reduce the statistical power, but bogs in regions receiving higher P deposition are characterised by higher P accumulation and more efficient decomposition (higher N:C and lower Δ N:C ratios). This leads to slower average rates of C

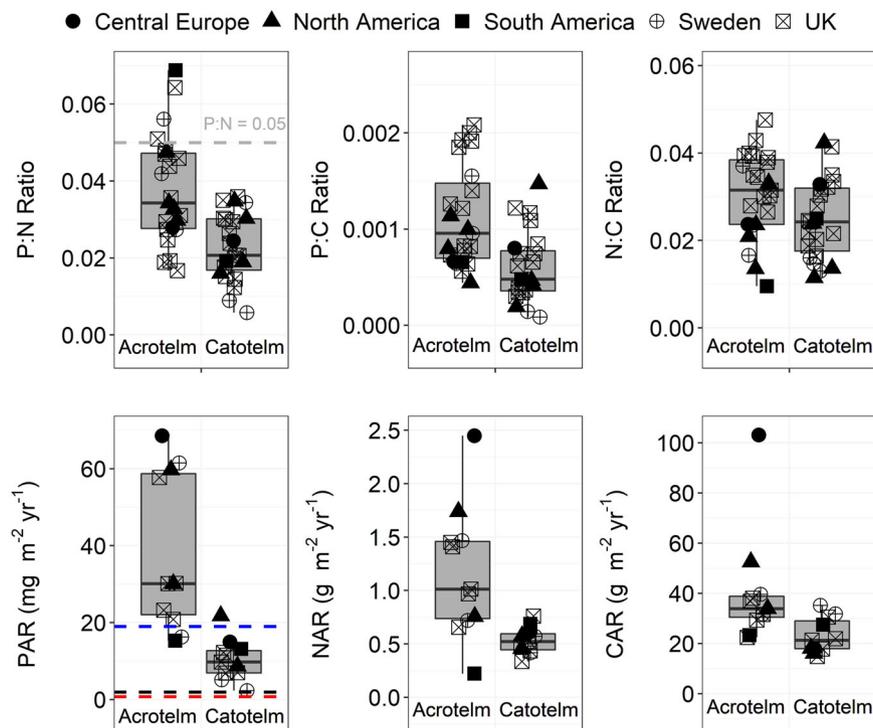


Fig. 2 Mean single-site stoichiometric ratios and accumulation rates measured in the acrotelm and catotelm at 23 mid-latitude peatlands. Horizontal offsets between points are solely for visualisation. Mean P:C, P:N and N:C stoichiometric ratios in catotelm peat are 0.0006, 0.023 and 0.024, respectively, and significantly lower than material in the acrotelm ($p < 0.05$). Rates of phosphorus (PAR), nitrogen (NAR) and carbon (CAR) accumulation include values in the catotelm that represent true burial rates, whereas the acrotelm represent apparent rates. Depths of the acrotelm/catotelm boundary were taken from each publication or, where unreported, a depth of 40 cm was used after sensitivity testing^{86,87} (see ‘Methods’). The horizontal dashed grey line on the P:N ratio plot denotes the critical stoichiometric threshold for P limitation (P:N = 0.05) in terrestrial ecosystems^{59,60}. Horizontal black and red dashed lines on the PAR plot are modelled values of present-day and pre-industrial atmospheric deposition, respectively, from Brahney et al.¹⁹ (see ‘Methods’). Modelled P constitutes only the long-range transport of fine mineral dust particles. The blue dashed line represents mean directly measured P deposition at nearby sampling stations reported in Tipping et al.⁵⁴ (see ‘Methods’). That acrotelm PAR exceeds monitored P deposition illustrates the effects of internal P recycling. More importantly for long-term peatland development, catotelm PAR is greater than the modelled long-distance mineral dust contribution. This holds true throughout the Holocene (Supplementary Fig. 3). This strongly suggests that bogs rely on local and regional nutrient input from nearby soils and ecosystems (see text for discussion), in line with recent findings on mineral dust deposition in Swedish bogs⁵¹.

burial over the Holocene (Fig. 5D; bivariate regression of P deposition on catotelm ARCA across individual sites yields $r^2 = 0.58$, $p < 0.01$). The two-fold difference in catotelm CAR across our sites is equal to that of atmospheric P deposition, so such a large effect is plausible (Fig. 5C). We acknowledge that modern measured P deposition accounts poorly for short-range transfers that are important at the site scale⁵⁴ and may differ from past rates, influenced for example by land-cover change and intensity of biomass burning. To our knowledge, no independent estimates of regional atmospheric P emission and deposition through the Holocene and Brahney et al.¹⁹ model pre-industrial global atmospheric P transfers using fluxes directly proportional to 20th-century values. We interpret the spatial pattern presented in Fig. 5 as representing the biogeochemical response to long-term, background P supply, which differs markedly from that of large, abrupt injections of nutrients, such as local dust input²⁷ or tephra^{26,28}. These events stimulate rapid C accumulation as ecosystem productivity ramps up but fertilisation effects are fairly short-lived (a few centuries). Indeed long-term P accumulation rates are low in bogs in southern Sweden (Figs. 3 and 5) despite receiving episodic pulses of nutrient-enriched dust sourced locally during the mid-Holocene²⁷.

Data on pre-industrial atmospheric nutrient deposition are scarce, but catotelm PAR sets a firm lower limit on long-term P input because of recycling and retention in the acrotelm. Catotelm P exceeds modelled P deposition from long-distance

mineral dust^{19,53} at all sites (Fig. 3) throughout the Holocene (Supplementary Fig. 3). The modelled fine dust fraction explains, on average, $30 \pm 9\%$ of catotelm PAR (mean \pm SE). The site in central Europe accumulates P rapidly and receives higher mineral dust input (45% of catotelm PAR), presumably from the Sahara⁷¹. P recycling in the acrotelm does not increase total P in the system, so this underlines that bogs must rely on contributions from external sources in addition to long-distance mineral dust. Local P sources and sinks remain quite poorly understood but biological inputs (plant fragments, bird strike, microorganisms) from neighbouring ecosystems able to acquire P through mineral weathering as well as locally sourced dust are primary candidates^{27,51,54,56}. Importantly, these localised pathways are almost certain to be spatially heterogeneous and temporally dynamic. Adding the more representative contribution of biological particulates from Tipping et al.⁵⁴ brings P input and peat burial values more in line ($P_{\text{dep}} = 76\%$ of catotelm PAR), although these are large generalisations.

Wang et al.²⁴ postulated peatlands bury P at approximately the same rate as P inputs, whilst acknowledging deposition rates in eastern Canada range between 0.07 and $0.34 \text{ mg m}^{-2} \text{ yr}^{-1}$. From our data (Figs. 4 and 5), such a degree of long-term spatial variability has substantial implications for decomposition and C cycling at individual peat bogs. Furthermore, the virtual absence of data on modern P deposition across the high latitudes (Supplementary Fig. 5) makes it difficult to judge the importance of altered

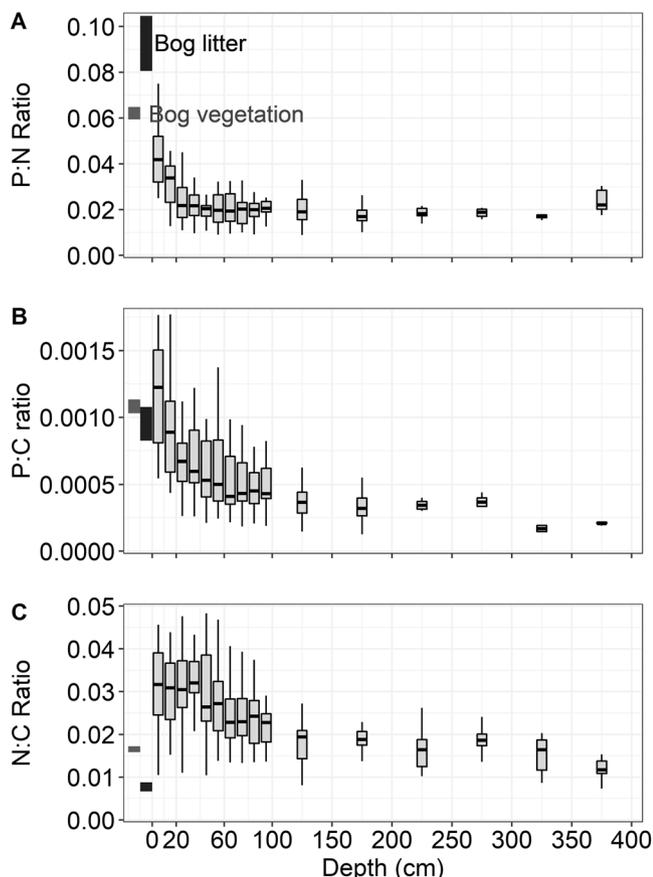


Fig. 3 Nutrient stoichiometric ratios against depth for all sites. Boxes are plotted for the ratios between (A) P and N, (B) P and C and (C) N and C at 10 cm horizontal intervals between 0 and 100 cm depth and then 50 cm intervals. Whiskers extend to 1.5 times the inter-quartile range. Dark and light grey rectangular boxes encapsulate the stoichiometric ratios for bog vegetation and bog litter across North America and Europe compiled by Wang et al.²⁴. Vertical limits for each source material rectangle (bog vegetation or litter) are the mean \pm standard error and their horizontal position is illustrative.

nutrient supply relative to amplified warming and permafrost melting for the stability of northern peatlands, or indeed how these factors may interact. Given the apparent importance of short-distance P inputs on long-term peatland functioning and C sequestration, there is a clear need to understand where bog P comes from at much greater spatial resolution.

PAR appears to scale linearly with P deposition (Fig. 5C); intuitively, so should hydrological P export. This presents a way of estimating the P balance for mid-latitude ombrotrophic peatlands. The y -intercept in Fig. 5C is not significantly different from zero, meaning on average 60% of P deposition becomes permanently buried in the catotelm and 40% is lost via hydrological runoff. This yields a P export range of 0.0002–0.13 $\text{g m}^{-2} \text{yr}^{-1}$. Measurements of peatland P loss via leaching are scarce but regional modelling of fluvial DOP fluxes⁷² are within 10% of our estimates.

Our database also provides the first estimate of the total Holocene P pool in mid-latitude peatlands from spatially aggregated measurements. Using C stocks calculated for northern¹ and southern hemisphere⁷³ peatlands, the minimum, mean and maximum catotelm P:C ratios yield estimates of 0.04, 0.23 and 0.64 Gt P, respectively. This encapsulates the sole prior estimate from Wang et al. (2015) of 0.34 Gt P calculated from peatlands in

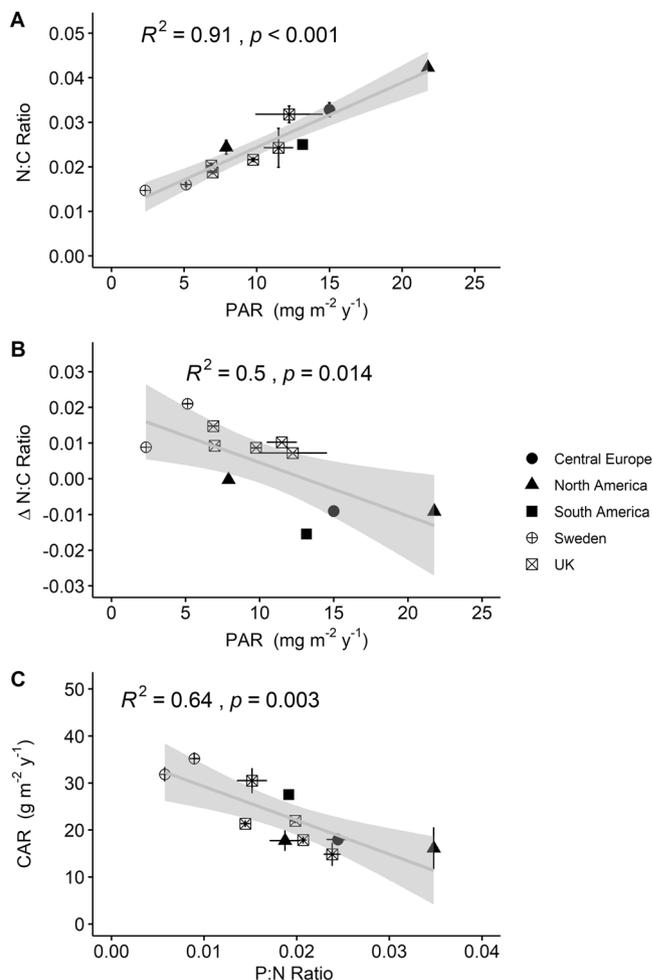


Fig. 4 Comparisons of catotelm P and C accumulation with catotelm stoichiometric indicators from eleven sites. A PAR in the catotelm is strongly correlated with the N:C ratio, interpreted as a decomposition proxy, across all sites. Each data point represents the mean value and error bars represent the standard error for catotelm peat at each dated site. B PAR in the catotelm is negatively correlated with the Δ N:C ratio, the difference between N:C in the acrotelm and catotelm. Lower Δ N:C indicates proportionally greater decomposition and loss of C as organic material moves through the acrotelm into the catotelm. C Sites that bury proportionally greater amounts of P relative to N are associated with slower C burial. PAR and NAR in isolation are only weakly correlated with CAR ($r^2 = 0.26$ and 0.05 , $p > 0.1$). Regression coefficients using acrotelm depths of 30 and 20 cm are extremely similar (Supplementary Table 4).

Ontario, Canada. The C accumulation rate at our site in the southern hemisphere (Skyring, Chile: $22 \text{ gC m}^{-2} \text{yr}^{-1}$) is the same as existing mean estimates for all peatlands across southerly mid-latitudes⁷³, so we consider Skyring stoichiometry to be appropriately representative of hemispheric values. The global soil P budget is stacked with uncertain inputs and outputs^{74,75} but two independent central estimates using our database suggest approximately 1.7% of global soil P is stored in mid-latitude ombrotrophic peatlands (Supplementary Table 5), albeit with high uncertainty.

P supply affects the interplay between peatland productivity and decomposition. We find evidence supporting the hypothesis that the amount of P supplied to a bog over long timescales influences its biogeochemical cascade from surface vegetation to catotelm peat as well as its long-term C burial rate. The amount

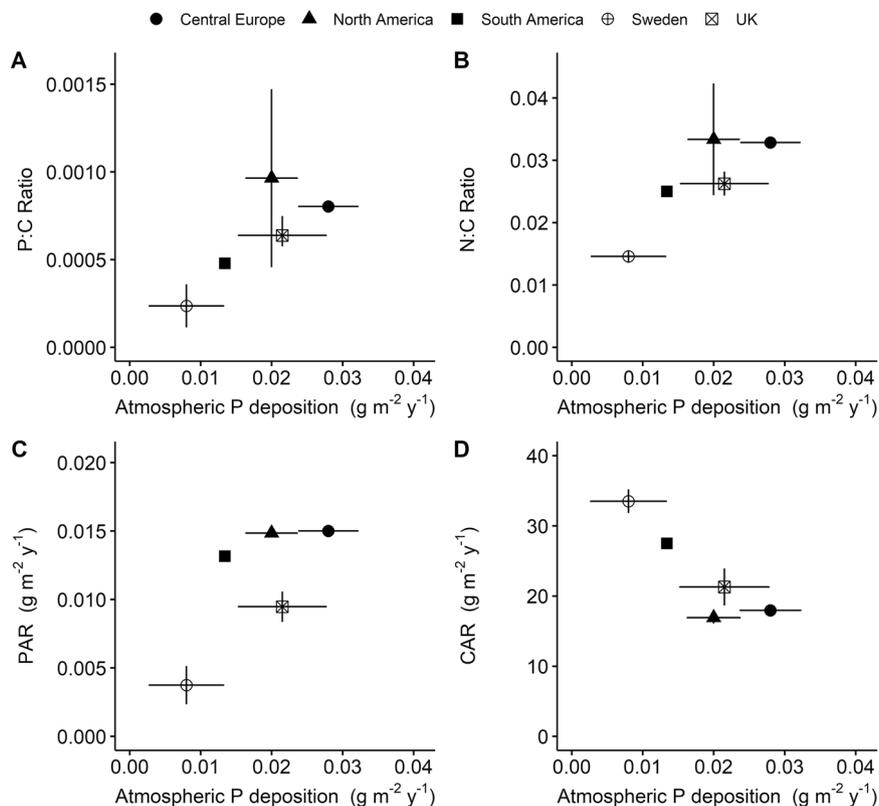


Fig. 5 Comparisons of modern measured atmospheric P deposition and peatland catotelm stoichiometry and C burial. The positive associations between P deposition and catotelm P:C (**A**) and PAR (**C**) fit our expectations because phosphorus depends exclusively on external supply. The negative relationships observed between P deposition, the intensity of decomposition (inferred from the N:C ratio; **B**) and rates of catotelm carbon burial (**D**) are more notable, pointing to an effect of P supply on carbon dynamics. Data points are regional median \pm standard error. Atmospheric P deposition (P_{dep}) represents the median of between 1 and 28 monitoring stations to account for local variance and bars represent standard errors where more than one monitoring station was used (see Fig. 1 and ‘Methods’). The equivalent values for acrotelm peats are presented in Supplementary Fig. 4 and show similar associations.

of C buried in peatlands reflects the difference between primary productivity and decomposition. Hydroclimate and vegetation are known to influence both processes; our data suggest P has an important and overlooked role. We propose the following governing mechanisms (Fig. 6), informed by published experimental evidence, whilst recognising that controlled field manipulations spanning hours to years and that apply a P loading up to two orders of magnitude higher than natural input^{29,37,76} do not necessarily replicate long-term dynamics.

Greater P supply should promote biomass production because mosses efficiently trap and utilise aerial nutrient inputs^{29,30}. At the same time, elevated nutrient deposition increases the size, activity and diversity of the microbial pool in the acrotelm^{31,77}, which has the potential to accelerate the decomposition of more recalcitrant C compounds that usually become buried in the catotelm. This would lead to higher gaseous and hydrological export. The inverse correlation between P input and CAR (Figs. 4A, 5D and 6) suggests fertilisation promotes more rapid decomposition relative to biomass production, thereby slowing long-term C sequestration. This differs from other ecosystems⁷⁸, including mineral soils⁷⁹, where amounts of P and C typically increase in tandem. Individual peat profiles also exhibit a positive relationship when abrupt injections of P from local dust input^{27,80} or tephra^{26,28} during the Holocene trigger episodes of rapid C accumulation. This could represent a threshold effect, whereby sufficiently high background P deposition to a bog over a prolonged period allows intensified decomposition to overcome

increased productivity. Much more work is needed to directly observe and quantify such an effect.

Such biogeochemical processing would require the soil microbial community to be more tightly P-limited than surface vegetation. This is plausible: Van den Elzen et al.⁴¹ found diazotrophic activity to be more sensitive than *Sphagnum* growth to P addition and Wang et al.²³ showed microbial stoichiometry is notably different to living plant material and litter in Mer Bleue bog. Moreover, Lin et al.^{32,45} used metagenomics to show P availability imposes a limiting effect on the microbial communities of decomposers and N₂ fixers. There is also strong evidence for direct effects of P on N₂ fixation rates from fertilisation plots^{40–42,44,46} and surface peat measurements⁴³. This is another mechanism by which P supply may influence the intensity of organic matter decay. Taken together, we propose that spatial variation in long-term P deposition appears to be an important and widely overlooked driver of long-term peatland functioning and C sequestration. We acknowledge that direct measurements of soil microbial activity and N₂ fixation rates for all sites would strengthen these causal inferences, but sufficiently long-term data are unavailable. A numerical model of peatland development that allows P, N and C to co-vary through time and depth would also offer valuable insight.

Human activities have amplified both atmospheric P and N deposition during the 20th century^{13,19,75}, with profound effects on the nutrient and carbon balance of forests^{13,14}, lakes¹⁹ and other global ecosystems¹⁵. Anthropogenically enhanced N

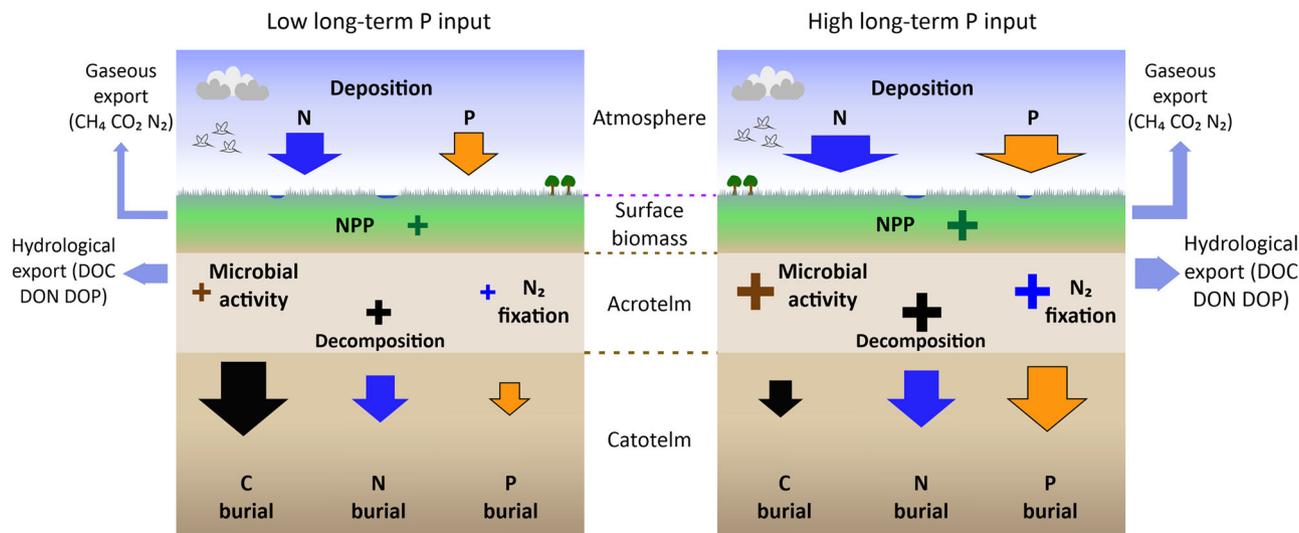


Fig. 6 Conceptual model illustrating the biogeochemical cascade in regions of low and high long-term P input. We propose that bogs in receipt of more P over the course of their development will, on average, bury less C. This is because higher nutrient input stimulates proportionally greater microbial decomposition, leading in turn to more gaseous and hydrological export from the acrotelm, than the fertilisation effects on surface productivity. See text for a more detailed explanation of the proposed governing mechanisms. Arrow sizes represent approximate proportions of input and output fluxes. Crosses represent the relative magnitude of internal processes within the biogeochemical cascade. NPP = net primary productivity. DOC, DON and DOP = dissolved organic carbon, nitrogen and phosphorus.

deposition to peatlands has been widely observed to alter plant structure^{47,70} and trigger C loss¹⁶. Whilst some experimental evidence suggests P can ameliorate the toxicity of excess N input^{30,46}, our findings support the idea¹⁸ that areas of prolonged high nutrient deposition could have reinforcing effects on C loss (Fig. 6). We similarly must better understand how P will influence peatlands that are no longer N-limited due to elevated atmospheric deposition in recent decades¹⁸. Given P and N deposition are predicted to remain above pre-industrial levels for at least another century¹³, our findings also raise important questions as to whether anthropogenic perturbations to the global P cycle, alone and in conjunction with N, may be sufficient to alter the trajectory of mid-latitude peatland development and slow future C sequestration. The capacity of peatlands to continue as a strong C sink is a key uncertainty in climate model projections, usually attributed to complex temperature and vegetation feedbacks^{81–83}. We contend that changes in nutrient supply should also be considered. Furthermore, global models of atmospheric nutrient cycling tend to focus on long-distance fluxes and often under-predict when compared to measured deposition, especially for P^{13,19,53}. This could be explained by models not capturing local nutrient input, which we have shown to be an important source of P to ombrotrophic peatlands. Continued urbanisation and expansion of intensive agriculture, both anthropogenic nutrient emission hotspots^{14,25}, place the future carbon sink of peatlands in those regions at particular risk.

Methods

Database compilation. A careful literature search was conducted to identify peer-reviewed publications that report P, N and C concentrations from deep profiles in ombrotrophic peatlands. Sites reporting chronological and bulk density data were recorded separately. The following selection criteria were then applied: (i) sites must be ombrotrophic (rain-fed) peatlands. Where a peat was known to have developed on a basal fen, data from peat below the bog/fen transition and with C < 40% were excluded; (ii) sites known to have been afforested, fertilised or drained were excluded although an influence from indirect or undocumented landscape modification at the sites used in this meta-analysis cannot be ruled out; and (iii) measurements must extend into the catotelm.

Mean values for P, N and C concentration, accumulation rate and stoichiometry were determined for the acrotelm and catotelm. We acknowledge the diplotelmic model is simplistic because the shift from aerobic to anaerobic conditions often

occurs across a transition zone, may differ between hummocks and hollows and seasonal water table fluctuations and long-term hydrological variability means this acrotelm/catotelm boundary depth may be time-transgressive^{84,85}. Where the depth of the acrotelm/catotelm boundary was not reported in the source publication (Supplementary Table 1), we conducted sensitivity tests using boundary depths of 20, 30 and 40 cm (Supplementary Table 4). Differences were minimal: catotelm PAR, NAR and CAR vary by 10%, 6% and 3%, respectively, which is considerably less than observed differences between acrotelm and catotelm means. We therefore used a depth of 40 cm as a conservative choice that is informed by literature^{86,87} and captures biogeochemical differences between the definitively active zone (acrotelm) and deeper burial zone (catotelm). To maximise data availability, basal samples in shorter cores (<100 cm) were assumed to represent the long-term mean provided penetration into the catotelm was confirmed.

By combining published data with new data from a bog in southern Sweden (Davids Mosse), we collated rates of P, N and C accumulation in the acrotelm and catotelm for 11 sites worldwide (Supplementary Table 1). These required reliable measurements of C and nutrients as well as bulk density and chronological information. Accumulation rates are apparent rather than true rates because the effects of long-term decomposition or nutrient recycling cannot be differentiated^{1,2}. The age-depth models for bogs in North America and Sweden incorporate at least five and up to 19 ¹⁴C ages while Seno Skyring (Chile) was dated using radiocarbon and tephra. The chronology for each UK site is based on three ¹⁴C ages, including one basal date, while the age-depth model for Etang de la Gruère (Switzerland) combines a ²¹⁰Pb profile with one basal ¹⁴C age. These chronological resolutions may overlook some decadal or centennial-scale variability, but long-term aggregated fluxes should be accurate. Elemental concentrations were measured on different instruments, but source publications confirm total P was measured and that certified standards were used in each case. Estimated measurement errors across the instruments are smaller in magnitude than differences between acrotelm and catotelm means (Supplementary Table 6). Owing to the different research questions being asked in each source publication, reconstructions of peat decomposition rates, peat vegetation type, pH or water table depth are not available for all sites.

A further 13 sites reported P, N and C concentrations to suitable depth but lacked chronological information (Supplementary Table 1). Concentrations are reported as the mean of each sample extracted from either the acrotelm or the catotelm. The relatively low number of sites imposes limitations and may reduce statistical power but is similar in number to those used by Charman et al.²¹ to evaluate climate-carbon interactions in northern peatlands. For the Seno Skyring, Mer Bleue and Marcell Experimental Forest sites, measurements of P, N and C, bulk density or the age-depth model published in separate source publications were merged. This was justified by cross-correlating bulk density or stoichiometric values reported in both papers (see Supplementary Methods). We collate data into wide bins (10 and 50 cm; Fig. 2) and use a conservative estimate for acrotelm/catotelm boundary depth to smooth effects of merging cores that may use different sampling resolutions.

We use the N:C ratio as a proxy of decomposition because it is generally suitable at *Sphagnum*-dominated peatlands⁸⁸. N:C profiles are intended to capture the preferential loss of carbon during decomposition, but its representativeness can

be confounded by vegetation changes, especially the appearance of more recalcitrant vascular species. Cores in our database with available palaeoecological data show *Sphagnum*-dominated stratigraphies. Some peat cores exhibit fine-resolution variability in degree of decomposition, often linked to hydroclimate, which can also confound the N:C ratio⁸⁹. Our use of mean values for the acrotelm and catotelm minimises this potential source of uncertainty. Integrating independent measures of decomposition is recommended⁸⁹ so, using source publications, we collated additional proxies of decomposition (FTIR spectroscopy, $\delta^{15}\text{N}$) for six sites. Each shows good agreement with the down-core N:C profile. We acknowledge that this congruence does not guarantee that N:C is the preferred decomposition proxy at the other sites.

We report stoichiometric ratios inversely to the standard convention: P:N, P:C and N:C. This approach is, in our view, more representative of the biogeochemical mechanisms at play because C content responds to nutrient dynamics.

Statistical tests. All statistical analyses were performed using R version 3.5.2 (R Development Core Team, 2018) in RStudio v1.2.1335. The normal distribution of each parameter was tested using Shapiro-Wilk tests. Associations between nutrients and physical factors were estimated by linear regressions, reduced major axis regressions and Pearson product moment correlation coefficients using the R packages 'ggpubr' (v0.2⁹⁰) and 'lmodel2' (v1.7.3⁹¹). Output is plotted in the 'ggplot2' environment (v3.1.1⁹²).

Measurements of modern P and N deposition. We extracted direct measurements of total P deposition from Tipping et al.⁵⁴ and Brahney et al.¹⁹. We decided to use regionally representative values because P deposition measured at monitoring stations within a 30 km radius vary by up to one order of magnitude. This uncertainty will derive from short-distance lateral P exchange along landscape gradients of nutrient enrichment⁵⁴, which is poorly quantified, and that P deposition sampling strategies purposefully exclude larger biological aerosols, such as bird faeces. P_{dep} values used in our analysis are therefore the median of all monitoring stations that operated for at least 12 months within a 350 km radius of a bog in our database (Fig. 1). For the UK, we used the median of all national monitoring sites because each is within 350 km of a studied bog. As a result, spatially representative data points for P deposition used in our analysis are based on between one and 28 monitoring stations.

Similarly, we extracted the most localised measurements of N deposition and so acquired data from a variety of publications. For the UK, mean N deposition since 1800 was extracted from the LTLS model⁹³. Values for Etang de la Gruère (central Europe) and Seno Skyring (South America) were reported by Bragazza and Limpens⁹³ and Fritz et al.³⁰, respectively. For North America, we used measurements by Hill et al.³⁸ at the Marcell Experimental Forest and Turunen et al.⁹⁴ for Mer Bleue. For southern Sweden we used values reported in Lund et al.⁹⁵

Data availability

The biogeochemical data synthesised in this study are presented in Supplementary Table 2, an extractable version is available as Supplementary Data 1 and also downloadable under a CC-BY licence on the King's Open Research Data System: https://kcl.figshare.com/articles/dataset/SupplementaryData1_csv/16810489/1.

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Author contributions

D.N.S. led the data compilation, analysis and wrote the initial draft. R.C.C. and J.F.B. contributed to analysis, interpretation and writing. J.K.S. and M.E.K. provided new data and contributed to analysis, interpretation and writing. H.T. and J.A.C.D. were involved in data collection for the UK sites and contributed to analysis. E.T. conceived the original project, contributed to data compilation, analysis and interpretation and writing. All authors contributed to the final version.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Daniel N. Schillereff.

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