Nitrogen-rich organic soils under warm well-drained conditions are global nitrous oxide emission hotspots

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Nitrous oxide (N\textsubscript{2}O) is a powerful greenhouse gas and the main driver of stratospheric ozone depletion. Since soils are the largest source of N\textsubscript{2}O, predicting soil response to changes in climate or land use is central to understanding and managing N\textsubscript{2}O. Here we find that N\textsubscript{2}O flux can be predicted by models incorporating soil nitrate concentration (\text{NO}_3^{-}), water content and temperature using a global field survey of N\textsubscript{2}O emissions and potential driving factors across a wide range of organic soils. N\textsubscript{2}O emissions increase with \text{NO}_3^{-} and follow a bell-shaped distribution with water content. Combining the two functions explains 72\% of N\textsubscript{2}O emission from all organic soils. Above 5 mg \text{NO}_3^{-}-N kg\textsuperscript{-1}, either draining wet soils or irrigating well-drained soils increases N\textsubscript{2}O emission by orders of magnitude. As soil temperature together with \text{NO}_3^{-} explains 69\% of N\textsubscript{2}O emission, tropical wetlands should be a priority for N\textsubscript{2}O management.
Organic soils make up more than one-tenth of the world’s soil nitrogen (N) pool and are a significant global source of the greenhouse gas nitrous oxide (N₂O). We do not fully understand the underlying microbial production and consumption processes and how these interact with environmental drivers such as the microclimate, physics, and chemistry of the soil. N₂O can be emitted as a by-product of both incomplete nitrification and incomplete denitrification. Under anaerobic conditions, N is primarily conserved in organic compounds, and nitrification (the conversion of ammonium (NH₄⁺) to NO₃⁻) is limited to the rooting zone or is absent. The normally low availability of NO₃⁻ also restricts rates of denitrification (the conversion of NO₃⁻ to N₂) in anaerobic soil; if sufficient NO₃⁻ is present but oxygen remains restricted, denitrification may go to completion, producing atmospheric N₂. Reduction of soil moisture promotes mineralisation of organic N to NH₄⁺, which can be nitrified to NO₃⁻, and produces the partially-denitrified conditions that are conducive to incomplete denitrification, a major source of N₂O. N₂O emission has been both positively and negatively correlated with soil moisture, as water-filled pore space (WFPS) or volumetric water content (VWC) depending upon water status; intermediate levels of around 50–80% WFPS or VWC appear to be optimal for N₂O production.

Increases in soil temperature normally enhance N₂O production up to about 24 °C, where bacterial denitrification reaches an optimum above which N₂O eflux drops. However, denitrifier communities may adapt to higher temperatures, leading to further increases in N₂O emissions. A review of laboratory and field studies shows inconsistent relationships between temperature and N₂O emissions from strongly positive to negative, illustrating that temperature alone cannot explain N₂O fluxes but must be considered in the context of other drivers, especially soil moisture. At near-zero soil temperatures, the freeze-thaw effect may produce significant amounts of N₂O.

As growing population pressure has increased the extent of fertilised and drained organic soil, nitrogen-rich organic soils will become increasingly important global N₂O sources. Currently N₂O contributes 12% of CO₂-equivalent GHG emissions from land use in tropics. Quantifying the influence of both increasing rates of land drainage and climate change on organic soil N₂O fluxes is thus critically important. However, emission factors used to assess N₂O fluxes from different land uses and ecosystems are usually simple proportions of the application rate of fertiliser (or atmospheric reactive N deposition for non-cultivated soils) and broad land-use categories; these models also do not take into account climate-related changes. Thus we lack an inclusive model to quantify the potential of organic soils to be a globally important source of N₂O. To address this challenge we undertook a standardised global survey of in situ N₂O fluxes from organic soils, together with ancillary measurements of key drivers, to derive a model of N₂O emissions that would be applicable to a wide range of biomes and environmental conditions. We find that N₂O emission from organic soils increases with rising soil NO₃⁻, follows a bell-shaped distribution with soil moisture, and increases with rising soil temperature. This emphasises the importance of warm drained fertile soils to climate change.
Results

Principal component analysis. Site-mean N₂O fluxes by study region superimposed on a global organic-soil map are shown in Fig. 1. The principal component analysis (PCA) differentiated tropical sites from temperate and boreal ones, and low agricultural-intensity sites (index 0 and 1) from arable sites (index 3) (p < 0.05; Fig. 2a, b). Soil NO₃⁻ was positively related to N₂O emission; VWC and water table were strongly negatively correlated with N₂O emissions, and C/N, C, and organic matter were less strongly negatively correlated with N₂O emissions, and soil temperature was positively related to N₂O emissions (Fig. 2c). Soil-available P was orthogonal to the N₂O-flux vectors, indicating no correlation. The difference between N₂O emissions from drained and natural sites was clear in all three major climate types (Supplementary Table 1).

Global models. Of the 18 parameters assessed (Supplementary Data 1), soil NO₃⁻ was the strongest predictor of site-mean N₂O, explaining 60% of the variation in log N₂O flux (Fig. 3a). The generalised additive model (GAM) trend was similar to concave log-log quadratic. Inclusion of site-mean VWC (Fig. 3b) raised the explanatory power of the multiple-regression GAM to 72% (n = 58; R² = 0.72; p < 0.001; Eq. (1); Fig. 4a). The regression surface was similar to a convex paraboloid with an apex at approximately 50% VWC:

$$\log(N_2O - N + 1) = 0.035 + 0.39 \log(NO_3 - N) + 0.025(\log(NO_3 - N))^2 + 4.8 \text{VWC} - 5.2 \text{VWC}^2$$  \hspace{1cm} (1)

In an independent comparison of the model with published data, relative N₂O emissions were represented well. The relationship between the mean N₂O fluxes (relative to the maximum value in the respective external data set) and VWC was best described by a bell-shaped GAM regression curve (R² = 0.78; p < 0.001; Fig. 5) similar to the VWC component of our global model (Fig. 3b). Both curves peaked at around 50% soil moisture.

Both our model and the literature support the idea that fluctuation around the intermediate VWC (~0.5 m³ m⁻³) creates variability in the oxygen content within the soil profile. That, in turn, stimulates mineralisation and nitrification which contribute to higher NO₃⁻ content9,51,52. Intermediate VWC also promotes incomplete denitrification, in agreement with early conceptualisations25,40. Previous regional-scale studies28,33–35 and experiments9,51,52. The maximum N₂O emission at the intermediate VWC means that both wetting from lower moisture values and drying from higher moisture will increase N₂O emissions. At a VWC of ~0.8 m³ m⁻³, oxygen concentration in the pore water is 5–9% of saturation, which is low enough to trigger N₂O production but insufficient for complete denitrification9,51,52.

There was no significant relationship between N₂O flux and NH₄⁻N among our observations (p = 0.79), suggesting that denitrification was probably the main source of N₂O emissions rather than nitrification. Only one site (Tasmania drained fen 2) directly received mineral fertiliser, whereas the nitrate in the other 57 sites originated from livestock and natural sources such as nitrification, atmospheric deposition, runoff and groundwater. Thus our global model describes N₂O emission due to grazing and naturally transported nitrate.

We found only a weak relationship between N₂O fluxes and soil temperature (40 cm–depth temperature log GAM R² = 0.21, p < 0.001; Fig. 3c). The soil temperatures normalised to local annual air-temperature maxima gave even lower correlation values (e.g. with temperature at 40 cm–depth log GAM R² = 0.09, p = 0.018). This may have been partially due to the short time span of our measurements per site. However, that is consistent with the meta-analysis of published data in eleven papers showing no correlation between long-term N₂O fluxes and soil temperature17,24,31,32,34,35–38. The test for an upper boundary59 in our temperature data was negative (p > 0.05). Therefore we accepted the H₀ hypothesis that our data are from a bivariate normal process and so the envelope of the data points does not represent a boundary. This also suggests that the high N₂O fluxes were measured in soils where temperature was not the limiting factor. A multiple-regression GAM model containing soil temperature at 40 cm depth and log NO₃⁻...
explained 69% of log N₂O fluxes \((n = 58; R^2 = 0.69; p < 0.001; Eq. (2); Fig. 4b):\)

\[
\log(N_2O-N + 1) = -0.15 - 0.50 \log NO_3^- - N \\
+ 0.10 (\log NO_3^- - N)^2 \\
+ 0.036^\circ C + 1.9 \times 10^{-5} ^\circ C^2
\]

Within our drained sites (Supplementary Data 1; \(n = 27\)) the temperature relationship was somewhat stronger \((R^2 = 0.27; p < 0.0078; Fig. 3c)\). This shows that organic soils exposed to warmer conditions, such as in the tropics, can act as N₂O-emission hotspots where soil moisture is optimal (Fig. 3b) and NO₃⁻ is above a threshold of 5 mg N kg⁻¹ (Fig. 3a).

Because we sampled each site for only a few days and that we visited temperate and boreal sites during the growing seasons this study was not designed to detect the effect of seasonal or synoptic-scale variation of temperature, soil nitrate, and other factors within each site. Thus our global models are only applicable to estimate daily N₂O emissions based on instantaneous environmental conditions at organic-soil sites. Annual-average N₂O emissions at sites under a seasonal climate may be
more difficult to draw from our model. Yet the model could be useful to estimate N2O emissions at sites under a lack of seasonal variation in environmental conditions such as the humid tropical climate. Upscaling our three tropical sites with intensive land use (the Malaysian oil palm plantation, and the Myanmar and Uganda arable sites; Supplementary Data 1) to a year’s duration and comparing them with the special default emission values (EF2) in IPCC Guidelines 2006 for tropical organic soils60 (16 kg N2O-N ha−1 y−1, range 5–48 kg ha−1 y−1) gave us the following results. For the Malaysian site, soil temperature was 27–30 °C, the mean emission rate was 294.3 ± s.e.m. within the respective soil-moisture class. The curve is the GAM regression (k = 3) between average relative N2O fluxes and VWC. The light blue area marks the 95% confidence limits of the regression line regimes than heretofore developed. This highlights the importance of soil nitrate, moisture, and temperature in organic soils as significant global contributors to climate change and stratospheric ozone depletion. Our global-scale models show that constantly high soil moisture results in low N2O emissions, whereas drainage creates fluctuation around the intermediate soil moisture and thus increases N2O emissions from organic soils. The temperature effect on N2O emissions emphasises the importance of considering the warm fertile soils in the global N2O budget. The implication of this work is that wetland conservation should be a priority for climate change mitigation, particularly given the evidence for future increases in the magnitude and frequency of summer droughts65. The anticipated large N2O emissions from N-rich drained organic soils can be mitigated through wetland conservation and restoration, and through appropriate soil management, such as reduced tillage, nutrient management and improved crop rotations66. These have been implemented to some extent in developed countries but need to be further expanded and extended, as a matter of urgency, to tropical and sub-tropical regions.

Methods

Study sites. Our global soil- and gas-sampling campaign was conducted during the vegetation periods between August 2011 and March 2017, following a standard protocol. We sampled 58 organic-soil sites using criteria for organic soils (>12% soil carbon content in the upper 0.1 m) adapted from the FAO World Reference Base65. Pools of soil in 23 regions throughout the A (rainy tropical), C (temperate), and D (boreal) climates of the Köppen classification (Fig. 1; Supplementary Data 1). Both natural and artificially drained sites were identified, based on the proximity of drainage ditches, water table height, and characteristic vegetation. The hydrology and trophic status of the natural sites ranged from groundwater-fed swamps and fens to ombrotrophic peat bogs. We measured the most important environmental drivers that were possible.

Field and laboratory measurements. Within each region, we established sites to capture the full range of environmental conditions as described above. The depth of the topsoil organic horizon ranged from 0.1 to 6 m across the sites. Land use ranged from natural mire and swamp forest to managed grassland and arable land. A four-grade agricultural-intensity index was used to quantify the effect of land conversion: 0—no agricultural land use (natural mire, swamp, or bog forest), 1—moderate grazing or mowing (more than once a year), and 3—arable land (directly fertilised or unfertilised). The agricultural intensity index was estimated based on observation and contacts with site managers and local researchers.

Fig. 5 Relative N2O fluxes versus volumetric water content (VWC) in 11 published annual time series. The N2O fluxes are scaled to the maximum value measured at each respective site. The dots and whiskers are average ± s.e.m. within the respective soil-moisture class. The curve is the GAM regression (k = 3) between average relative N2O fluxes and VWC. The light blue area marks the 95% confidence limits of the regression line.

Other potential drivers. The logarithm of C:N ratio, a common scalar explanatory variable used to predict N2O emissions65, was correlated with N2O emissions (R2 = 0.16; p = 0.001; Supplementary Fig. 1) but was not significant in a model that contained NO3 −. Agricultural intensity explained 25% of the variability in N2O fluxes (log GAM R2 = 0.25; p < 0.001), but again was not significant in a model containing NO3 − and VWC as proximal controllers of N2O emission. The effect of agriculture on N2O emissions was mainly related to cultivation (Fig. 2b). We could detect no significant difference between N2O emissions from agriculturally unused sites and pastures or hay fields. Thus non-agricultural sources of elevated N (e.g. from chronically elevated atmospheric N deposition), and lower soil water content (e.g. reductions in precipitation) would likely have a similar impact on N2O emissions as agricultural fertilisation and drainage.

Discussion

This is the first time that simple, robust global models of N2O emissions driven by nitrate, moisture, and temperature of organic soils have been identified. It is notable that the models encompass temperate, continental, and tropical biomes. Our findings provide more accurate models of the drivers of N2O emissions from organic soils across a wide range of biomes and management
In the laboratory, plant-available phosphorus (P) was determined on a FiaStar5000 flow-injection analyser (KCl extractable). Plant-available potassium (K) was determined from the same solution by the flame-photometric method, and plant-available magnesium (Mg) was determined from a 100-mL NH₄-acetate solution with a titanium-yellow reagent on the flow-injection analyser. Available calcium (Ca) was analysed using the same solution by the flame-photometrical method. Soil pH was determined from a 1 N KCl solution. Soil NH₄-N and NO₃-N were determined on a 2 M KCl extract of soil by flow-injection analysis. Total nitrogen and carbon contents of oven-dry samples were determined using a dry-combustion method on a varioMAX CNS elemental analyser. The organic-matter content of oven-dry soil (SOM) was determined by loss on ignition at 360 °C. We determined gross water content (GWC) as the difference between the fresh and oven-dry weight divided by the oven-dry weight. Bulk density was determined as follows:

\[ BD = \frac{D_{\text{om}} - D_{\text{bm}}}{(\text{SOM} \cdot D_{\text{om}} + (1 - \text{SOM}) \cdot D_{\text{bm}})} \]

where:

- \( BD \) is bulk density, g cm\(^{-3} \)
- \( D_{\text{om}} \) is the empirically determined bulk density of the mineral fraction (2.65 g cm\(^{-3} \))
- \( D_{\text{bm}} \) is the empirically determined bulk density of the organic fraction (0.305–0.23 g cm\(^{-3} \) according to the von Post humification scale), and
- SOM is the organic content of the oven-dry soil, g g\(^{-1} \).

We determined VWC as:

\[ \text{VWC} = \text{GWC} \cdot \text{BD} \]

where:

- VWC is volumetric water content, m\(^3\) m\(^{-3} \)
- GWC is gravimetric water content, Mg Mg\(^{-1} \)
- BD is bulk density, Mg m\(^{-3} \)

For normalising the soil temperature to possible local optima we divided our soil-temperature measurements with the mean air temperature at the nearest weather station in the warmest month of the year (Klimatni Ekspert http://climexp.knmi.nl; Supplementary Data 1).

### Statistical analysis

Principal component analysis (PCA), Spearman’s rank correlation and stepwise multiple regression of site-mean efflux vs. the environmental parameters were used. The tests were run using both untransformed and log-transformed NO\(_2\) fluxes. Before the log-transformation, a constant value was added to all fluxes to account for negative values. Normality of the variables and the residuals was checked by the Shapiro–Wilk test. Neither the NO\(_2\) fluxes nor their logarithms were normally distributed (p < 0.05); this is a commonly reported issue with N\(_2\)O. Therefore only a nonparametric test such as Spearman’s rank correlation and generalised additive models (GAM) could be applied. We used the mgcv package of the R Project to calculate the GAM regressions using minimal smoothness (k = 3). We reported p-values (significance level p < 0.05) from the summaries of the GAM regressions produced by the summary.gam package of the R Project. We only reported GAM regressions when the residuals were normally distributed. As a presumption for the stepwise multiple regression, the independent variables were checked for GAM concurrency—but only reported multiple relations with a variance inflation factor < 10 between the independent variables. We tested the presence of a boundary in our data. The test compared the density of points in the region of the data set’s upper envelope to the expected density of the upper envelope of a bivariate normally distributed data set of the same size.

### Literature analysis

In order to compare our model with independent external data, we surveyed literature referenced in the Thomson Reuters Web of Science. The search terms were: N\(_2\)O and organic soil and nitrous oxide and organic soil. We only included publications that reported time series of at least a year under these criteria. The study sites were fairly evenly distributed throughout major organic soil regions of the world. Only three of these papers reported soil NO\(_3\) emissions. Therefore only a nonparametric test such as Spearman’s rank correlation and denitrification to N\(_2\)O production in peat, clay and loamy sand soils under different soil moisture conditions. Nutr. Cycl. Agroecosys. 70, 111–121 (2004).

### Data availability

The data reported in this paper are deposited in the PANGAEA repository https://doi.pangaea.de/10.1594/PANGAEA.885897.

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### References

1. Batjes, N. H. Total carbon and nitrogen in the soils of the world. Eur. J. Soil Sci. 65, 10–21 (2014).
2. Butterbach-Bahl, K., Baggs, E. M., Dannenmann, M., Kiese, R. & Zechmeister-Boltenstern, S. Nitrous oxide emissions from soils: how well do we understand the processes and their controls? Philos. Trans. R. Soc. Lond. B Biol. Sci. 368, 1621 (2013).
3. Jones, C. M., Stres, B., Rosenquist, M. & Hallin, S. Phylogenetic analysis of nitrite, nitric oxide, and nitrous oxide respiratory enzymes reveal a complex evolutionary history for denitrification. Mol. Biol. Evol. 25, 1955–1966 (2008).
4. Meng, W., Moore, T. R., Talbot, J. & Pierre, J. H. R. The cascade of CNP stoichiometry in an ombrotrophic peatland: from plants to peat. Environ. Res. Lett. 9, 024003 (2014).
5. Scherbak, L., Millar, N. & Robertson, G. P. Global metaanalysis of the nonlinear response of soil nitrous oxide (N\(_2\)O) emissions to fertilizer nitrogen. Proc. Natl Acad. Sci. USA 111, 9199–9204 (2014).
6. Meng, W., Moore, T. R., Talbot, J. & Riley, J. L. The stoichiometry of carbon and nutrients in peat formation. Glob. Biogeochem. Cycl. 29, 113–121 (2015).
7. Martikainen, P. J., Nykänen, H., Crill, P. & Silvola, J. Effect of a lowered water table on nitrous oxide fluxes from northern peatlands. Nature 366, 51–53 (1993).
8. Golovchenko, A. V., Tikhonova, E. E. & Zvyagintsev, D. G. Abundance, biomass, structure, and activity of the microbial complexes of minerotrophic and ombrotrophic peatlands. Microbiology 76, 650–657 (2007).
9. Rubol, S., Silver, W. L. & Bellin, A. Hydrologic control on edox and nitrogen dynamics in a peatland soil. Sci. Total Environ. 432, 37–46 (2012).
10. Clayton, H., McTaggart, I. P., Parker, J., Swan, L. & Smith, K. A. Nitrous oxide emissions from fertilised grassland: a 2-year study of the effects of N fertiliser form and environmental conditions. Biol. Fertil. Soils 25, 252–260 (2004).
11. Skiba, U. M., Sheppard, L. J., MacDonald, J. & Fowler, D. Some key environmental variables controlling nitrous oxide emissions from agricultural and semi-natural soils in Scotland. Atmos. Environ. 32, 3311–3320 (1998).
12. Dobbie, K. E., McTaggart, I. P. & Smith, K. A. Nitrous oxide emissions from intensive agricultural systems: variations between crops and seasons, key driving variables, and mean emission factors. J. Geophys. Res. Atmos. 104, 26891–26899 (1999).
13. Dobbie, K. E. & Smith, K. A. The effects of temperature, water-filled pore space and land use on N\(_2\)O emissions from an imperfectly drained gley soil. Eur. J. Soil Sci. 52, 667–673 (2001).
14. Dobbie, K. E. & Smith, K. A. Nitrous oxide emission factors for agricultural soils in Great Britain: the impact of soil water-filled pore space and other controlling variables. Glob. Change Biol. 9, 204–218 (2003).
15. Pihlatie, M., Simojoki, A., Esala, M. & Regina, K. Contribution of nitification and denitrification to N\(_2\)O production in peat, clay and loamy sand soils under different soil moisture conditions. Nutr. Cycl. Agroecosys. 70, 111–121 (2004).
16. Dobbie, K. E. & Smith, K. A. The effect of water table depth on emissions of N\(_2\)O from a grassland soil. Soil Use Manag. 22, 22–28 (2006).
17. Takakai, F. et al. Effects of agricultural land-use change and forest fire on N\(_2\)O emission from tropical peatlands, Central Kalimantan, Indonesia. Soil Sci. Plant Nutr. 52, 662–674 (2006).
18. Couwenberg, J., Dommain, R. & Joosten, H. Greenhouse gas fluxes from tropical peatlands in South-East Asia. Glob. Change Biol. 16, 1715–1732 (2010).
19. Schaurer, G. et al. Greenhouse gas emissions from European soils under different land use: effects of soil moisture and temperature. Eur. J. Soil Sci. 61, 683–696 (2010).
20. Leschen, J. P., Veithof, G. L., de Vries, W. & Kros, J. Differentiation of nitrous oxide emission factors for agricultural soils. Environ. Pollut. 159, 3215–3222 (2011).
21. Teh, Y. A. et al. Large greenhouse gas emissions from a temperate peatland pasture. Ecosystems 14, 311–325 (2011).
22. Toma, Y. et al. Nitrous oxide emission derived from soil organic matter decomposition from tropical agricultural peat soil in central Kalimantan, Indonesia. Soil Sci. Plant Nutr. 57, 436–451 (2011).
23. van der Weerden, T. J., Kelliker, F. M. & de Klein, C. A. M. Influence of pore size distribution and soil water content on nitrous oxide emissions. Soil Res. 50, 125–135 (2012).
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24. Weslien, P. Ruttig, T. Kasmir-Kledtsson, A. & Kledtsson, L. Carrot cropping on organic soil is a hotspot for nitrous oxide emissions. Nutr. Cycl. Agroecosys. 94, 249–253 (2012).

25. Davidson, E. A., Keller, M., Erickson, H. E., Verchot, L. V. & Veldkamp, E. A conceptual model of soil emissions of nitrous and nitric oxides. Bioscience 50, 667–680 (2000).

26. Schmidt, U., Thöni, H. & Kauppenjohann, M. Using a boundary line approach to analyze N<sub>2</sub>O flux data from agricultural soils. Nutr. Cycl. Agroecosys. 57, 119–120 (2000).

27. Inubushi, K., Furukawa, Y., Hadi, A., Purnomo, E. & Tsuruta, H. Seasonal changes of CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O fluxes in relation to land-use change in tropical peatlands located in coastal area of South Kalimantan. Chemosphere 52, 603–608 (2003).

28. Batty, T., Smith, K. A. & Moncrieff, J. B. Effect of stand age on greenhouse gas fluxes from a Sitska spruce Picea sitchensis (Bong.) Carr. chronosequence on a peaty gley soil. Glob. Change Biol. 13, 2128–2142 (2007).

29. Goldberg, S. D., Knorr, K. H., Blodau, C., Lischke, G. & Gebauer, G. Impact of altering the water table height of an acidic fen on N<sub>2</sub>O and NO fluxes and soil concentrations. Glob. Change Biol. 16, 220–233 (2010).

30. Tomás, V. et al. Effect of environmental factors on temporal variation in annual carbon dioxide and nitrous oxide emissions from an unfertilized bare field on Gray Lowland soil in Mikasa, Hokkaido, Japan. Soil Sci. Plant Nutr. 56, 663–675 (2010).

31. Christiansen, J. R. & Gundersen, P. Stand age and tree species affect N<sub>2</sub>O and CH<sub>4</sub> exchange from afforested soils. Biogeosciences 8, 2353–2356 (2011).

32. Christiansen, J. R., Vesterdal, L. & Gundersen, P. Nitrous oxide and methane exchange in two small temperate forest catchments—effects of hydrological gradients and implications for global warming potentials of forest soils. Biochemistry 107, 437–454 (2012).

33. Balaine, N. et al. Changes in relative gas diffusivity explain soil nitrous oxide flux dynamics. Soil Sci. Soc. Am. J. 77, 1496–1505 (2013).

34. Benanti, G., Saunders, M., Tobin, B. & Osborne, B. Contrasting impacts of afforestation on nitrous oxide and methane emissions. Agric. For. Meteorol. 198, 82–93 (2014).

35. Leppel, T. et al. Nitrous oxide emission budgets and land-use-driven hotspots for organic soils in Europe. Biogeosciences 11, 6595–6612 (2014).

36. Sgouridis, F. & Ullah, S. Soil greenhouse gas fluxes, environmental controls and the partitioning of N<sub>2</sub>O sources in UK natural and semi-natural land use types. J. Geophys. Res. 112, F01023 (2007).

37. Holtan-Hartwig, L., Dörsch, P. & Bakken, L. R. Low temperature control of Heterotrophic respiration in drained tropical peat is greatly affected by temperature—A passive ecosystem cooling experiment. Environ. Res. Lett. 9, 105013 (2014).

38. Rysgaard, S., Glud, R. N., Risagaard-Petersen, N. & Dalsgaard, T. Denitrification and anammox activity in Arctic marine sediments. Limnol. Oceanogr. 49, 1493–1502 (2004).

39. Jauhiainen, J., Kerojoki, O., Silvennoinen, H., Limin, S. & Vasander, H. Heterotrophic respiration in drained tropical peat is greatly affected by temperature—a passive ecosystem cooling experiment. Environ. Sci. Technol. 49, 14110–14119 (2015).

40. Holttan-Hartwig, L., Dörsch, P. & Bakken, L. R. Low temperature control of soil denitrifying communities: kinetics of N<sub>2</sub>O production and reduction. Soil Biol. Biochem. 34, 1797–1806 (2002).

41. Rysgaard, S., Risagaard-Petersen, N. & Dalsgaard, T. Denitrification and anammox activity in Arctic marine sediments. Limnol. Oceanogr. 49, 1493–1502 (2004).

42. Jauhiainen, J., Kerouki, O., Silvennoinen, H., Limin, S. & Vasander, H. Heterotrophic respiration in drained tropical peat is greatly affected by temperature—a passive ecosystem cooling experiment. Environ. Res. Lett. 9, 105013 (2014).

43. Faqir, R. & Baldock, J. Concepts in modelling N<sub>2</sub>O emissions from land use. Plant Soil 309, 147–167 (2008).

44. Dijkstra, F. A. et al. Effects of elevated carbon dioxide and increased temperature on methane and nitrous oxide fluxes: evidence from field experiments. Front. Ecol. Environ. 10, 520–527 (2012).

45. Koponen, H. T. & Martikainen, P. J. Soil water content and freezing temperature affect freeze–thaw related N<sub>2</sub>O production in organic soil. Nutr. Cycl. Agroecosys. 69, 213–219 (2004).

46. Matzner, E. & Borken, W. Do freeze–thaw events enhance C and N losses from soils of different ecosystems? A review. Eur. J. Soil Sci. 59, 274–284 (2008).

47. Pihlatie, M. K. et al. Greenhouse gas fluxes in a drained peatland forest during spring frost–thaw event. Biogeosciences 7, 1715–1727 (2010).

48. Wagner-Riddle, C. et al. Globally important nitrous oxide emissions from croplands induced by freeze–thaw cycles. Nat. Geosci. 10, 279–283 (2017).

49. Paustian, K. et al. Climate-smart soils. Nature 532, 49–57 (2016).

50. Roman-Cuesta, R. M. et al. Hotspots of gross emissions from the land use sector: patterns, uncertainties, and leading emission sources for the period 2000–2005 in the tropics. Biogeosciences 13, 4213–4269 (2016).

51. Alm, J. et al. Emission factors and their uncertainty for the exchange of CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O in Finnish managed peatlands. Boreal Environ. Res. 12, 191–209 (2007).

52. Syakila, A. & Kroese, C. The global nitrous oxide budget revisited. Greenh. Gas. Meas. Manag. 11, 1–17 (2011).

53. Kasimir-Kledtsson, A. et al. Greenhouse gas emissions from farmed organic soils: a review. Soil Use Manag. 13, 2245–2250 (1997).

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Author Contributions
U.M. conceived the study and planned the field campaign. J.P. managed the field campaign in most regions. S.E., J.A., K.K., A.K., E.D.L., M.M., T.P., J.-O.S., K.Soh., K.Soo., A.T., G.V., and U.M. performed the field work. S.U., F.L.-D., E.D.L., M.M., W.J.M., E.S., K.S., J.A.V., and S.S.Z. provided local expertise in site selection and interpretation. A.T. measured the gas samples. J.P., U.M., K.Soh. and A.A. compiled and analysed the data, and created the map in Fig. 1. M.E. and J.T. performed the principal
component analysis. J.T.A.V., K.B.B., N.B.D., S.U., J.Ja., L.K., A.K., F.L.-D., E.D.L., A.L., K.L., W.J.M., C.M., Ü.N., B.O., F.S., and J.A.V. made suggestions for the analyses and the paper. J.P. and Ü.M interpreted the results and wrote the paper.

**Additional information**

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