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

Pärn, Jaan; Verhoeven, Jos T. A.; Butterbach-bahl, Klaus; Dise, Nancy B.; Ullah, Sami; Aasa, Anto; Egorov, Sergey; Espenberg, Mikk; Järveoja, Järvilu; Jauhiainen, Jyrki; Kasak, Kuno; Klemedtsson, Leif; Kull, Ain; Laggoun-défarge, Fatima; Lapshina, Elena D.; Lohila, Annalea; Lõhmus, Krista; Maddison, Martin; Mitsch, William J.; Müller, Christoph

DOI: 10.1038/s41467-018-03540-1

License: Creative Commons: Attribution (CC BY)

Citation for published version (Harvard):
Pärn, J, Verhoeven, JTA, Butterbach-bahl, K, Dise, NB, Ullah, S, Aasa, A, Egorov, S, Espenberg, M, Järveoja, J, Jauhiainen, J, Kasak, K, Klemedtsson, L, Kull, A, Laggoun-défarge, F, Lapshina, ED, Lohila, A, Lõhmus, K, Maddison, M, Mitsch, WJ, Müller, C, Niinemets, U, Osborne, B, Pae, T, Salm, J, Sgouridis, F, Sohar, K, Soosaar, K, Storey, K, Teemusk, A, Tenywa, MM, Tournebize, J, Truu, J, Veber, G, Villa, JA, Zaw, SS & Mander, Ü 2018, 'Nitrogen-rich organic soils under warm well-drained conditions are global nitrous oxide emission hotspots', Nature Communications, vol. 9, 1135. https://doi.org/10.1038/s41467-018-03540-1

Link to publication on Research at Birmingham portal

Publisher Rights Statement:
Published in Nature Communications on 19/03/2018
DOI: 10.1038/s41467-018-03540-1

General rights
Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

• Users may freely distribute the URL that is used to identify this publication. 
• Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research. 
• User may use extracts from the document in line with the concept of ‘fair dealing’ under the Copyright, Designs and Patents Act 1988 (?) 
• Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy
While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

Download date: 09. Mar. 2020
Nitrogen-rich organic soils under warm well-drained conditions are global nitrous oxide emission hotspots

Jaan Pärn 1,2,3, Jos T.A. Verhoeven4, Klaus Butterbach-Bahl5, Nancy B. Disé6, Sami Ullah3, Anto Aasa1, Sergey Egorov1, Mikk Espenberg1, Järvi Järveoja1, Jyrki Jauhiainen8, Kuno Kasak1, Leif Klemmedsson9, Ain Kull1, Fatima Laggoun-Défarge10, Elena D. Lapshina11, Annalea Lohila12, Krista Löhms13, Martin Maddison1, William J. Mitsch14, Christoph Müller15,16, Ülo Niinemets17, Bruce Osborne16, Taavi Pae1, Jüri-Ott Salm18, Fotis Sgouridis19, Kristina Sohar1, Kaido Soosaar1, Kathryn Storey20, Alar Teemusk1, Moses M. Tenywa21, Julien Tournebize22, Jaak Truu1, Gert Veber1, Jorge A. Villa23, Seint Sann Zaw24 & Ülo Mander1

Nitrous oxide (N₂O) is a powerful greenhouse gas and the main driver of stratospheric ozone depletion. Since soils are the largest source of N₂O, predicting soil response to changes in climate or land use is central to understanding and managing N₂O. Here we find that N₂O flux can be predicted by models incorporating soil nitrate concentration (NO₃⁻), water content and temperature using a global field survey of N₂O emissions and potential driving factors across a wide range of organic soils. N₂O emissions increase with NO₃⁻ and follow a bell-shaped distribution with water content. Combining the two functions explains 72% of N₂O emission from all organic soils. Above 5 mg NO₃⁻-N kg⁻¹, either draining wet soils or irrigating well-drained soils increases N₂O emission by orders of magnitude. As soil temperature together with NO₃⁻ explains 69% of N₂O emission, tropical wetlands should be a priority for N₂O management.

1Department of Geography, Institute of Ecology and Earth Sciences, University of Tartu, Tartu 51014, Estonia. 2School of Geography, Geology and the Environment, Keele University, Newcastle ST5 5BG, UK. 3School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham B15 2TT, UK. 4Ecology and Biodiversity, Department of Biology, Utrecht University, Utrecht 3584 CH, The Netherlands. 5Institute of Meteorology and Climate Research, Karlsruhe Institute of Technology, Garmisch-Partenkirchen 82467, Germany. 6Centre for Ecology and Hydrology, Edinburgh EH26 0QF, UK. 7Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå 901 83, Sweden. 8Natural Resources Institute Finland (Luke), Helsinki FIN-00790, Finland. 9Department of Earth Sciences, University of Gothenburg, Gothenburg SE405 30, Sweden. 10Institute of Earth Sciences, National Center for Scientific Research (CNRS) and University of Orleans, Orleans 45100, France. 11UNESCO Chair of Environmental Dynamics and Climate Change, Yurga State University, Khanty-Mansiysk 628012, Russia. 12Atmospheric Composition Research, Finnish Meteorological Institute, Helsinki FIN-00100, Finland. 13Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu, Tartu 51014, Estonia. 14Everglades Wetland Research Park, Kapnick Center, Florida Gulf Coast University, Naples 33940 FL, USA. 15Institute of Plant Ecology, Justus Liebig University Giessen, Giessen 35392, Germany. 16University College Dublin (UCD) School of Biology and Environmental Science UCD Earth Institute, Dublin 4, Ireland. 17Department of Plant Physiology, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Tartu 51014, Estonia. 18Estonian Fund for Nature, Tartu 51014, Estonia. 19School of Geographical Sciences, University of Bristol, Bristol BS8 1SS, UK. 20Department of Primary Industries, Parks, Water and Environment, Tasmanian Government Hobart 7001 TAS, Australia. 21Department of Agricultural Production, College of Agricultural and Environmental Sciences, Makerere University, Kampala 7062, Uganda. 22Hydrosystems and Bioprocesses Research Unit National Research Institute of Science and Technology for Environment and Agriculture (IRSTEA), Antony 92160, France. 23Grupo de Investigación Aplicada al Medio Ambiente, Corporacion Universitaria Lasallista, Caldas 51118, Colombia. 24Forest Resource Environment Development and Conservation Association, Yangon 0951, Myanmar. Correspondence and requests for materials should be addressed to J.Pär. (email: jaan.parn@ut.ee)
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-oxidised 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 efflux 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.

Fig. 1 Site-mean N₂O fluxes by study region superimposed on a global organic-soil map. Country and region codes are defined after ISO 3166-2. The distribution of organic soil was defined as >150 t Corg ha⁻¹ from the Global Soil Organic Carbon Estimates (courtesy of the European Soil Data Centre) + 0.5 geographical-degrees buffer for visual generalisation.
Soil-available P was orthogonal to the N2O emissions, and soil temperature was positively related to N2O emissions (Fig. 2c). N2O emissions were less 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). N2O emission used as passive variable. 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:

$$\log(N_2O - N + 1) = 0.035 + 0.39 \log NO_3 - N$$

$$+ 0.025 (\log NO_3 - N)^2$$

$$+ 4.8 \text{VWC} - 5.2 \text{VWC}^2$$

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− content. Intermediate VWC also promotes incomplete denitrification, in agreement with early conceptualisations of previous regional-scale studies and experiments. 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 denitrification.

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 temperature. The test for an upper boundary 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 \( (n = 58; R^2 = 0.69; p < 0.001; \text{Eq. (2); Fig. 4b}) \):  
\[
\log(N₂O-N + 1) = -0.15 - 0.50 \log NO₃-N + 0.10 (\log NO₃-N)^2 + 0.036 \frac{°C}{C} + 1.9 \times 10^{-5} °C^2
\]

Within our drained sites (Supplementary Data 1; \( n = 27 \)) the temperature relationship was somewhat stronger \( (R^2 = 0.27; p < 0.0078; \text{Fig. 3c}) \). 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...
The mean emission rate was 294.3 ± s.e.m. within the respective soil-moisture class. The curve is the GAM (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 soils (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 μg N₂O-N m⁻² h⁻¹ = 25.8 kg N₂O-N ha⁻¹ y⁻¹. For Myanmar, 14–19 °C (upland), the figures were 125.5 μg N₂O-N m⁻² h⁻¹ = 11.0 kg N₂O-N ha⁻¹ y⁻¹. For Uganda, 17–20 °C (upland), the figures were 507.3 μg N₂O-N m⁻² h⁻¹ = 44.5 kg ha⁻¹ y⁻¹. Thus the annual fluxes obtained by this simple upscaling all fell within the IPCC tropical default range.

Other potential drivers. The logarithm of C:N ratio, a common scalar explanatory variable used to predict N₂O emissions, 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 N₂O 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 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 emphasizes 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 droughts. 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 rotations. 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 Base. Tools were deployed 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 (once a year or less), 2—intensive 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.

At each site, i.e., 4 stations were established 15–50 m apart to maximise the environmental variance. Each station was instrumented with 3–5 white opaque PVC 65 L truncated conical chambers 1.5–5 m apart and a 1-m-deep observation well (a 50-mm-diameter perforated PP-HT pipe wrapped in geotextile). The total number of chambers was 444. N₂O fluxes were measured using the static chamber method64 using PVC collars of 0.5 m diameter and 0.1 m depth installed in the soil. A stabilisation period of 3–12 h was allowed before gas sampling to reduce the disturbance effect on fluxes from inserting the collars. The chambers were placed into water-filled rings on top of the collars. Gas was sampled from the chamber headspace into a 50 mL glass vial every 20 min during a 1-h session. The vials had been evacuated in the laboratory 2–6 days before the sampling. At least three sampling sessions per location were conducted over 3 days. The gas samples were brought to the University of Tartu and analysed for N₂O concentration within the database and included in the analyses.

Water-table height was recorded daily from the observation wells during the gas sampling at least 8 h after placement. Soil temperature was measured at 10, 20, 30, and 40 cm depth. Soil samples of 150–200 g were collected from the chambers at 0–10 cm depth after the final gas sampling. Humification was rated on the von Post scale, 1 to 10 grades from completely undecomposed to completely decomposed peat65. The soil samples were brought to Estonian University of Life Sciences for chemical and physical analyses. During transport, the samples were kept below the ambient soil temperature at which they were collected.
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 on a 1 N KCl solution16. Soil NH4-N and NO3-N were determined on a 2 M KCl extract of soil by flow-injection analysis53. 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 graminic water content (GWC) as the difference between the fresh and oven-dry weight divided by the oven-dry weight66. Bulk density was determined as follow66:

\[
BD = (D_m - D_h) / (SOM \cdot D_m + (1 - SOM) \cdot D_h) 
\]

where:
- **BD** is bulk density, g cm⁻³;
- **D_m** is the empirically determined bulk density of the mineral fraction (2.65 g cm⁻³)66;
- **D_h** is the empirically determined bulk density of the organic fraction (0.035–0.23 g cm⁻³ according to the von Post humification scale65), and
- **SOM** is the organic content of the oven-dry soil, g g⁻¹.

We determined VWC as follows66:

\[
VWC = GWC \cdot BD 
\]

where:
- **VWC** is volumetric water content, m³ m⁻³;
- **GWC** is gravimetric water content, Mg Mg⁻¹, and
- **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 year69 (KNMI Climate Explorer 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 N₂O flows. Before the log-transformation, a constant value was added to all flows to account for negative values. Normality of the variables and the residuals was checked by the Shapiro–Wilk test. Neither the N₂O flows nor their logarithms were normally distributed (p < 0.05); this is a commonly reported issue1.

**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: N₂O and organic soil and nitrous oxide and organic soil. We only included publications that reported time series of at least a year’s duration that reported N₂O flows and simultaneous soil temperature and soil moisture observations (either VWC or WFPS). Eleven papers17,24,32,53,54,58 qualified 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 NO3 concentration17,24,32. We converted the WFPS values to VWC as follows66:

\[
VWC = WFPS \cdot TP 
\]

where:
- **VWC** is volumetric water content, m³ water m⁻³ fresh soil, WFPS is water-filled porosity, m³ water m⁻³ pore space, and TP is total porosity, m³ pore space m⁻³ soil.

To standardise the highly different absolute N₂O values among data sets we normalised them by scaling to the maximum value measured at each site70. We calculated average relative N₂O flows in 15 soil temperature classes: 0 °C to 2 °C, 2 °C to 4 °C, … and 28 °C to 30 °C, and 10 soil moisture classes: 0% to 10%, 10% to 20%, … and 90% to 100%. Linear and GAM regressions with minimal smoothness (κ = 3) were determined between soil temperature, soil moisture and both the individual and average relative N₂O flows.

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

Received: 9 July 2017 Accepted: 21 February 2018

Published online: 19 March 2018

**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. & Zecheimaster-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. Phylotaxonomic analysis of non-methylated, nitrous 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 C:N:P stoichiometry in an ombrotrophic peatland: from plants to peat. *Environ. Res. Lett.* **9**, 024003 (2014).

5. Shcherbak, L., Millar, N. & Robertson, G. P. Global metaanalysis of the nonlinear response of soil nitrous oxide (N₂O) 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. & Yzyginsteine, D. G. Abundance, biomass, structure, and activity of the microbial complexes of minerotrophic and ombrotrophic peatlands. *Microbiology* **76**, 650–657 (2007).

9. Rubol, A., Silver, W. L. & Bellin, A. Hydrologic control on redox 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 (2014).

11. Sikka, 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 N₂O 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., Syväolso, A., Simojoki, A., Esaala, M. & Regina, K. Contribution of nitrification and denitrification to N₂O production in peat, clay and loamy sand soils under different soil moisture conditions. *Natur. Cycl. Agroecosys.* **70**, 111–141 (2004).

16. Dobbie, K. E. & Smith, K. A. The effect of water table depth on emissions of N₂O from a grassland soil. *Soil Use Manage.* **22**, 22–28 (2006).

17. Takai, F., et al. Effects of agricultural land-use change and forest fire on N₂O emission from tropical peatlands, Central Kalimantan, Indonesia. *Soil Sci. Plant Nutr.* **52**, 662–674 (2006).

18. Couwenberg, J., Domman, R. & Joosten, H. Greenhouse gas fluxes from tropical peatlands in South-East Asia. *Glob. Change Biol.* **16**, 1715–1732 (2010).

19. Schueller, 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., Vethof, 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., Kellihier, 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).
33. Balaine, N. et al. Changes in relative gas diffusivity explain soil nitrous oxide emissions. NATURE COMMUNICATIONS | 2018 9:1135 | DOI: 10.1038/s41467-018-03540-1 | www.nature.com/naturecommunications

24. Weslien, P., Rutting, T., Kasimir-Klemedtsson, A. & Klemedtsson, L. Carrot NATURE COMMUNICATIONS | DOI: 10.1038/s41467-018-03540-1 ARTICLE

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

25. Davidson, E. A., Keller, M., Erickson, H. E., Verchot, L. V. & Veldkamp, E. Changes in relative gas diffusivity explain soil nitrous oxide emissions from an unfertilized bare field on Gray Lowland soil in Mikasa, Hokkaido, Japan. Soil Sci. Plant Nutr. 56, 663–675 (2010).

30. Christiansen, J. R. & Gundersen, P. Stand age and tree species affect N2O and CH4 exchange from afforested soils. Biogeochemistry 8, 2353–2346 (2011).

31. Christiansen, J. R., Vesterald, 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).

34. Benanti, G., Saunders, M., Tobin, B. & Osborne, B. Contrasting impacts of temperature on greenhouse gas emissions from soils. Glob. Change Biol. 16, 284–290 (2010).

36. Sgouridis, F. & Ullah, S. The global nitrous oxide budget revisited. Biogeosciences 11, 4361–4379 (2014).

44. Pihlatie, M. K. et al. Greenhouse gas emissions from farmed organic soils: a review. Soil Use Manag. 13, 2245–2250 (1997).

45. Wagner-Riddle, C. et al. Globally important nitrous oxide emissions from croplands induced by freeze-thaw cycles. Environ. Res. Lett. 11, 105013 (2016).

46. Paustian, K. et al. Climate-smart soils.

47. Roman-Cuesta, R. M. et al. Hotspots of gross emissions from the land use transition in tropical Southeast Asian riparian ecosystems. J. Geophys. Res. Atmos. 49, 11190–11198 (2014).
component analysis. J.T.A.V., K.B.B., N.B.D., S.U., J.Ja., L.K., K.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
Supplementary Information accompanies this paper at https://doi.org/10.1038/s41467-018-03540-1.

Competing interests: The authors declare no competing interests.

Reprints and permission information is available online at http://npg.nature.com/reprintsandpermissions/

Publisher’s note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit http://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2018