Feedback and comments are very welcome. Please write to the lead author Dr Daniel Schillereff via email (daniel.schillereff@kcl.ac.uk) or on Twitter @dschillereff.

Title: Phosphorus supply controls the long-term functioning of mid-latitude ombrotrophic peatlands

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Phosphorus (P) supply is pivotal to global ecological functioning and carbon cycling. Ombrotrophic peatlands are waterlogged, nutrient-limited ecosystems where plant litter production exceeds decomposition rates, creating an important soil carbon (C) store (~500 Pg). Published experimental evidence demonstrates that the tight stoichiometric balance between P, nitrogen (N) and C regulates present-day peatland behaviour and carbon sequestration. We know little about the dynamics and importance of P in long-term bog development, limiting understanding of how the global peatland carbon sink may respond to prolonged human-perturbed and elevated P deposition. Here we show that P supply imposes a strong and overlooked control on long-term biogeochemical cycling and carbon storage across a range of individual bogs. Holocene stoichometric (P, N and C) profiles from 23 ombrotrophic, *Sphagnum* peatlands across Europe, North and South America confirm the importance of P recycling and retention by living vegetation in the acrotelm. Phosphorus accumulation in the catotelm shows a strong, positive correlation with site-specific proxies for decomposition ($r^2 = 0.91$) and the P:N balance appears linked to long-term C burial ($r^2 = 0.63$). More significantly, we find that modern measured P deposition in each study region is associated with greater decomposition and lower carbon accumulation in the catotelm. As ombrotrophic bogs source P solely from the atmosphere, the P supply to a particular bog appears to drive its biogeochemical cascade from surface vegetation to catotelm storage. We propose, supported by published experimental evidence, that P constrains productivity and microbial nutrient turnover over Holocene timescales. In turn, this dictates the intensity of organic matter decomposition, the amount of C export prior to permanent burial and, ultimately, the size of globally significant carbon and nutrient stores. We also calculate the P pool in mid-latitude ombrotrophic peatlands to be 0.23 Gt, representing 1.7% of global soil P. Our findings identify P supply as an overlooked driver of long-term peatland development and raises the prospect that increased post-industrial P deposition may degrade the global peatland carbon sink.

Peatlands have sequestered around 500 ±100 Pg of carbon since the Last Glacial Maximum[1–3], equal to a third of the global soil organic carbon pool[4]. 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 influences subsurface peat formation and decay[9]. Nutrient availability also governs productivity and microbial activity, creating an intrinsic link between P:N:C stoichiometry and carbon cycling[10]. Ombrotrophic peatlands receive nutrients exclusively via atmospheric inputs[11,12], so small changes in external P or N supply could have substantial effects. Large databases of peat C and N profiles have been compiled, which link accumulation rates to climate drivers and floral stratigraphy[1,13–15], but phosphorus measurements are restricted to a handful of individual case studies[16–19]. These present evidence that occasional, localised injections of P-enriched dust[20] or tephra[19,21] triggered short-lived spikes in C accumulation. The extent to which spatially variable P supply controlled the long-term 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[22,23]. Phosphorus supply also correlates positively with microbial biomass, activity and diversity in sub-surface peat[24–26], which accelerates subsurface respiration[27–29] and decomposition[30,31] and slows carbon sequestration. Provided ample phosphorus is available[32], terrestrial ecosystems also acquire N through biological N_2 fixation. There is good evidence from field manipulations for a direct influence of P on N_2 fixation in peatlands[33–37], probably by modulating the nitrogenase activity of diazotrophs[38]. But field studies span hours to years[23,30,39,40], whereas carbon burial has been on-going for thousands of years[41]. 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 observations[39].

Earlier work noted a general concordance between rates of P accumulation in deep peat and directly-measured aerial P deposition[17,42] 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[43], are likely to be missed. Long-distance transport of fine mineral dust is important for global biogeochemical cycling[44], but an imbalance between this flux and far higher directly-measured rates of P deposition requires additional, presumably short-distance, aerial contributions[45]. Combustion sources may represent up to 50% of the global atmospheric P budget[46], although much less prior to industrialisation. Gorham and Janssens[18] 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 Holocene[45]. These represent short-range and spatially heterogeneous and temporally dynamic transfers[45,47]. 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 drives the biogeochemical cascade from surface vegetation to burial in the catotelm at the individual bog-level. 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 carbon sequestration over long (centuries to millennia) timescales.

Results

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 stoichiometric profiles and accumulation rate curves through the acrotelm and catotelm for 11 sites that stretch across northerly and southerly mid-latitudes (45° - 60°) (Figure 1, Supplemental 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.

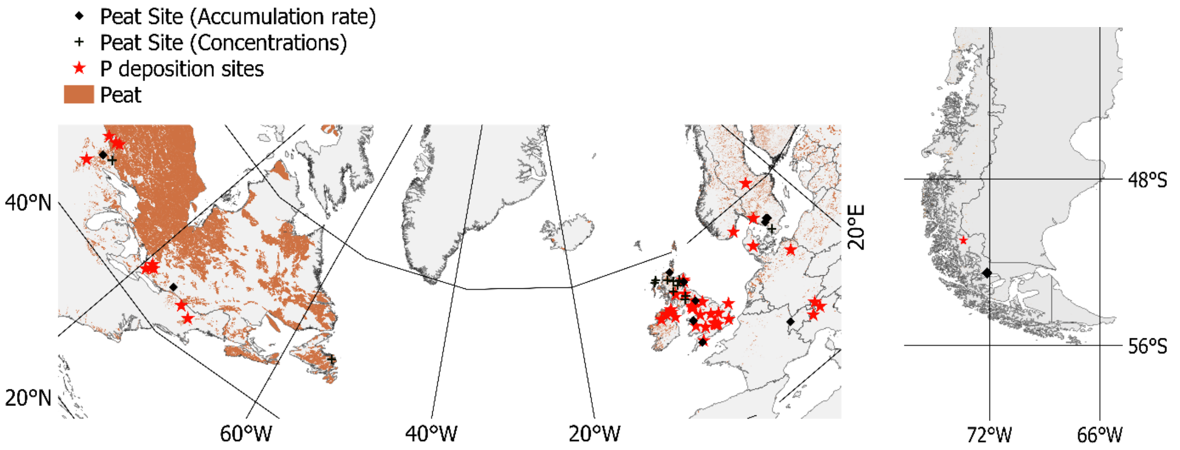


Figure 1. Location of bog stoichiometric profiles and monitoring sites for P deposition. We collated P, N and C concentration data for 23 mid-latitude sites (crosses), of which 11 also provided accumulation rates (diamonds). Red stars represent the locations of regional monitoring stations for P deposition used in the analysis, originally reported by Tipping et al.[45] and Brahney et al.[48]. The distribution of peatlands is taken from the PEATMAP of Xu et al.[49].

Phosphorus follows a fundamentally different stoichiometric cascade from living biomass to buried peat from that of N (Figure 2). Near-surface phosphorus enrichment is observed at every site, with maximum P concentrations measured in the shallowest 20-cm of peat (Supplemental Figure 1). Nitrogen concentrations and N:C ratios rise towards the surface at only half of our sites and decline or remain stable at the others. Furthermore, P:C and P:N ratios move progressively away from those of vegetation with depth (and time) whereas peat N:C below 100-cm depth is not significantly different (one-tail *t*-test) to living biomass. This divergent stoichiometric behaviour is best explained by efficient recycling of P in the acrotelm, which is necessary because external inputs are insufficient to maintain ecological functioning. In other terrestrial ecosystems where plant biomass becomes the sink, P:N of the material being buried approaches that of the living vegetation[50]. That we do not see this trend in ombrotrophic peatlands (Figure 2) is consistent with the idea that average plant biomass is continuously being buried in the catotelm, while P is recycled and retained in the acrotelm by living vegetation.

Rates of P, N and C accumulation in catotelm peat, (i.e., long-term burial), average 10.2 ± 1.6 mg m^{-2} y1, 0.53 ± 0.04 g m^{-2} y^{-1} and 23.0 ± 2.1 g m^{-2} y^{-1} (mean ± standard error) (Figure 3; Supplemental Table 2). Our mean N and C burial rates are very similar to larger published syntheses (0.50 gN m^{-2} y^{-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 in global peatlands, and is substantially lower than earlier estimates (~18 mg m^{-2} y^{-1} [42,51]). The higher values in previous studies are derived by averaging all samples through the full peat profile, so are strongly influenced by rapid apparent rates of accumulation in the acrotelm (Supplemental Figure 3). This highlights the importance of differentiating biogeochemical behaviour across the diplotelmic cascade.

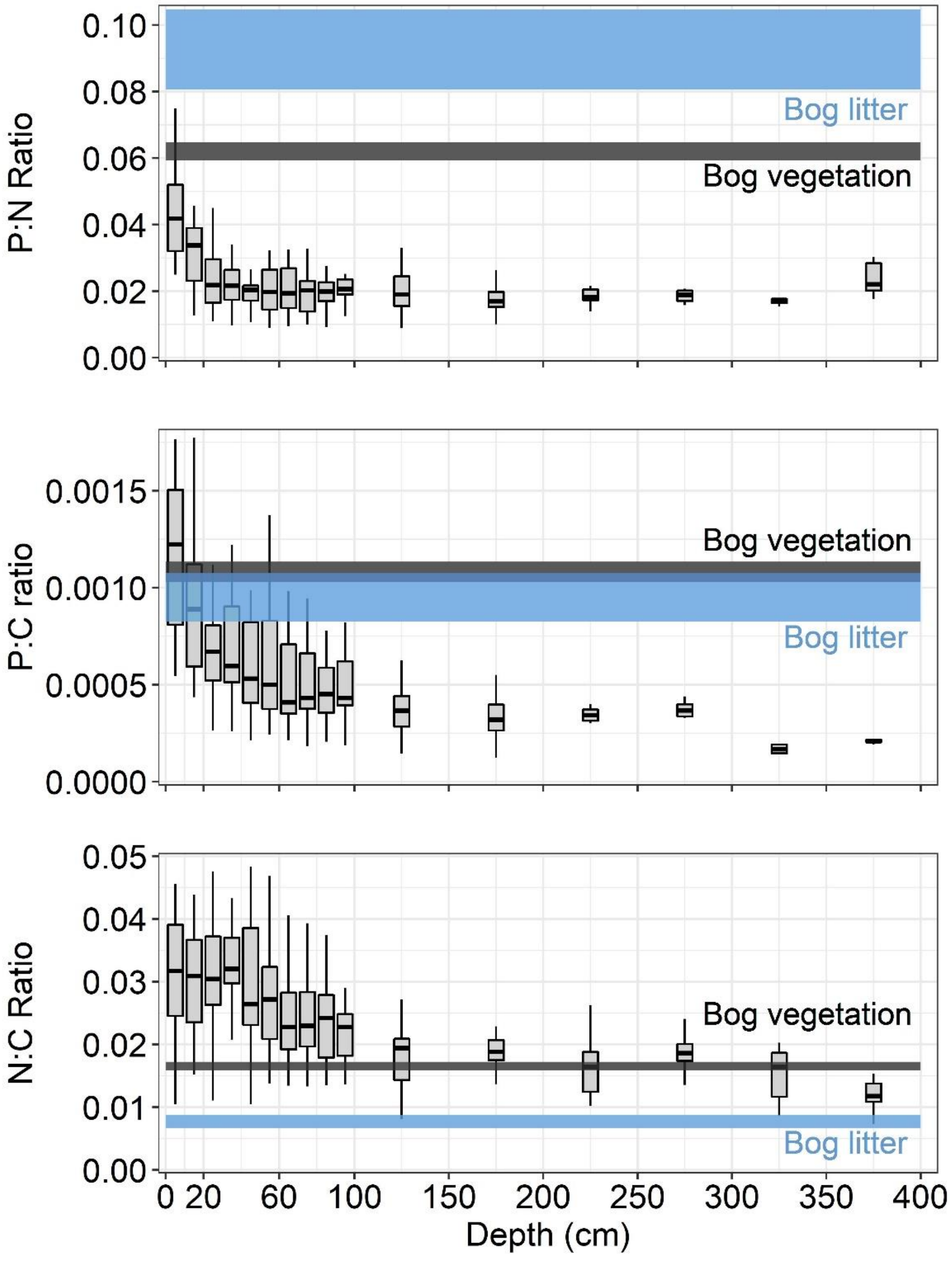


Figure 2. Nutrient stoichiometric ratios against depth for all sites. Boxes are plotted for 10-cm horizonal intervals between 0 and 100-cm depth and then 50-cm intervals. Whiskers extend to 1.5 times the inter-quartile range. Dark and light grey rectangular boxes encapsulate the stoichiometric ratios for bog vegetation and bog litter across North America and Europe compiled by Wang et al[17]. Vertical limits for each source material rectangle are the mean plus and minus the standard error.

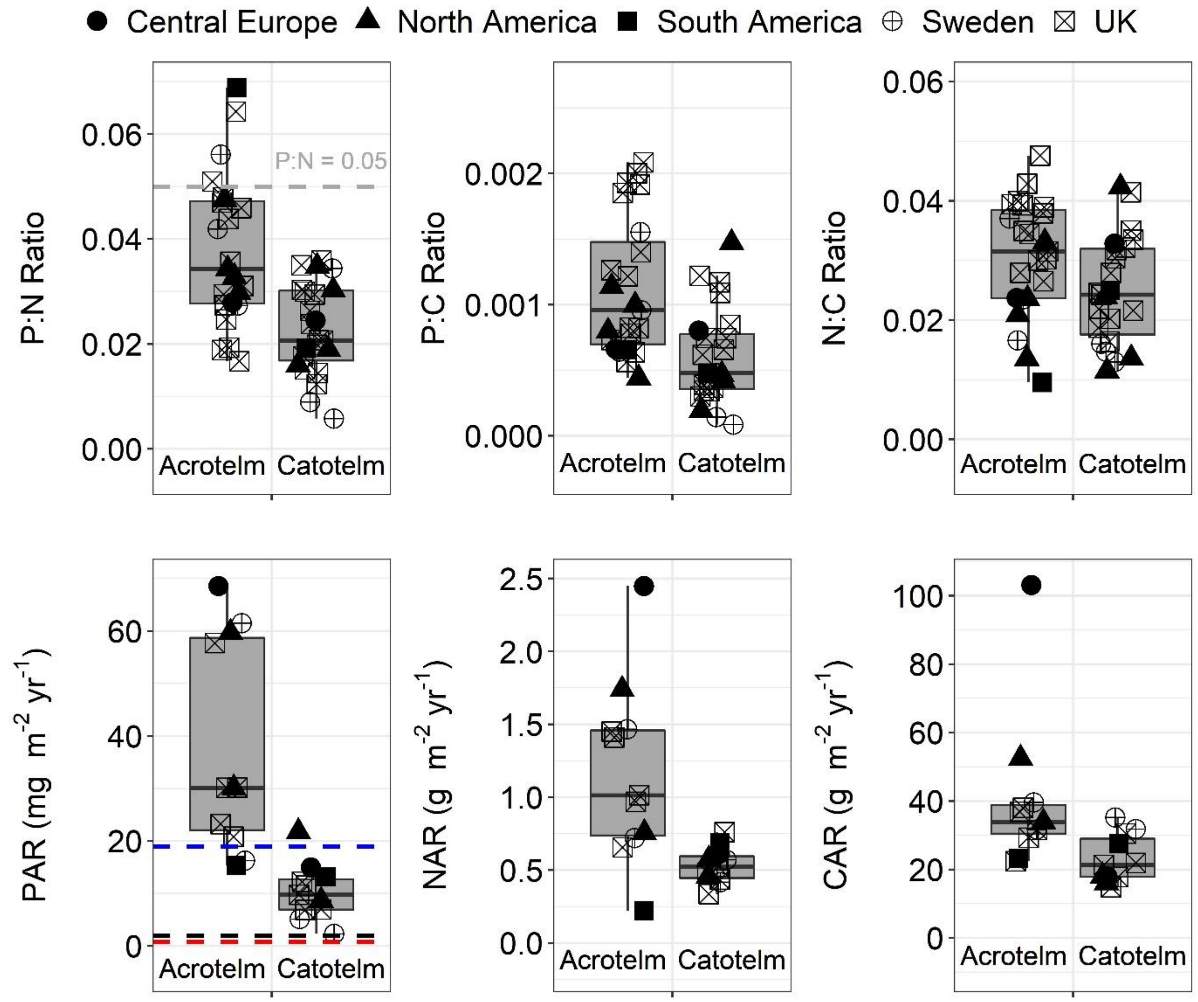


Figure 3. Mean single-site stoichiometric ratios and accumulation rates measured in the acrotelm and catotelm at 23 mid-latitude peatlands. Horizontal offsets between points are solely for visualisation. Mean P:C, P:N and N:C stoichiometric ratios in catotelm peat are 0.0006, 0.023 and 0.024, respectively, 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[52,53] (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[54,55]. Horizontal dashed lines on the PAR plot are modelled values of present-day (black) and pre-industrial (red) atmospheric deposition from Brahney et al[48] (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.[45] (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 mineral dust contribution. This holds true throughout the Holocene (Supplemental Figure 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 bogs[43].

Nutrients and carbon accumulate in the catotelm significantly more slowly ($p < 0.05$) than the acrotelm (Figure 3) because of anoxic conditions 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 dating resolution. The range of P, N and C is 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 PAR shows a similar degree of variance between sites (RSD = 52%). Phosphorus also shows the largest difference between mean acrotelm and catotelm accumulation rates (3.5 times lower). The marked narrowing of inter-site NAR in the catotelm suggests spatial variability in N inputs (deposition plus fixation) are balanced by N loss via denitrification and hydrological export. This suggests that differences in P inputs at individual sites may persist through the surface-to-catotelm biogeochemical cascade.

The effects of spatially variable P burial on peatland functioning is illustrated by the striking relationship we observe between PAR and N:C ratio in the catotelm ($r^2 = 0.91$, $p < 0.001$; Figure 4A). Down-core N:C is commonly interpreted as a decomposition proxy because carbon is preferentially lost as organic matter passes through the acrotelm[56–59]. PAR is negatively correlated with ΔN:C (the difference between acrotelm and catotelm N:C ratios), which is likely to be more representative of relative decay intensity during peatland development (Figure 4B). Bogs that accumulate more P are characterised by higher N:C (lower ΔN:C) ratios, indicative of more efficient decomposition. We propose this is a widespread and largely overlooked biogeochemical characteristic of ombrotrophic peatlands, whereby P supply influences the intensity of organic matter decay by promoting N fixation[33–37] and microbial activity[24–26]. Furthermore, bogs that experience proportionally greater burial of P relative to N seem to sequester carbon more slowly ($r^2 = 0.64$, $p = 0.003$; Figure 4C), showcasing a direct link between nutrient stoichiometry and long-term carbon cycling. CAR is not significantly correlated with P or N in isolation in the acrotelm and catotelm ($p > 0.1$, Supplemental Table 3). This differs from studies of single sites, which find strong, positive correlations between down-core nutrient and C profiles[16,19,60]. Furthermore, we do not find evidence of a climatic effect on short- or long-term C sequestration (regressions of mean annual precipitation and temperature on acrotelm and catotelm CAR: $r^2 < 0.04$, $p > 0.1$) across the sites in our database.

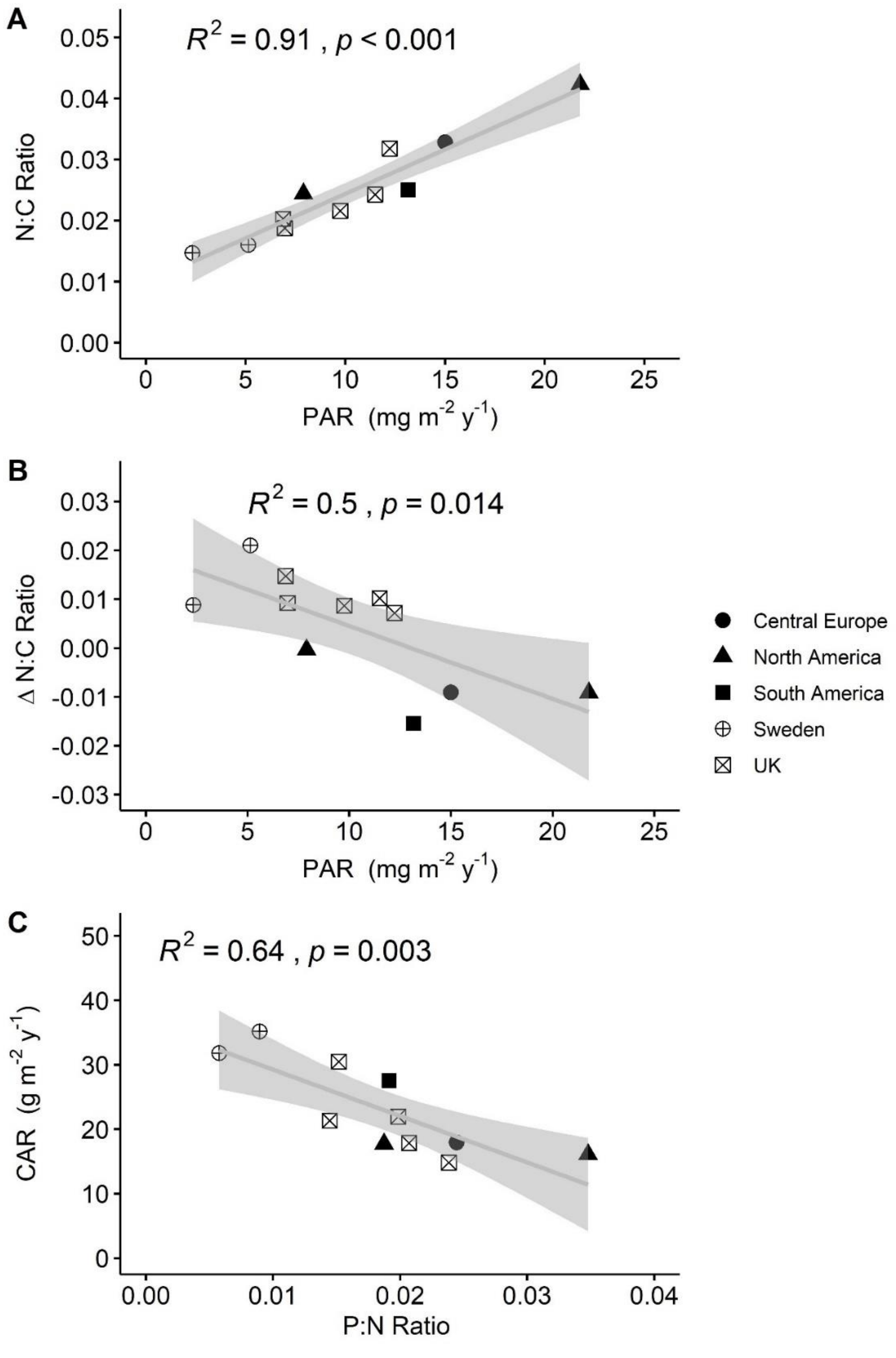


Figure 4. Comparisons of catotelm phosphorus and carbon accumulation with catotelm stochiometric indicators from eleven sites. A) PAR in the catotelm is strongly correlated with the N:C ratio, interpreted as a decomposition proxy, across all sites. Each datapoint represents the mean value for catotelm peat at each dated site. B) PAR in the catotelm is negatively correlated with the ΔN:C ratio, the difference between N:C in the acrotelm and catotelm. Lower ΔN:C indicates proportionally greater decomposition and loss of carbon 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 carbon burial. PAR and NAR in isolation are only weakly correlated with CAR (r^2 = 0.26 and 0.05, p > 0.1).

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 (Figure 5). The scarcity of P deposition monitoring stations means regional median values are used, 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 ΔN:C ratios). This leads to slower average rates of carbon burial over the Holocene (Figure 5D; bivariate regression of P deposition on catotelm ARCA across individual sites yields $r^2 = 0.58$, $p < 0.01$; Supplemental Table 3). 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 (Figure 5C). We acknowledge modern measured P deposition may differ from past rates, influenced for example by land-cover change and intensity of biomass burning. Nevertheless, we are aware of no independent estimates of regional atmospheric P emission and deposition through the Holocene and Brahney et al.[48] model pre-industrial global atmospheric P transfers using fluxes directly proportional to 20th-century values. The spatial pattern presented in Figure 5 represents a different biogeochemical response to that of large, abrupt injections of nutrients, such as local dust input[20] or tephra[19,21]. These events stimulate rapid carbon 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 (Figures 3, 5) despite receiving episodic pulses of nutrient-enriched dust sourced locally during the mid-Holocene[20].

Data on pre-industrial atmospheric nutrient deposition are scarce, but catotelm PAR sets a firm lower limit on long-term P input because of recyling and retention in the acrotelm. This value exceeds modelled P deposition from long-distance mineral dust[44,48] at all sites (Figure 3) throughout the Holocene (Supplemental Figure 3). The modelled fine dust fraction explains, on average, 30 ± 9 % of catotelm PAR (mean ± SE). The site in central Europe accumulates P rapidly and receives higher mineral dust input (45% of catotelm PAR) from the Sahara[61]. 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 mineral dust. Global P sources and sinks remain quite poorly understood but biological inputs (plant fragments, bird strike, microorganisms) and dispersal from neighbouring ecosystems able to acquire P through mineral weathering are primary candidates[20,45,47]. 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.[45] brings P input and peat burial values more in line (P_{dep} = 76% of catotelm PAR), although these are large generalisations. Given the apparent importance of short-distance P inputs on long-term peatland functioning and carbon sequestration, there is a clear need to understand where bog P comes from at much greater spatial resolution.

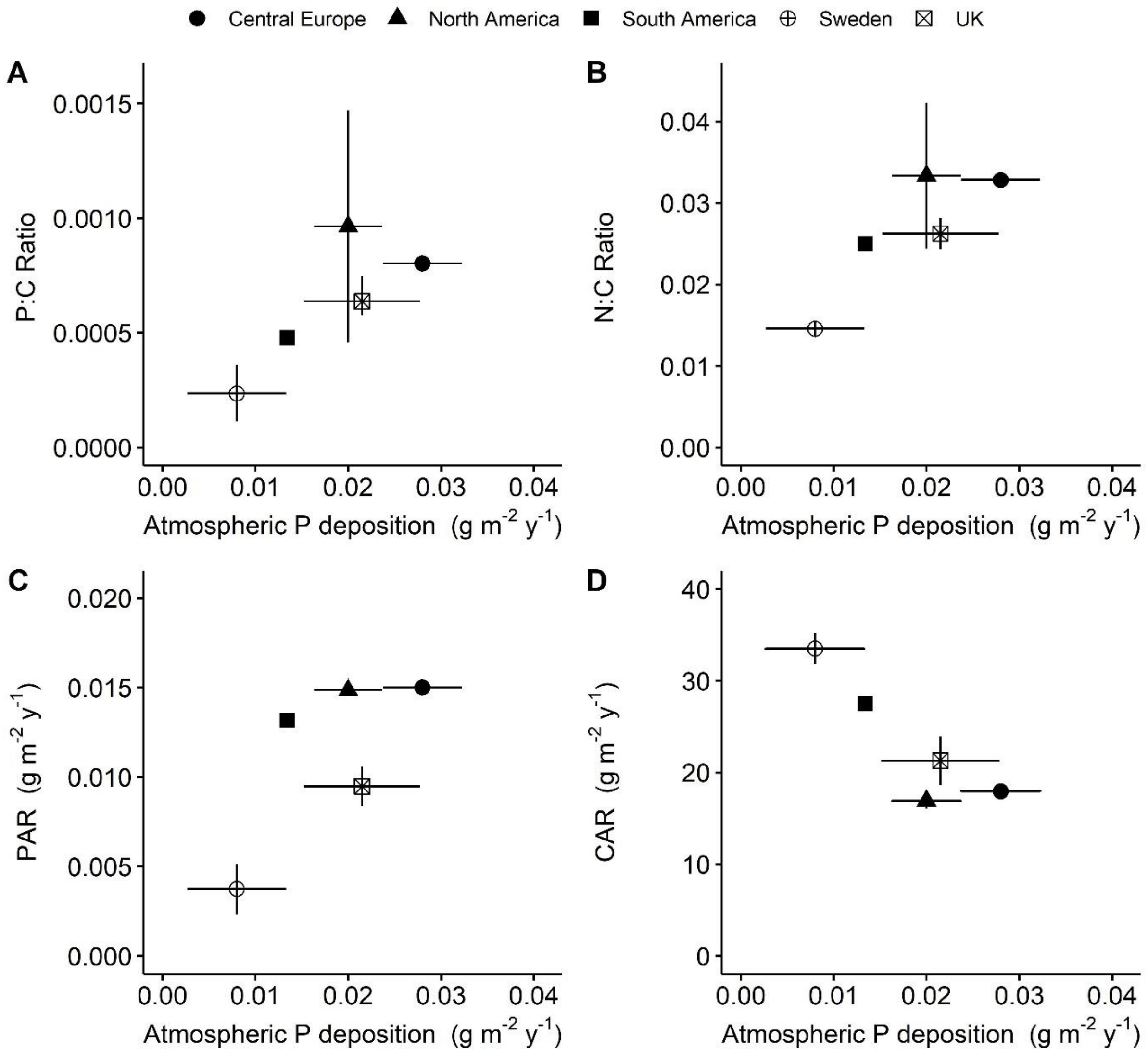


Figure 5. Comparisons of modern measured atmospheric phosphorus deposition and peatland catotelm stoichiometry and carbon burial. We find, as expected, a positive and negative association between P deposition and catotelm PAR (Figure 5C) and CAR (Figure 5D), respectively. Datapoints are regional medians ± standard error. Atmospheric P deposition (P_{dep}) represents the median of between 1 and 28 monitoring stations to account for local variance (see Figure 1 and Methods). Bars represent standard errors where more than one monitoring station was used. The y-intercept in Figure 5C is not significantly different from zero, meaning on average 60% of P_{dep} becomes permanently buried in the catotelm and 40% is lost via hydrological runoff.

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 northern[1] and southern hemisphere[62] 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 Ontario, Canada.

The carbon accumulation rate at our site in the southern hemisphere (Skyring, Chile: 22 gC m^{-2} y^{-1}) is the same as existing estimates for all peatlands across southerly mid-latitudes[62], so we consider Skyring stoichiometry to be appropriately representative of hemispheric values. The global soil P budget is stacked with uncertain inputs and outputs[63,64] but two independent central estimates using our database suggest approximately 1.7% of global soil P is stored in mid-latitude ombrotrophic peatlands (Supplemental Table 4), albeit with high uncertainty.

Discussion

We find evidence supporting the hypothesis that the amount of P supplied to a bog over the Holocene influences its biogeochemical cascade between surface vegetation and catotelm peat. Specifically, sites in Europe and the Americas with higher P input are characterised by more efficient decomposition (higher N:C and lower ΔN:C ratios) and lower long-term carbon burial. We propose the following governing mechanisms (Figure 6), informed by published experimental evidence and recognising that controlled field manipulations spannings hours to years do not necessarily replicate long-term dynamics.

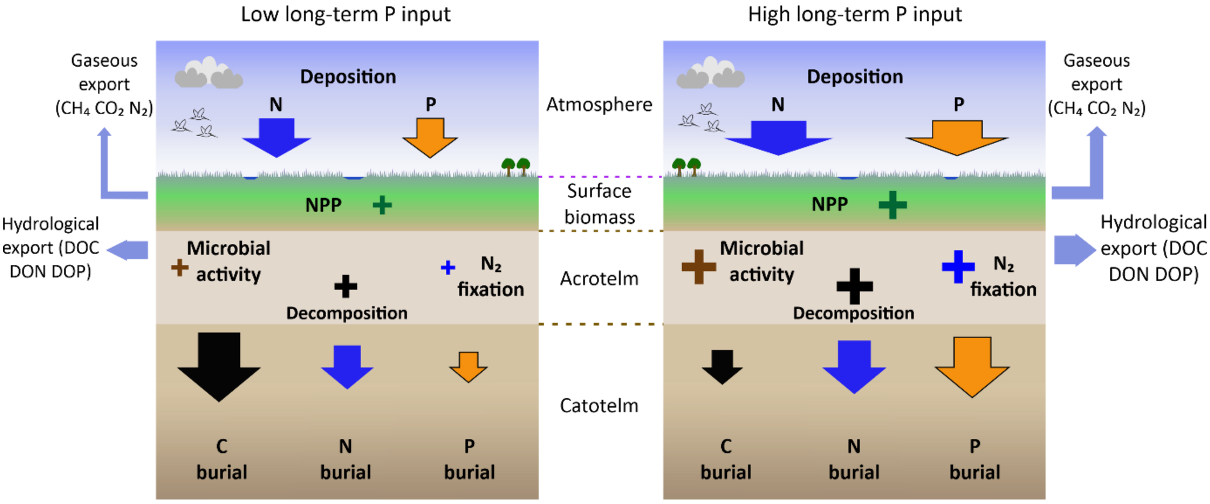


Figure 6. Conceptual model illustrating the biogeochemical cascade in regions of low and high long-term P input. We propose that bogs in receipt of more P over the course of their development will, on average, bury less carbon because losses of C from the acrotelm are proportionally greater than the 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.

The amount of carbon buried in a particular bog reflects the difference between primary productivity and decomposition. Greater P supply should promote biomass production because mosses efficiently trap and utilise aerial nutrient inputs[22,23]. At the same time, elevated nutrient deposition increases the size, activity and diversity of the microbial pool in the acrotelm[24,25]. Lin et al.[26] showed P availability imposes a limiting effect on the microbial communities of decomposers and N_2 fixers, and there is strong evidence for direct effects of

P on N_2 fixation rates from fertilisation plots[33–35,38] and surface peat measurements[36]. This would accelerate decomposition of the more recalcitrant compounds that usually become buried in the catotelm. The inverse correlation between P input and CAR (Figures 4A; 5D; 6) suggests fertilisation promotes more rapid decomposition relative to biomass production, thereby slowing long-term carbon sequestration. Spatial variation in long-term P deposition appears to be an important and widely overlooked driver of peatland functioning.

P:C and P:N profiles move progressively further from that of source vegetation with depth and time (Figure 2), in contrast to other terrestrial ecoystems[50], and catotelm peats fall below the stoichiometric threshold for P limitation[54,55] at all sites (Figure 3). This suggests that P is the nutrient most in demand by living biomass and that continuous recycling of within the acrotelm is necessary to sustain peat growth. The mechanisms by which P is retained are not fully understood but root, shoot or mycorrhizal uptake are probably involved[11,16,17]. While N, P and occasionally K can each limit the growth of contemporary peatlands[65], our data indicate P availability has had an important long-term effect on productivity and peatland development over Holocene timescales. Other drivers of carbon dynamics include competitive displacement of *Sphagnum* by vascular plants, which has been widely reported under enhanced 20th-century N deposition[30,39,66,67]. Vascular plants decompose more efficiently but peat stratigraphic profiles in our database are dominated by *Sphagnum* throughout the Holocene. Variability in water table depth also influences peat decomposition[9], but our database consists of long-term site-specific averages, which should smooth hydroclimate effects.

We assert that the potential impacts of P and N deposition on peatland biogeochemical cycling should be considered in combination rather than in isolation. Profound effects of anthropogenically-enhanced 20th-century N deposition on peatland plant structure[39,67] and carbon storage[68] have been widely observed. Wang et al.[17] postulated peatlands bury P at approximately the same rate as P inputs, whilst acknowledging deposition rates in eastern Canada range between 7 and 34 mg m^{-2} y^{-1}. From our data (Figures 4 and 5), such a degree of long-term spatial variability has substantial implications for decomposition and carbon cycling at individual peat bogs. Our findings also showcase the need to better understand local and regional sources of phosphorus and its short-distance transport mechanisms[45,47].

The capacity of peatlands to continue as a strong carbon sink is a key uncertainty in climate model projections, which is attributed to complex temperature and vegetation feedbacks[69–71]. The influence of phosphorus has not yet been considered. Elevated atmospheric P loading has altered the trophic status of lakes around the world in recent decades[48] and Gorham and Janssens[18] attributed long-term P content in North American bogs to agricultural dust deposition. More recently, Wang et al.[46] proposed up to half of modern P deposition can be attributed to combustion sources. If this is accurate[48], such a dramatic post-industrial acceleration of P input has substantial implications for long-term peatland carbon dynamics. Furthermore, the virtual absence of modern P deposition data across the high latitudes (Supplemental Figure 4) makes it difficult to judge the importance of altered nutrient supply relative to amplified warming and permafrost melting for the stability of northern peatlands, or indeed how these factors may interact. Our findings raise important questions as to whether anthropogenic perturbations to P cycling may be sufficient to alter the trajectory of mid-latitude peatland development and slow carbon sequestration.

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; (iii) Measurements must extend into the catotelm. Where the depth of the acrotelm/catotelm boundary was not stated in a publication, we assumed a depth of 40 cm[52,53]. We acknowledge the shift 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 the acrotelm/catotelm boundary may be time-transgressive[72,73]. A 40-cm subdivision is a pragmatic choice that is informed by literature, should return accurate accumulation rates over thousands of years and facilitates statistical comparisons of biogeochemical dynamics in the acrotelm and 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. Where it was not stated, reported P and N concentrations were assumed to represent the total fraction. Owing to the different research questions being asked in each original publication, reconstructions of peat decomposition rates, botanical assemblage or water table depth are not available for each site.

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 (Supplemental Table 1). These required reliable measurements of carbon 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 ^{14}C ages while Seno Skyring (Chile) was dated using radiocarbon and tephra. The chronology for each UK site is based on three ^{14}C ages, including one basal date, while the age-depth model for Etang de la Gruère (France) combines a ^{210}Pb profile with one basal ^{14}C age. These chronological resolutions may overlook some decadal or centennial-scale variability, but long-term aggregated fluxes should be accurate.

A further 13 sites reported P, N and C concentrations to suitable depth but lacked chronological information (Table 1). Concentrations are reported as the mean of each sample extracted from either the acrotelm or 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.[14] 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 papers by independent research groups were merged. This was justified by cross-correlating stoichiometric values reported in both papers (see Methods in Supplemental Information).

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 carbon 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’ (v0.2[74]) and ‘lmodel2’ (v1.7.3[75]). Output is plotted in the ‘ggplot2’ environment (v3.1.1[76]).

Modern measurements of P deposition

We extracted direct measurements of total P deposition from Tipping et al.[45] and Brahney et al.[48]. We decided to used regionally representative values because P_{dep} measured at monitoring stations within a 30-km radius vary by up to one order of magnitude. 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 (Figure 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 representive P_{dep} datapoints used in our analysis are based on between one and 28 monitoring stations.

References

1. Loisel, J. *et al.* A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. *The Holocene* **24**, 1028–1042 (2014).
2. Loisel, J. *et al.* Insights and issues with estimating northern peatland carbon stocks and fluxes since the Last Glacial Maximum. *Earth-Sci. Rev.* **165**, 59–80 (2017).
3. Yu, Z., Loisel, J., Brosseau, D. P., Beilman, D. W. & Hunt, S. J. Global peatland dynamics since the Last Glacial Maximum. *Geophys. Res. Lett.* **37**, (2010).
4. Scharlemann, J. P., Tanner, E. V., Hiederer, R. & Kapos, V. Global soil carbon: understanding and managing the largest terrestrial carbon pool. *Carbon Manag.* **5**, 81–91 (2014).
5. Chambers, F. M., Barber, K. E., Maddy, D. & Brew, J. A 5500-year proxy-climate and vegetation record from blanket mire at Talla Moss, Borders, Scotland. *The Holocene* **7**, 391–399 (1997).
6. Charman, D. J., Blundell, A., Chiverrell, R. C., Hendon, D. & Langdon, P. G. Compilation of non-annually resolved Holocene proxy climate records: stacked Holocene peatland palaeo-water table reconstructions from northern Britain. *Quat. Sci. Rev.* **25**, 336–350 (2006).

7. Swindles, G. T. *et al.* Widespread drying of European peatlands in recent centuries. *Nat. Geosci.* **12**, 922–928 (2019).
8. van der Linden, M. & van Geel, B. Late Holocene climate change and human impact recorded in a south Swedish ombrotrophic peat bog. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **240**, 649–667 (2006).
9. Clymo, R. S. The Limits to Peat Bog Growth. *Philos. Trans. R. Soc. B Biol. Sci.* **303**, 605–654 (1984).
10. Hessen, D. O., Ågren, G. I., Anderson, T. R., Elser, J. J. & de Ruiter, P. C. CARBON SEQUESTRATION IN ECOSYSTEMS: THE ROLE OF STOICHIOMETRY. *Ecology* **85**, 1179–1192 (2004).
11. Damman, A. W. H. Distribution and movement of elements in ombrotrophic peat bogs. *Oikos* **30**, 480–495 (1978).
12. Malmer, N. Patterns in the Growth and the Accumulation of Inorganic Constituents in the Sphagnum Cover on Ombrotrophic Bogs in Scandinavia. *Oikos* **53**, 105–120 (1988).
13. Charman, D. J. *et al.* Drivers of Holocene peatland carbon accumulation across a climate gradient in northeastern North America. *Quat. Sci. Rev.* **121**, 110–119 (2015).
14. Charman, D. J. *et al.* Climate-related changes in peatland carbon accumulation during the last millennium. *Biogeosciences* **10**, 929–944 (2013).
15. Beilman, D. W., MacDonald, G. M., Smith, L. C. & Reimer, P. J. Carbon accumulation in peatlands of West Siberia over the last 2000 years. *Glob. Biogeochem. Cycles* **23**, (2009).
16. Wang, M., Moore, T. R., Talbot, J. & Richard, P. J. H. The cascade of C:N:P stoichiometry in an ombrotrophic peatland: from plants to peat. *Environ. Res. Lett.* **9**, 024003 (2014).
17. Wang, M., Moore, T. R., Talbot, J. & Riley, J. L. The stoichiometry of carbon and nutrients in peat formation. *Glob. Biogeochem. Cycles* **29**, 113–121 (2015).
18. Gorham, E. & Janssens, J. a. The distribution and accumulation of chemical elements in five peat cores from the mid-continent to the eastern coast of North America. *Wetlands* **25**, 259–278 (2005).

19. Ratcliffe, J. L. *et al.* Rapid carbon accumulation in a peatland following Late Holocene tephra deposition, New Zealand. *Quat. Sci. Rev.* **246**, 106505 (2020).

20. Kylander, M. E. *et al.* Mineral dust as a driver of carbon accumulation in northern latitudes. 1–10 (2018) doi:10.1038/s41598-018-25162-9.

21. Hughes, P. D. M. *et al.* The impact of high tephra loading on late-Holocene carbon accumulation and vegetation succession in peatland communities. *Quat. Sci. Rev.* **67**, 160–175 (2013).

22. Limpens, J., Berendse, F. & Klees, H. How Phosphorus Availability Affects the Impact of Nitrogen Deposition on Sphagnum and Vascular Plants in Bogs. *Ecosystems* **7**, 793–804 (2004).

23. Fritz, C. *et al.* Nutrient additions in pristine Patagonian Sphagnum bog vegetation: Can phosphorus addition alleviate (the effects of) increased nitrogen loads. *Plant Biol.* **14**, 491–499 (2012).

24. White, J. R. & Reddy, K. R. Influence of Phosphorus Loading on Organic Nitrogen Mineralization of Everglades Soils. *Soil Sci. Soc. Am. J.* **64**, 1525 (2000).

25. Bledsoe, R. B., Goodwillie, C. & Peralta, A. L. *Long-term nutrient enrichment of an oligotroph-dominated wetland increases bacterial diversity in bulk soils and plant rhizospheres*. http://biorxiv.org/lookup/doi/10.1101/2020.01.08.899781 (2020) doi:10.1101/2020.01.08.899781.

26. Lin, X. *et al.* Microbial community stratification linked to utilization of carbohydrates and phosphorus limitation in a Boreal Peatland at Marcell Experimental Forest, Minnesota, USA. *Appl. Environ. Microbiol.* **80**, 3518–3530 (2014).

27. Sjögersten, S., Cheesman, A. W., Lopez, O. & Turner, B. L. Biogeochemical processes along a nutrient gradient in a tropical ombrotrophic peatland. *Biogeochemistry* **104**, 147–163 (2011).

28. Cheesman, A. W., Turner, B. L. & Ramesh Reddy, K. Soil Phosphorus Forms along a Strong Nutrient Gradient in a Tropical Ombrotrophic Wetland. *Soil Sci. Soc. Am. J.* **76**, 1496–1506 (2012).

29. Kivimäki, S. K., Sheppard, L. J., Leith, I. D. & Grace, J. Long-term enhanced nitrogen deposition increases ecosystem respiration and carbon loss from a Sphagnum bog in the Scottish Borders. *Environ. Exp. Bot.* **90**, 53–61 (2013).
30. Moore, T. R., Knorr, K.-H., Thompson, L., Roy, C. & Bubier, J. L. The effect of long-term fertilization on peat in an ombrotrophic bog. *Geoderma* **343**, 176–186 (2019).
31. Hill, B. H. *et al.* Ecoenzymatic stoichiometry and microbial processing of organic matter in northern bogs and fens reveals a common P-limitation between peatland types. *Biogeochemistry* **120**, 203–224 (2014).
32. Vitousek, P. M. *et al.* Towards an ecological understanding of biological nitrogen fixation. in *The Nitrogen Cycle at Regional to Global Scales* (eds. Boyer, E. W. & Howarth, R. W.) 1–45 (Springer Netherlands, 2002). doi:10.1007/978-94-017-3405-9_1.
33. Larmola, T. *et al.* Methanotrophy induces nitrogen fixation during peatland development. *Proc. Natl. Acad. Sci.* **111**, 734–739 (2014).
34. van den Elzen, E. *et al.* Symbiosis revisited: phosphorus and acid buffering stimulate N<sub>2</sub> fixation but not <i>Sphagnum</i> growth. *Biogeosciences* **14**, 1111–1122 (2017).
35. van den Elzen, E., Bengtsson, F., Fritz, C., Rydin, H. & Lamers, L. P. M. Variation in symbiotic N2 fixation rates among Sphagnum mosses. *PLOS ONE* **15**, e0228383 (2020).
36. Toberman, H. *et al.* Dependence of ombrotrophic peat nitrogen on phosphorus and climate. *Biogeochemistry* **125**, 11–20 (2015).
37. Basilier, K., Granhall, U., Stenström, T.-A. & Stenstrom, T.-A. Nitrogen Fixation in Wet Minerotrophic Moss Communities of a Subarctic Mire. *Oikos* **31**, 236 (1978).
38. Kox, M. A. R. *et al.* Effects of nitrogen fertilization on diazotrophic activity of microorganisms associated with Sphagnum magellanicum. *Plant Soil* **406**, 83–100 (2016).
39. Bubier, J. L., Moore, T. R. & Bledzki, L. A. Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog. *Glob. Change Biol.* **13**, 1168–1186 (2007).

40. Fritz, C., Lamers, L. P. M., Riaz, M., Berg, L. J. L. van den & Elzenga, T. J. T. M. Sphagnum Mosses - Masters of Efficient N-Uptake while Avoiding Intoxication. *PLOS ONE* **9**, e79991 (2014).
41. Morris, P. J. *et al.* Global peatland initiation driven by regionally asynchronous warming. *Proc. Natl. Acad. Sci.* **115**, 4851–4856 (2018).
42. Schillereff, D. N. *et al.* Long-term macronutrient stoichiometry of UK ombrotrophic peatlands. *Sci. Total Environ.* **572**, 1561–1572 (2016).
43. Sjöström, J. K. *et al.* Paleodust deposition and peat accumulation rates – Bog size matters. *Chem. Geol.* **554**, 119795 (2020).
44. Mahowald, N. *et al.* Global distribution of atmospheric phosphorus sources, concentrations and deposition rates, and anthropogenic impacts. *Glob. Biogeochem. Cycles* **22**, 1–19 (2008).
45. Tipping, E. *et al.* Atmospheric deposition of phosphorus to land and freshwater. *Env. Sci Process. Impacts* **16**, 1608–1617 (2014).
46. Wang, R. *et al.* Significant contribution of combustion-related emissions to the atmospheric phosphorus budget. *Nat. Geosci.* **8**, 48–54 (2015).
47. Newman, E. I. Phosphorus Inputs to Terrestrial Ecosystems. *J. Ecol.* **83**, 713–726 (1995).
48. Brahney, J., Mahowald, N., Ward, D. S., Ballantyne, A. P. & Neff, J. C. Is atmospheric phosphorus pollution altering global alpine Lake stoichiometry? *Glob. Biogeochem. Cycles* 1369–1383 (2015) doi:10.1002/2013GB004593.Received.
49. Xu, J., Morris, P. J., Liu, J. & Holden, J. PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. *Catena* **160**, 134–140 (2018).
50. Vitousek, P. M., Porder, S., Houlton, B. Z. & Chadwick, O. A. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. *Ecol. Appl.* **20**, 5–15 (2010).
51. Worrall, F., Moody, C. S., Clay, G. D., Burt, T. P. & Rose, R. The total phosphorus budget of a peat-covered catchment. *J. Geophys. Res. Biogeosciences* **121**, 1814–1828 (2016).
52. Limpens, J., Heijmans, M. M. P. D. & Berendse, F. The Nitrogen Cycle in Boreal Peatlands. *Boreal Peatl. Ecosyst.* **188**, 195–230 (2006).

53. Rydin, H. & Jeglum, J. *The Biology of Peatlands*. (Oxford University Press, 2013).

54. Güsewell, S. N : P ratios in terrestrial plants: variation and functional significance: Tansley review. *New Phytol.* **164**, 243–266 (2004).

55. Bedford, B. L., Walbridge, M. R. & Aldous, A. Patterns in Nutrient Availability and Plant Diversity of Temperate North American Wetlands. *Ecology* **80**, 2151–2169 (1999).

56. Kuhry, P. & Vitt, D. H. Fossil Carbon/Nitrogen Ratios as a Measure of Peat Decomposition. *Ecology* **77**, 271–275 (1996).

57. Kuhry, P., Halsey, L. A., Bayley, S. E. & Vitt, D. H. Peatland development in relation to Holocene climatic change in Manitoba and Saskatchewan (Canada). *Can. J. Earth Sci.* **29**, 1070–1090 (1992).

58. Malmer, N. & Wallén, B. Input rates, decay losses and accumulation rates of carbon in bogs during the last millennium: internal processes and environmental changes. *The Holocene* **14**, 111–117 (2004).

59. Malmer, N. & Holm, E. Variation in the C/N-Quotient of Peat in Relation to Decomposition Rate and Age Determination with 210 Pb. *Oikos* **43**, 171–182 (1984).

60. Larsson, A., Segerstrom, U., Laudon, H. & Nilsson, M. Holocene carbon and nitrogen accumulation rates and contemporary carbon export in discharge: a study from a boreal fen catchment. *Holocene* 48–48 (2016) doi:10.1177/0959683616675936.

61. Lequy, É., Legout, A., Conil, S. & Turpault, M. P. Aeolian dust deposition rates in Northern French forests and inputs to their biogeochemical cycles. *Atmos. Environ.* **80**, 281–289 (2013).

62. Yu, Z. Holocene carbon flux histories of the world's peatlands: Global carbon-cycle implications. *The Holocene* **21**, 761–774 (2011).

63. Schlesinger, W. H. & Bernhardt, E. S. *Biogeochemistry*. (Elsevier, Amsterdam, 2013).

64. Peñuelas, J. *et al.* Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. *Nat. Commun.* **4**, (2013).

65. Bridgham, S. D., Pastor, J., Janssens, J. A., Chapin, C. & Malterer, T. J. Multiple limiting gradients in peatlands: A call for a new paradigm. *Wetlands* **16**, 45–65 (1996).

66. Berendse, F. *et al.* Raised atmospheric CO2 levels and increased N deposition cause shifts in plant species composition and production in Sphagnum bogs. *Glob. Change Biol.* **7**, 591–598 (2001).

67. Juutinen, S., Bubier, J. L. & Moore, T. R. Responses of Vegetation and Ecosystem CO2 Exchange to 9 Years of Nutrient Addition at Mer Bleue Bog. *Ecosystems* **13**, 874–887 (2010).

68. Bragazza, L. *et al.* Atmospheric nitrogen deposition promotes carbon loss from peat bogs. *Proc. Natl. Acad. Sci.* **103**, 19386–19389 (2006).

69. Gallego-Sala, A. V. *et al.* Latitudinal limits to the predicted increase of the peatland carbon sink with warming. *Nat. Clim. Change* **8**, 907–913 (2018).

70. Wilson, R. M. *et al.* Stability of peatland carbon to rising temperatures. *Nat. Commun.* **7**, 13723 (2016).

71. Dorrepaal, E. *et al.* Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature* **460**, 616–619 (2009).

72. Clymo, R. S. & Bryant, C. L. Diffusion and mass flow of dissolved carbon dioxide, methane, and dissolved organic carbon in a 7-m deep raised peat bog. *Geochim. Cosmochim. Acta* **72**, 2048–2066 (2008).

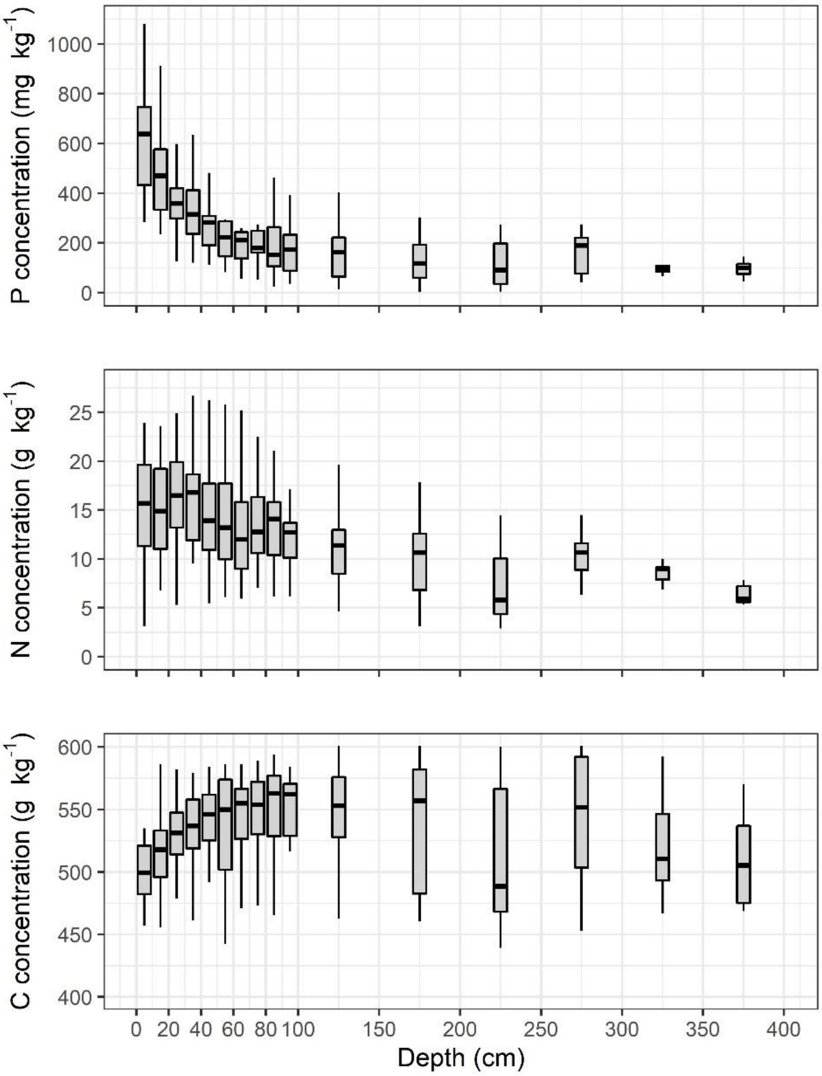
73. Morris, P. J., Waddington, J. M., Benscoter, B. W. & Turetsky, M. R. Conceptual frameworks in peatland ecohydrology: looking beyond the two-layered (acrotelm-catotelm) model. *Ecohydrology* **4**, 1–11 (2011).

74. Kassambara, A. ggpubr. (2019).

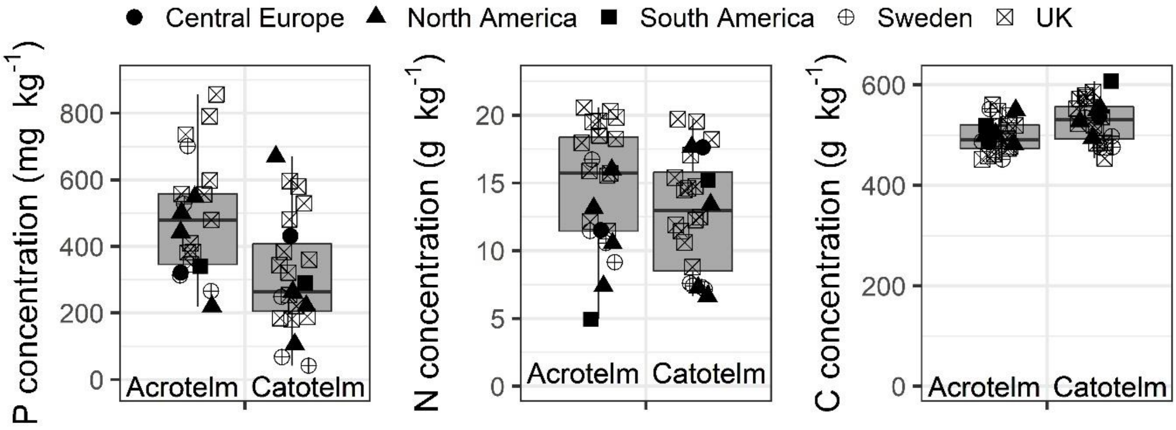
75. Oksanen, J. Package ‘lmodel2’. (2018).

76. Wickham, H. ggplot2. (2016).

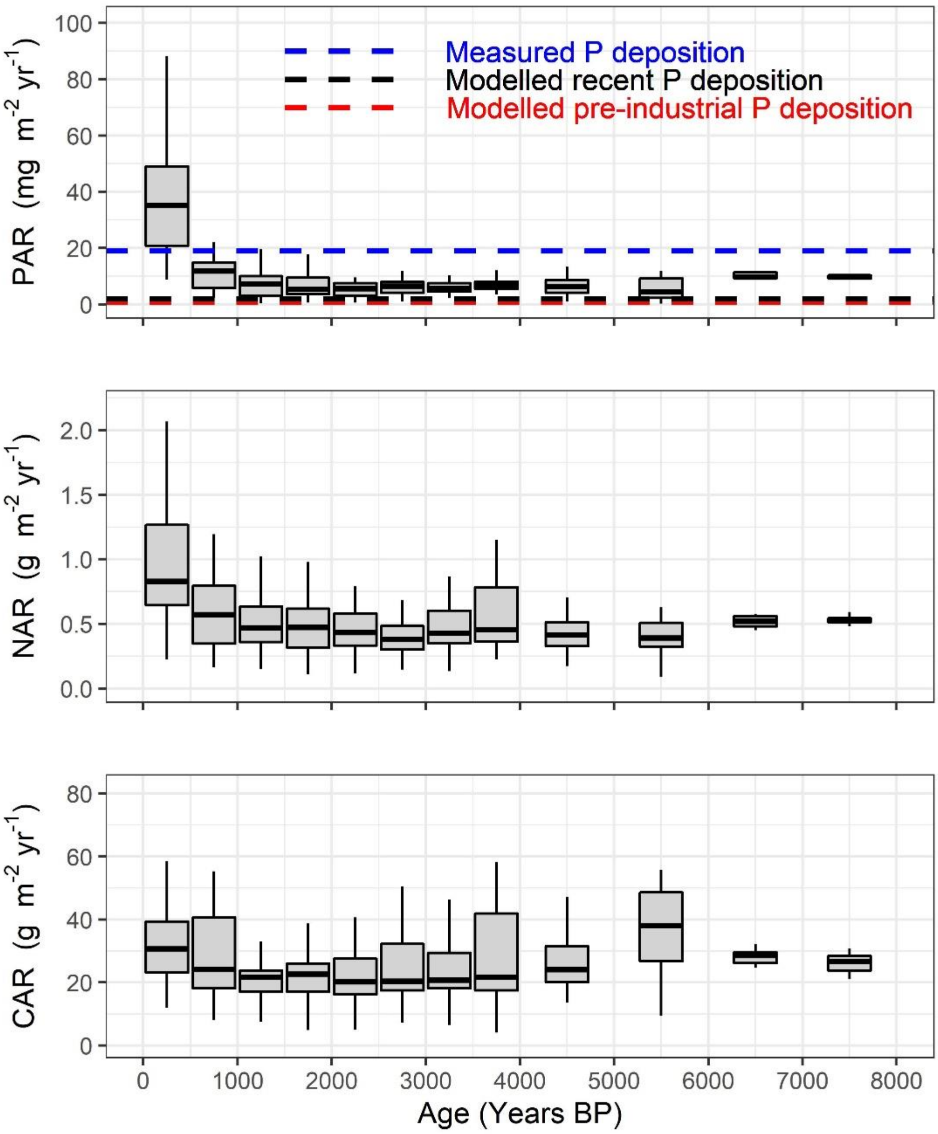
SUPPLEMENTAL INFORMATION



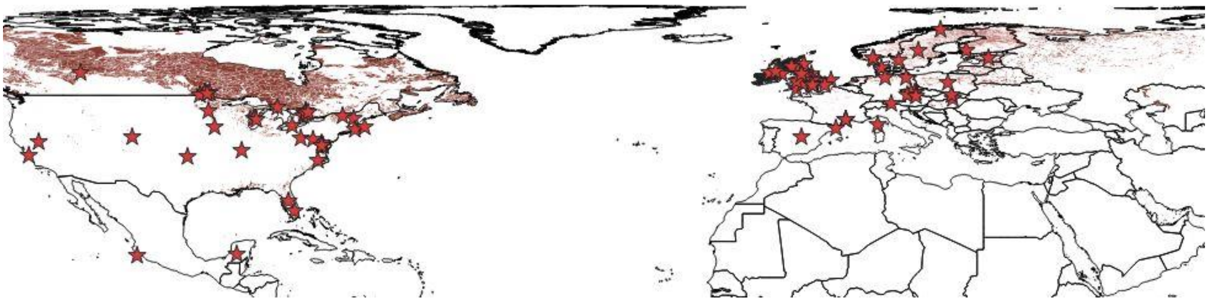
Supplemental Figure 1. Nutrient concentration against depth for all sites. Box-and-whiskers represent all samples grouped into 10-cm intervals between 0 and 100-cm depth and then 50-cm intervals.



Supplemental Figure 2. Mean single-site concentrations measured in the acrotelm and catotelm at 23 mid-latitude peatlands. Horizontal offsets between point markers are solely for visualisation.



Supplemental Figure 3. Phosphorus, nitrogen and carbon accumulation rates through time for all sites. Boxes represent all samples grouped into 500-year (0 - 4000 yr BP) and 1000-year (4000 – 8000 yr BP) intervals. Modelled P deposition (black and red dashed horizontal lines) are the mean value for each grid cell[1] containing a site in our database. The measured P deposition rate (blue line) is a mean calculated from the nearest atmospheric deposition sampling site[2] to each bog in our database.



Supplemental Figure 4. Coverage of mid-latitude peatlands in the northern hemisphere by direct measurements of P deposition. Red stars mark P deposition monitoring stations compiled by Tipping et al.[2]. Peatland extent (brown shaded area) is taken from the PEATMAP of Xu et al.[3]. The paucity of measurement sites in northern Canada and Siberia is stark and represents a notable gap in our capacity to judge potential effects of spatially variable P deposition on past and future peat carbon dynamics.

Supplemental Table 1. Location and peat profile overview. Forsinard, Glensaugh, Moor House, Migneint and Dartmoor are reported as mean values from triplicate cores. Basal ages are reported as calibrated years before present (yr BP), rounded to the nearest 10 years. Superscript numerals in the acrotelm/catotelm boundary column denote the reference stating a depth different from 40-cm (1 = Leifeld et al.[4]; 2 = Knorr et al.[5]; 3 = Wang et al.[6]; 4 = Tfaily et al.[7]; 5 = Damman[8].

Site name	**Country**	**Latitude (°N)**	**Longitude (°E)**	**Peat core depth (cm)**	**Basal age (yr BP)**	**Depth of acrotelm / catotelm boundary (cm)**
Accumulation rates						
Forsinard	UK (Scotland)	58.369	-3.895	290	7370	40
Glensaugh	UK (Scotland)	56.895	-2.541	120	3920	40
Moor House	UK (England)	54.683	-2.267	190	5300	40
Migneint	UK (Wales)	52.969	-3.819	123	5880	40
Dartmoor	UK (England)	50.495	-3.950	90	2640	40
Etang de la Gruère	Switzerland	47.240	7.049	102	2110	25[1]
Draftinge Mosse	Sweden	57.108	13.715	241	5430	40

Davids Mosse	Sweden	56.986	13.009	413	4450	40
Seno Skyring	Chile	-52.509	-72.127	120	1850	30[2]
Mer Bleue	Canada	45.400	-75.500	260	6440	50[3]
Marcell Experimental Forest	USA	47.503	-93.483	190	7920	30[4]
Concentrations only						
Creag Dubh	UK (Scotland)	57.435	-4.000	80		40
Rubha Mor	UK (Scotland)	58.080	-6.752	100		40
Meall Chrombaig	UK (Scotland)	56.900	-3.643	85		40
Queensberry	UK (Scotland)	55.284	-3.576	105		40
Sheilhope Hill	UK (Scotland)	55.567	-3.267	120		40
Tom Roiseneabhat	UK (Scotland)	58.271	-6.437	105		40
Cock Hill	UK (Scotland)	56.910	-2.658	75		35
Carn nan Aighean	UK (Scotland)	57.781	-4.692	50		40
Dun Mount	UK (Scotland)	57.267	-2.996	100		40
Red Lake	USA	48.150	-92.370	323		40
Carmanville	Canada	49.220	-54.190	418		40
Traneröds Mosse	Sweden	56.060	13.100	400		35[5]

Supplemental Table 2. Nutrient and carbon accumulation rates, concentrations and stoichiometric ratios for each site in the data base. Mean values for the acrotelm and catotelm at each site are reported separately.

Site	PAR (mg m^{-2} y^{-1})	NAR (g m^{-2} y^{-1})	CAR (g m^{-2} y^{-1})	P (mg kg^{-1})	N (g kg^{-1})	C (g kg^{-1})	P:N Ratio	P:C Ratio	N:C Ratio
Acrotelm									
Forsinard	30.2	1.41	38.0	382.0	19.8	548.4	0.017	0.00056	0.035
Glensaugh	23.2	0.66	22.4	556.1	15.7	539.7	0.031	0.00082	0.028
Moor House	30.1	0.97	31.6	480.0	15.9	522.2	0.027	0.00083	0.030
Migneint	57.7	1.45	36.9	791.2	20.6	519.3	0.036	0.00140	0.039
Dartmoor	20.8	1.01	29.3	408.9	19.6	560.7	0.019	0.00064	0.034
Etang de la Gruère	68.6	2.45	103.1	321.9	11.5	485.6	0.028	0.00066	0.024
Draftinge Mosse	16.3	0.72	31.7	313.1	11.5	487.8	0.027	0.00064	0.023
Davids Mosse	61.5	1.47	39.6	701.5	16.7	451.9	0.042	0.00155	0.037
Seno Skyring	15.3	0.22	23.3	340.5	5.0	519.4	0.069	0.00066	0.010
Mer Bleue	26.1	0.69	30.5	420.7	13.2	550.0	0.033	0.00076	0.024
Marcell	21.8	1.74	52.5	548.0	16.0	481.8	0.032	0.00114	0.033
Red Lake				500.8	10.5	503.2	0.048	0.00100	0.021
Carmanville				220.2	7.4	498.8	0.030	0.00044	0.014
Creag Dubh				383.6	15.55	493.25	0.025	0.00078	0.032
Rubha Mor				598	20.3	473.7	0.029	0.00126	0.043
Meall Chrombaig				994.8	22.7	477.3	0.044	0.00208	0.048
Queensberry				856.75	18.25	462.9	0.047	0.00185	0.039
Sheilhope Hill				934.75	19.5	487.8	0.048	0.00192	0.040
Tom Roiseneabhat				346.3	17.95	473.65	0.019	0.00073	0.038
Cock Hill				943	18.5	471.1	0.051	0.00200	0.039
Carn nan Aighean				557.5	12.15	458.55	0.046	0.00122	0.026

Dun Mount				736.3	11.45	381.75	0.064	0.00193	0.030
Traneröds Mosse				528.6	9.16	552.2	0.056	0.00096	0.017
Number of sites	11	11	11	23	23	23	23	23	23
Average (± SE)	37.2 ± 6.1	1.16 ± 0.19	39.9 ± 6.8	559.3 ± 46.9	15.2 ± 0.97	495.7 ± 8.5	0.038 ± 0.003	0.00112 ± 0.00011	0.031 ± 0.002
Minimum	15.3	0.22	22.4	220.2	4.95	381.8	0.017	0.00044	0.010
Maximum	68.6	2.45	103.1	994.8	22.7	560.7	0.069	0.00208	0.048

Site	**PAR (mg m^{-2} y^{-1})**	**NAR (g m^{-2} y^{-1})**	**CAR (g m^{-2} y^{-1})**	**P (mg kg^{-1})**	**N (g kg^{-1})**	**C (g kg^{-1})**	**P:N Ratio**	**P:C Ratio**	**N:C Ratio**
Catotelm									
Forsinard	6.9	0.44	21.3	184.7	12.3	586.2	0.014	0.00030	0.020
Glensaugh	7.0	0.34	17.8	220.5	10.6	564.3	0.021	0.00039	0.019
Moor House	9.8	0.48	21.9	254.0	12.5	572.5	0.020	0.00043	0.021
Migneint	12.2	0.52	14.8	481.5	19.5	578.8	0.024	0.00074	0.032
Dartmoor	11.5	0.76	30.5	221.8	14.5	575.6	0.015	0.00037	0.024
Etang de la Gruère	15	0.61	18.0	431.5	17.5	537.6	0.024	0.00080	0.033
Draftinge Mosse	2.3	0.42	31.2	42.3	7.3	497.8	0.006	0.00008	0.015
Davids Mosse	5.1	0.57	35.2	68.0	7.6	475.1	0.009	0.00014	0.016
Seno Skyring	13.2	0.69	27.5	291.0	15.2	608.0	0.019	0.00048	0.025
Mer Bleue	7.9	0.45	17.7	251.2	13.4	550.0	0.019	0.00046	0.024
Marcell	21.8	0.57	16.1	670.0	17.6	494.8	0.035	0.00147	0.042
Red Lake				220.8	7.3	527.7	0.030	0.00042	0.014
Carmanville				106.4	6.6	554.1	0.016	0.00019	0.011

Creag Dubh				182.1	8.8	536.1	0.021	0.00034	0.016
Rubha Mor				321.4	18.2	519.9	0.018	0.00062	0.035
Meall Chrombaig				579.6	19.7	475.4	0.029	0.00122	0.041
Queensberry				596.5	17.1	509.3	0.035	0.00117	0.033
Sheilhope Hill				343.5	11.5	522.8	0.030	0.00066	0.022
Tom Roiseneabhat				189.9	15.4	552.3	0.012	0.00034	0.028
Cock Hill				529.5	14.8	485.4	0.036	0.00109	0.030
Carn nan Aighean				383.8	14.6	453.8	0.026	0.00085	0.032
Dun Mount				360.7	11.9	483.9	0.030	0.00075	0.025
Traneröds Mosse				248.9	8.8	535.3	0.034	0.00048	0.013
Number of sites	11	11	11	23	23	23	23	23	23
Average (± SE)	10.2 ± 1.6	0.53 ± 0.04	23.0 ± 2.1	327.1 ± 37.1	13.4 ± 0.9	530.0 ± 8.6	0.023 ± 0.002	0.00060 ± 0.00008	0.025 ± 0.002
Minimum	2.3	0.34	14.8	42.3	6.5	453.8	0.006	0.00008	0.011
Maximum	21.8	0.76	35.2	670.0	19.7	608.0	0.036	0.00147	0.042

Supplemental Table 3. Linear statistical associations between stoichiometry, accumulation rate and P deposition across the dipthotelmic cascade. All regression coefficients are non-significant except those reported in bold **(*p < 0.05).**

		Acrotelm						
		P_{dep}	PAR	NAR	CAR	P:N	P:C	N:C
Catotelm	P_{dep}	-------	0.06	0.21	0.22	0.18	0.08	0.03
	PAR	0.26	0.22	0.19	0.20	0.04	0.01	<0.01
	NAR	<0.01	0.03	0.03	0.05	0.09	<0.01	0.01
	CAR	**0.58***	0.09	0.09	0.08	0.03	<0.01	0.01
	P:N	**0.42***	0.21	0.15	0.14	0.01	0.02	<0.01
	P:C	0.24	0.31	0.25	0.21	0.01	0.05	<0.01
	N:C	0.30	0.32	0.28	0.26	<0.01	0.03	<0.01

Supplemental Table 4. Estimates of the total global soil P store that has accumulated in mid-latitude peatlands. The upper calculation uses an estimate of labile (organic) P in the upper 50 cm of global soils[64].

Variable (unit)	**Mean (range)**	**Source**
P held in mid-latitude peatlands (Gt)	0.23 (0.04-0.64)	Our database
Labile P in global soils (Gt)	13.8	[64]
Proportion of global soil P held in peatlands (%)	**1.67** (0.29-4.6)	Our calculation
	Central estimate (range)	
P in global soils (Gt)	120 (40 – 200)	[65]
Labile fraction in global soils (%)	11 (2 – 20)	[65]
Proportion of global soil P held in peatlands (%)	**1.74** (0.1-80)	Our calculation

Supplemental methods

Compiling the P:N:C database

United Kingdom

Phosphorus, N and C were calculated as long-term mean concentrations for Dartmoor, Migneint, Moor House, Glensaugh and Forsinard and first reported in Schillereff et al.[9]. Cores at these sites were extracted in 2014, sub-sampled at 10-cm intervals and milled to fine, homogeneous powders. Phosphorus content was measured colorimetrically using a Seal Analytical AQ2 discrete analyser after digestion in H2SO4/H2O2. After drying at 105 °C, carbon and nitrogen were determined on an Elementar Vario-EL analyser using an ISO17025 accredited method. Peat bulk density was determined for each 10-cm slice and age-depth models are based on three radiocarbon ages near the top, middle and base of the ombrotropic stage in each profile. The raw measurements and chronological data are available through the NERC Environmental Information Data Centre[10].

The additional sites in Scotland were also reported in Schillereff et al.[9] and represent sites classed as deep blanket peat in the National Soil Inventory of Scotland[11]. This Inventory constituents 721 soil profiles sampled between 2007 and 2009. The ten deep blanket peat sites are 90-120 cm in thickness with at least three sampling depths per profile. Bulk density was measured in triplicate, C and N were determined on Flash EA 1112 Series Elemental Analyser connected via a Conflo III to a DeltaPlus XP isotope ratio mass spectrometer (all Thermo Finnigan, Bremen, Germany) and P was determined colorometrically following fusion with NaOH.

Sweden

The David Mosse and Draftinge Mosse records were retrieved in 2014, subsampled at 1-cm intervals, and freeze dried. The bulk density was calculated by weighing each subsample and recording the surface area. Phosphorous concentrations were retrieved through WD-XRF analysis while C and N was acquired by a Carlo Erba NC2500 elemental analyser. The chronology is based on AMS radiocarbon dates (Davids Mosse: n=6, Draftinge Mosse, n=16). The results for Draftinge Mosse are reported in Sjöström et al.[12] and the data is accessed through https://bolin.su.se/data/sjostrom-2020. Results for Davids Mosse are unpublished.

Central Europe

Peat depths, bulk density and carbon and nitrogen concentrations were reported by Leifeld et al.[4]. Elemental composition was measured on an elemental analyser (Hekatech, Germany). These were merged with measurements of phosphorus concentrations, analysed by wavelength-dispersive X-ray fluorescence spectroscopy (Geological Institute, Ukrainian Academy of Sciences, Kiev), and chronological information from Steinmann and Shotyk[13]. The age-depth model is constructed from a ^{210}Pb profile, a pollen marker horizon and a radiocarbon age from the basal sample.

North America

Phosporus, N and C concentrations and accumulation rates for Mer Bleue, Ontario, were taken from Wang et al.[6]. This site has been a focus of peatland fertilisation experiments for decades[14,15]. The peat stratigraphy and age-depth models for the cores used in this study were originally reported in Frolking et al.[16]. Acrotelm depth was reported at 50-cm. Total C and N were determined by combustion on a LECO CNS 2000 elemental analyser and total P was measured colorometrically by the ammonium molybdate-ascorbic acid method on a Lachat QuikChem AE flow-injection auto-analyser (Lachat Instruments, Milwaukee, WI), after digestion in concentrated sulfuric acid and hydrogen peroxide with selenium and lithium sulfate as catalysts.

The Marcell Experimental Forest has been the subject of numerous studies on peatland biogeochemistry[7,17–19]. Obtaining separate values required multiple sources to be merged. Bulk density estimations for two cores from the S1 bog[7] were merged with chronological information for equivalent depths from Wieder et al.[20] to obtain a mass accumulation rate curve. Tfaily et al.[7] also reported C and N content, measured via combustion on a ThermoFinnegan Delta XP elemental analyser. Mean P accumulation rate for the acrotelm and catotelm were the products of their respective mass accumulation rates and P concentration reported by Hill et al.[18]. Total P was measured via the molybdate-ascorbic acid protocol. Acrotelm thickness was reported as 30 cm[7].

Nutrient and C concentrations for two other sites in North America were originally reported by Gorham and Janssens[21]. These *Sphagnum*-dominated, ombrotrophic peatlands span a transect from the mid-continent to the Atlantic maritime zone. Peat cores were originally obtained in 1981 or 1982 and sub-sampled into 10-cm sections. Radiocarbon dates were obtained at approximately 1-m intervals in each core. Elemental composition was determined by ICP-ES and neutron-activation analysis while C was measured with a LECO analyser and N was determined by the Kjeldahl procedure. Mean concentrations and accumulation rates were weighted by the bulk density of each sample.

South America

Carbon, N and P measurements were tracked down for a single ombrotrophic bog in Patagonia (Skyring; Table S1). C, N and P concentrations for three separate depth intervals were reported by Knorr et al.[5]. Total P was measured by wavelength-dispersive X-ray fluorescence spectroscopy (WD-XRF), using a Rigaku Primus ZSX II (Rigaku, Tokyo, Japan), calibrated with certified reference materials. Total N and C were measured on an elemental analyzer (EA 3000, HekaTech, Wegberg, Germany) coupled to an isotope ratio mass spectrometer (NU instruments, Wrexham, UK), calibrated with IAEA standards. The values of Knorr et al. were multiplied by peat mass accumulation rates for the same site determined by Biester et al.[22].

References for Supplementary Information

1. Brahney, J., Mahowald, N., Ward, D. S., Ballantyne, A. P. & Neff, J. C. Is atmospheric phosphorus pollution altering global alpine Lake stoichiometry? *Glob. Biogeochem. Cycles* 1369–1383 (2015) doi:10.1002/2013GB004593.Received.
2. Tipping, E. *et al.* Atmospheric deposition of phosphorus to land and freshwater. *Env. Sci Process. Impacts* **16**, 1608–1617 (2014).
3. Xu, J., Morris, P. J., Liu, J. & Holden, J. PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. *CATENA* **160**, 134–140 (2018).
4. Leifeld, J., Steffens, M. & Galego-Sala, A. Sensitivity of peatland carbon loss to organic matter quality. *Geophys. Res. Lett.* **39**, 1–6 (2012).

5. Knorr, K.-H., Horn, M. A. & Borken, W. Significant nonsymbiotic nitrogen fixation in Patagonian ombrotrophic bogs. *Glob. Change Biol.* (2014) doi:10.1111/gcb.12849.

6. Wang, M., Moore, T. R., Talbot, J. & Richard, P. J. H. The cascade of C:N:P stoichiometry in an ombrotrophic peatland: from plants to peat. *Environ. Res. Lett.* **9**, 024003 (2014).

7. Tfaily, M. M. *et al.* Organic matter transformation in the peat column at Marcell Experimental Forest: Humification and vertical stratification: Organic matter dynamics. *J. Geophys. Res. Biogeosciences* **119**, 661–675 (2014).

8. Damman, A. W. H. Distribution and movement of elements in ombrotrophic peat bogs. *Oikos* **30**, 480–495 (1978).

9. Schillereff, D. N. *et al.* Long-term macronutrient stoichiometry of UK ombrotrophic peatlands. *Sci. Total Environ.* **572**, 1561–1572 (2016).

10. Toberman, H. *et al. Peat survey in England, Scotland and Wales carried out during 2014 [LTLS] (Dataset)*. https://doi.org/10.5285/9305b068-f417-4659-9966-d9456f22c331 (2016).

11. Lilly, A., Bell, J., Hudson, G., Nolan, A. & Towers, W. *National Soil Inventory of Scotland 2007–2009: Profile description and soil sampling protocols. (NSIS_2).* (2011).

12. Sjöström, J. K. *et al.* Paleodust deposition and peat accumulation rates – Bog size matters. *Chem. Geol.* **554**, 119795 (2020).

13. Steinmann, P. & Shotyk, W. Geochemistry, mineralogy, and geochemical mass balance on major elements in two peat bog profiles (Jura Mountains, Switzerland). *Chem. Geol.* **138**, 25–53 (1997).

14. Moore, T. R., Knorr, K.-H., Thompson, L., Roy, C. & Bubier, J. L. The effect of long-term fertilization on peat in an ombrotrophic bog. *Geoderma* **343**, 176–186 (2019).

15. Moore, T. R. & Bubier, J. L. Plant and Soil Nitrogen in an Ombrotrophic Peatland, Southern Canada. *Ecosystems* **23**, 98–110 (2020).

16. Frolking, S. *et al.* A new model of Holocene peatland net primary production, decomposition, water balance, and peat accumulation. *Earth Syst. Dyn. Discuss.* **1**, 115–167 (2010).

17. Urban, N. R. & Eisenreich, S. J. Nitrogen cycling in a forested Minnesota bog. *Can. J. Bot.* **66**, 435–449 (1988).

18. Hill, B. H. *et al.* Ecoenzymatic stoichiometry and microbial processing of organic matter in northern bogs and fens reveals a common P-limitation between peatland types. *Biogeochemistry* **120**, 203–224 (2014).

19. Hill, B. H. *et al.* Comparisons of soil nitrogen mass balances for an ombrotrophic bog and a minerotrophic fen in northern Minnesota. *Sci. Total Environ.* **550**, 880–892 (2016).

20. Wieder, R. K., Nov�k, M., Schell, W. R. & Rhodes, T. Rates of peat accumulation over the past 200 years in fiveSphagnum-dominated peatlands in the United States. *J. Paleolimnol.* **12**, 35–47 (1994).

21. Gorham, E. & Janssens, J. a. The distribution and accumulation of chemical elements in five peat cores from the mid-continent to the eastern coast of North America. *Wetlands* **25**, 259–278 (2005).

22. Biester, H., Martinez-Cortizas, A., Birkenstock, S. & Kilian, R. Effect of peat decomposition and mass loss on historic mercury records in peat bogs from patagonia. *Environ. Sci. Technol.* **37**, 32–39 (2003).