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Circumpolar assessment of permafrost C quality and its vulnerability over time using long-term incubation data

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Abstract

High-latitude ecosystems store approximately 1700 Pg of soil carbon (C), which is twice as much C as is currently contained in the atmosphere. Permafrost thaw and subsequent microbial decomposition of permafrost organic matter could add large amounts of C to the atmosphere, thereby influencing the global C cycle. The rates at which C is being released from the permafrost zone at different soil depths and across different physiographic regions are poorly understood but crucial in understanding future changes in permafrost C storage with climate change. We assessed the inherent decomposability of C from the permafrost zone by assembling a database of long-term (>1 year) aerobic soil incubations from 121 individual samples from 23 high-latitude ecosystems located across the northern circumpolar permafrost zone. Using a three-pool (i.e., fast, slow and passive) decomposition model, we estimated pool sizes for C fractions with different turnover times and their inherent decomposition rates using a reference temperature of 5 °C. Fast cycling C accounted for less than 5% of all C in both organic and mineral soils whereas the pool size of slow cycling C increased with C : N. Turnover time at 5 °C of fast cycling C typically was below 1 year, between 5 and 15 years for slow turning over C, and more than 500 years for passive C. We project that between 20 and 90% of the organic C could potentially be mineralized to CO_2 within 50 incubation years at a constant temperature of 5 °C, with vulnerability to loss increasing in soils with higher C : N. These results demonstrate the variation in the vulnerability of C stored in permafrost soils based on inherent differences in organic matter decomposability, and point toward C : N as an index of decomposability that has the potential to be used to scale permafrost C loss across landscapes.

Keywords: Alaska, boreal forest, C decomposition, climate change, Siberia, soil organic carbon, tundra

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Introduction

High-latitude ecosystems store about 1700 Pg of carbon (C) in soils of the permafrost region which is more than twice as much C as is currently contained in the atmosphere (Schuur *et al*., 2008; Tarnocai *et al*., 2009). This large C pool is mainly kept frozen in permafrost soils but is expected to undergo drastic changes (thaw, thermal erosion) with predicted global warming (Gruber *et al*., 2004; Schuur *et al*., 2008). Recent efforts to establish a publicly available database of polygon-based estimates of soil organic carbon (SOC) in permafrost-affected soils (including both the seasonally thawed active layer and perennially frozen permafrost) provide an excellent source of information on SOC storage in permafrost (the Northern Circum-polar Soil Carbon Database, Hugelius *et al*., 2013). Permafrost thaw will expose large quantities of previously frozen organic C to microbial decomposition and will likely transfer large amounts of C to the atmosphere (Oechel *et al*., 1993; Dutta *et al*., 2006; Schuur *et al*., 2009). Although most of the C released from thawed permafrost will occur through microbial decomposition, our understanding of the overall decomposability of permafrost C from different depths and different physiographic regions is still poor.

Soil OC quality, or decomposability, is one of the most important factors in determining the transfer rate of permafrost C to the atmosphere. Besides soil depth and geographical region, environmental factors (temperature, water, nutrient availability, soil pH) and

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physical protection by soil minerals highly influence permafrost C decomposition (Schmidt *et al.*, 2011). Decomposition rates of permafrost C also vary between different vegetation types and reflect the mechanisms by which C was incorporated into permafrost. More easily decomposable C is released early in decomposition and C of poor quality is then buried in peat and mineral soils (Schuur *et al.*, 2008). After thaw, the higher C content in organic-rich high-latitude soils results in higher decomposition rates measured as CO_2 flux compared to C poor mineral soils (Lavoie *et al.*, 2011). Generally, peat and mineral soils show low decomposition rates although there are exceptions found in Yedoma deposits where organic matter was buried deep into permafrost comparatively rapidly during past glacial periods (Dutta *et al.*, 2006; Zimov *et al.*, 2006b; Lee *et al.*, 2012). These Yedoma deposits in Alaska and Siberia contain approximately 2–5% of organic C to depths of ca. 25 m, which makes them relatively large global C stores (Zimov *et al.*, 2006b).

Total SOC is composed of a continuous spectrum of C pools characterized by different turnover times that range from less than a year to hundreds or even thousands of years (Jenkinson & Rayner, 1977; Trumbore, 1997; Amundson, 2001; Schmidt *et al.*, 2011). Each pool provides a substrate for microbial decomposition with an inherent decomposability although chemical recalcitrance and physical protection inhibit rapid decomposition of a large fraction of soil C (Schmidt *et al.*, 2011). For simplicity, SOC has been conceptually grouped into a fast decomposable fraction that turns over within a few days to a few months, a slower decomposing C pool that has a mean residence time (MRT) of a few years and a very passive, almost inert, soil C fraction which has been described to have turnover times of a few years to thousands of years (Jenkinson & Rayner, 1977; Parton *et al.*, 1987; Trumbore, 1997). Although those conceptual pools of soil C have been incorporated into most terrestrial carbon cycle models, they have not been well estimated using data from field and laboratory studies (Trumbore, 2000).

We have recently applied a deconvolution approach to quantify pool sizes and turnover times of different cohorts of C substrate quality based on information contained in soil CO_2 flux data from laboratory incubations (Schädel *et al.*, 2013). This deconvolution approach separates CO_2 efflux into pool-specific decay rates and allows for the calculation of MRT according to dynamic characteristics in the time-series data from soil incubation studies. Data from laboratory incubation studies, which usually have no new input of organic C sources, contain quantitative information on the depletion of the SOC pools. With increasing incubation duration, more C from slowly decomposing material is respired relative to the fast pools that become depleted, which provides insights into the turnover times of these slower SOC fractions (von Lützow & Kögel-Knabner, 2009). Laboratory studies are also a very useful way to isolate the effects of environmental factors such as temperature and moisture on respiration rates and allow comparisons across soil types of different C content and origin (Holland *et al.*, 2000).

In this synthesis study, we assessed the decomposability of thawed organic C from permafrost-affected soils (active layer and permafrost) across the arctic under aerobic conditions. We combined multiple long-term incubation studies (duration >1 year) and explored systematic variation in C quality from soils in the permafrost zone using a three-pool C decomposition model. The main objectives of this study were to (i) assess decomposability of C fractions with different turnover times across the permafrost zone; (ii) identify C quality differences in different vegetation types (boreal forest vs. tundra) and soil depths (0–22 m); (iii) estimate potential C loss from these soils over a projected 50 year incubation period at 5 °C using estimated pool-specific decay rates from this deconvolution analysis; and (iv) to identify the best overall predictors for soil quality (C pool sizes, turnover times and potential C loss) that would apply to soils across the permafrost zone. We expected C pool sizes, decay rates, and turnover times to vary between organic and mineral soils (larger fast turning over C pool with shorter turnover time in organic soils). In addition, we hypothesized that deep mineral soils would have a larger portion of passive C with very slow turnover times compared to shallow mineral soils as climate and vegetation history play a major role in C decomposability.

Materials and methods

Incubation datasets

Soil incubation datasets used in this analysis were obtained from participants of the Vulnerability of Permafrost Carbon Research Coordination Network (http://www.biology.ufl.edu/permafrostcarbon/) and one dataset was extracted from literature (Neff & Hooper, 2002). Most of the incubation studies have been published (Neff & Hooper, 2002; Dutta *et al.*, 2006; Shaver *et al.*, 2006; Lavoie *et al.*, 2011; Lee *et al.*, 2012; Elberling *et al.*, 2013; Knoblauch *et al.*, 2013) while one study was in preparation for publication (R. Bracho, E.A.G. Schuur, E. Pegoraro, S.M. Natali, J. Zhou, L. Wu, K. Xue, L. Cheng, M. Yuan, J. Zhang, Y. Deng, N.J.D. Van, Z. He, R. Penton, J. Cole, J.M. Tiedje, C. Luo, K. Konstantinidis, S. Xue, D. Li and Y. Luo, unpublished data) at the time of submission of this manuscript. Incubation experiments were chosen to be included in this synthesis according to the following criteria: (i) samples had to be collected within one of the different

permafrost zones according to Brown *et al.* (1997); (ii) aerobic CO_2 production had to be measured over the course of the incubation study; (iii) the incubation study had to last for 1 year or longer; (iv) initial C concentration needed to be available; and (v) CO_2 flux in the initial phase had to be higher than CO_2 flux at the end of the incubation to fit a first-order decay model. Soil samples came from upland aerobic sites and none of the used soil samples had undergone any type of environmental manipulation or treatment. More details on the laboratory incubation experiments, CO_2 sampling techniques and rates can be found in the corresponding literature (Neff & Hooper, 2002; Dutta *et al.*, 2006; Shaver *et al.*, 2006; Lavoie *et al.*, 2011; Lee *et al.*, 2012; Elberling *et al.*, 2013; Knoblauch *et al.*, 2013). For the unpublished incubation study details are provided in the supplementary material.

Incubation data for this synthesis were derived from study sites across the entire arctic region, with the majority of sampling sites located in Siberia and Alaska (Fig. 1). Vegetation types varied among sites (Table S1) and included boreal forest and three different tundra types: moist acidic, nonacidic tussock, and heath. Soil samples were taken from active layer or permafrost; however, a clear distinction was not always available. Each spatially explicit soil core was treated as an individual sample and only analytical replicates were pooled. Incubation temperatures varied from 4 to 15 °C across studies (Table S1) and we used the 15 °C treatment when more than one incubation temperature was available. Using this higher temperature allowed for more inference of the slower turning over C pools because more of the total C pool was respired over the incubation period.

Aerobic C flux from each soil sample, together with a three-pool C dynamics model and initial C concentration (% C), was used to estimate parameters of C decomposition (C pool-specific partitioning coefficients and pool-specific decay rates) of pools with different turnover times.

Soil C decomposition model

Soil organic C exists in complex forms and its dynamics usually have to be represented by models with more than one C pool (Trumbore, 1997). Time-series data from soil incubation experiments generally exhibit some inflection points, which indicate shifts of microbial decomposition of organic C from fast to slow or from slow to passive pools (Schädel *et al.*, 2013). A three-pool C decomposition model was used to separate total measured CO_2 production from the incubation into pool-specific decay rates using deconvolution analysis (Schädel *et al.*, 2013). The total observed respiration rate (R) in the three-pool model is the sum of pool-specific decomposition rates (Fig. S1) derived from a fast (C_1, short turnover time), a slow (C_2, longer turnover time), and a passive C pool (C_3, very long turnover time). Total soil respiration (R; in mg C gdw^{-1} d^{-1}) was modeled using Eqn (1)

$$R = \sum_{i=1}^{n} r_i = \sum_{i=1}^{n} k_i C_{\text{tot}} f_i \quad (1)$$

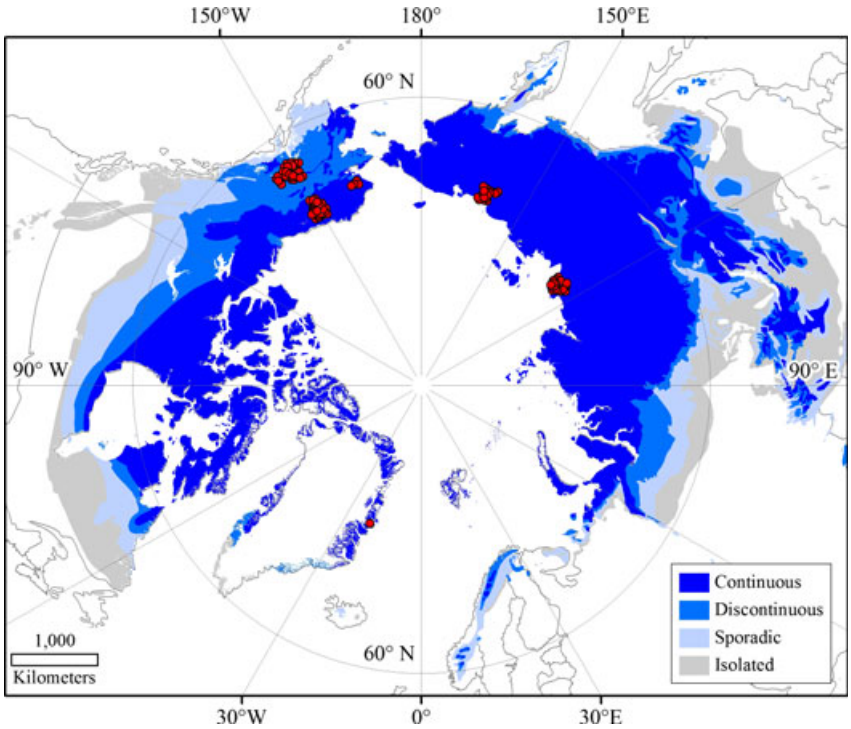

Fig. 1 Circum-Arctic map of permafrost zonation according to Brown *et al.* (1997) with sampling sites indicated by red dots. Exact site locations have been manipulated for cartographic representation; projection: Azimuthal Equidistant, datum: WGS84. Exact latitude and longitude for each sampling site can be found in Table S1.

where R is the sum of C released from all pools, r_i is a respiration rate from ith C pool C_i ($i = 1 \ldots n$, where $n = 3$ pools). Pool-specific respiration rates (r_i) were modeled as the product of inherent pool-specific decay rate (k_i, in d^{-1}), total initial C pool (C_{tot}, in mg C gdw^{-1}) and a partitioning coefficient (f_i, unitless). The partitioning coefficient describes the ratio of C in ith pool to the total C pool:

$$f_i = \frac{C_i}{C_{tot}}, \sum_{i=1}^{n} f_i = 1 \quad (2)$$

The sum of all C pool fractions equals 1 (Eqn 2). The change in C pool size for fraction i was modeled by a first-order differential equation (Eqn 3) with C pool i decaying at a temperature-dependent rate k_i over time (t) multiplied by the total initial organic C pool size (C_{tot}) times the partitioning coefficient (f_i)

$$\frac{dC_i(t)}{dt} = -k_i C_{tot} f_i \quad (3)$$

In this soil C decomposition model, C_{tot} and R are measured quantities. Parameters k_i and f_i need to be estimated with deconvolution analysis.

Deconvolution analysis

Deconvolution analysis is a method used to separate measured soil CO_2 efflux into source components, such as fast, slow, and passive soil organic matter (SOM). As each of the source components has a different kinetic rate of organic C decomposition, the method differentiates those source components according to the kinetic rates (Luo *et al.*, 2001). This deconvolution analysis uses Bayesian probabilistic inversion to optimize parameters (p) of the soil C decomposition model against measured CO_2 flux data. The inversion approach was developed by Xu *et al.* (2006) and is based on Bayes' theorem (Eqn 4), which states that the posterior probability density function $P(p \mid Z)$ of model parameters (p) can be obtained from prior knowledge of parameters, represented by a prior probability density function $P(p)$, and the information that is contained in the decomposition dataset, represented by a likelihood function $P(Z \mid p)$.

$$P(p \mid Z) \propto P(Z \mid p)P(p) \quad (4)$$

To perform the Bayesian inversion we first specified ranges of model parameters according to literature values (Jenkinson & Rayner, 1977; Trumbore, 1997; Dioumaeva *et al.*, 2002; Carrasco *et al.*, 2006; Craine *et al.*, 2010), assuming a uniform distribution over the specific parameter ranges. The *prior* parameter space was set as widely as possible for all types of soils in the initial model run to permit broad parameter search within the lower or upper limit (Table S2) and was narrowed down in a second model run to improve posterior parameter distribution. Some additional constraints need to be considered during the deconvolution analysis. For example, the sum of all C pool fractions (f) must equal 1 and decay rates (k) for the three pools followed the order of fast > slow > passive C pool. Literature provides some information of the turnover time (k^{-1}) of the fast and slow C pool, which could be used to set the parameter ranges for those parameters but there is very little information available for the passive C pool.

For organic soils we chose the shortest possible turnover time (upper limit in Table S2) for the passive C pool to be 50 years at 15 °C and the largest turnover time (lower limit in Table S2) could be indefinitely large. Furthermore, we assumed the passive C pool in mineral soils to be almost inert and not decomposable within a relevant timeframe and thus set the shortest possible turnover time (upper limit in Table S2) to be 1000 years at 15 °C. We chose the lower limit to be zero for all parameters as C pool fractions and decay rates tended to be very small.

The likelihood function $P(Z \mid p)$ (Eqn 5) was calculated with the assumption that errors between observed and modeled values followed a Gaussian distribution:

$$P(Z \mid p) \propto \exp\left\{\frac{-1}{2\sigma^2} \sum_{t \epsilon \mathrm{obs}(Z_i)} [Z_i(t) - X_i(t)]^2\right\} \quad (5)$$

where $Z(t)$ denotes the data obtained from measurements, $X(t)$ is the modeled value, and σ is the standard deviation of the observed CO_2-efflux. Within the parameter space the Metropolis-Hastings (M-H) algorithm, which is a Markov Chain Monte Carlo (MCMC) technique, was used to sample parameter sets that minimized the data-model error (Metropolis *et al.*, 1953; Hastings, 1970). The M-H algorithm was run 100 000 times with acceptance rates for parameter values between 3 and 20%. The combination of a Bayesian approach and a Markov chain Monte Carlo (MCMC) technique was done with Matlab (R2011b, MathWorks, Natick, Massachusetts).

The probabilistic inversion approach constructs posterior parameter distributions that allow inferences for parameter uncertainties by quantifying maximum likelihood estimates (MLEs) for well-constrained parameters, means for poorly constrained parameters and confidence intervals for all parameters. The estimated set of parameters for each soil was used to run the model forward giving an optimized model output for the MLE values together with confidence intervals of the estimations.

Schädel *et al.* (2013) originally developed the C decomposition model used for this synthesis and compared performance of a two-pool and three-pool C decomposition model using data from a 385 day incubation. Their comparison showed that both two- and three-pool models fit equally well with data from a 1 year incubation study. Given that we used C pool size estimates and decay rates to extrapolate C loss beyond the incubation period, we chose to use the three-pool model as it more accurately describes C dynamics over a long time period by accounting for a passive C pool with a long MRT (see Table S3 for model comparison). We applied the three-pool model to each of the 121 soil samples separately at the given incubation temperature but then standardized decay rates and C dynamics to a common temperature of 5 °C using a Q_{10} of 2.5 (R. Bracho, E.A.G. Schuur, E. Pegoraro, S.M. Natali, J. Zhou, L. Wu, K. Xue, L. Cheng, M. Yuan, J. Zhang, Y. Deng, N.J.D. Van, Z. He, R. Penton, J. Cole, J.M. Tiedje, C. Luo, K. Konstantinidis, S. Xue, D. Li and Y. Luo,

unpublished data). Estimated parameters from the model runs were used to calculate C loss (including 97.5% CI) over a projected incubation time period of 50 incubation years using an exponential decay function over time (Eqn 3) for each pool (n = 3 pools). For this potential C loss we projected with constant incubation conditions for 12 months over each year at 5 °C. Pool sizes and C loss were calculated in% of total C to look at relative differences between the large varieties of soils.

Statistics

We investigated differences in C pool sizes and C loss per timeframe between soil types with a one-way ANOVA in R (R Development Core Team, 2012) followed by Tukey–Kramer honestly significant difference (HSD) test if the ANOVA result was significant ($P < 0.05$).

We used linear regression in R to find the strongest explanatory variables that could predict C pool sizes and C loss over time using the given variables from the datasets. These included initial C (%) and N (%), C : N, average sampling depth, soil type, and vegetation. Soil type is a nominal variable with three levels that combines initial C concentration and average sampling depth and groups all samples into organic soils (initial C > 20%), shallow mineral soils (initial C < 20% and depth < 1 m) and deep mineral soils (initial C < 20% and depth > 1 m). This nominal variable was introduced to distinguish deep mineral soil samples (deeper than 1 m) from the shallow mineral ones that were taken at a depth <1 m. Organic soils ranged in depth between 0 and 1.2 m. Other variables such as mean annual temperature (MAT), mean annual precipitation (MAP), pH and bulk density were analyzed with a subset of soils that also reported those variables.

We used graphical inspection and variance inflation factors (VIF) with the full model to assess which variables contained collinearity and therefore needed to be excluded from the analysis. The cutoff VIF value to drop a variable was 3 as suggested by Zuur *et al.* (2010). We dropped the variable with the highest VIF first and continued until all variables had a VIF < 3. Random effects and variance structures were then optimized using the lowest Akaike Information Criterion (AIC) as model selection criterion following Zuur *et al.* (2010). We included incubation study and sampling site (nested within study) as random effects. The fixed effects to start the full model with were percentage N, C : N, average sampling depth and vegetation. The optimal model was selected by dropping the least significant individual explanatory variable one by one and refitting the model every time with the model selection criterion being the smallest AIC. The linear mixed effects model was fitted using the 'lme' command with restricted maximum likelihood from the 'nlme' package in R (Pinheiro *et al.*, 2012). We ran linear mixed effects models for each of the C pool sizes, turnover time of the fast and slow C pool and for simulated C loss for 1, 10, and 50 incubation years. Pool sizes were arcsine square root transformed and C loss was $\log_{10}$ transformed to meet the assumption of normality. Furthermore, we checked all residuals for normality and homogeneity of variance.

Results

Soil attributes

Soil samples had initial C concentrations ranging from 0.6% to 44% representing a range from mineral to organic soil types (Fig. 2a, Table S1). The lowest C concentration was found in a mineral soil from the Lena Delta in Siberia and the highest C concentration was found in organic soils from Chandalar, Interior Alaska, but this range spans what is typical for other organic and mineral soils around the region. Total N concentrations ranged from 0.03% to 2.6% (Fig. 2b; Table S1) and C : N ranged from 5.4 to 72.6 with the majority of soils between 10 and 50 (Fig. 2c).

Carbon pool sizes

In general, the fast C pool size was small (<5% of total C) and there were no differences among the three soil types (Fig. 3a). The slow C pool size was significantly different ($P < 0.001$) between the three soil types and was largest in organic soils and smallest in deep mineral soils (Fig. 3b). Organic soils also showed the largest range in slow C pool sizes, with very small C pool

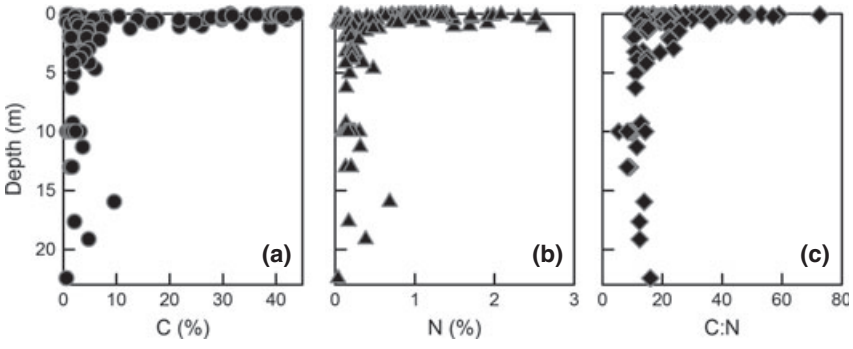

Fig. 2 Depth profile of (a) organic C (%), (b) organic N (%), and (c) C : N of all soil samples.

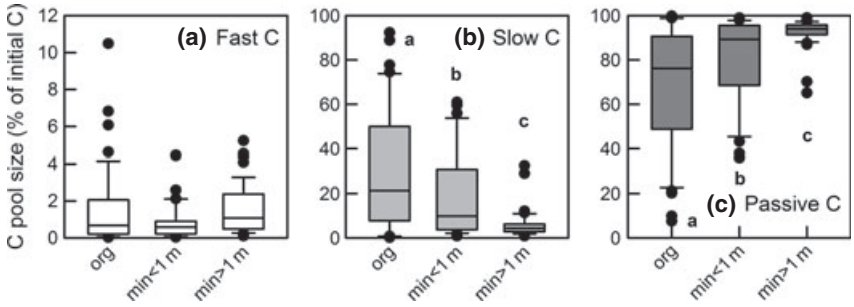

Fig. 3 Box plots showing the relative size (in percentage of initial C) of (a) the fast C pool, (b) the slow C pool, and (c) the passive C pool grouped by soil type with the following levels: organic (initial C > 20%), shallow mineral (initial C < 20% and depth <1 m) and deep mineral (initial C < 20% and depth > 1 m). Different letters indicate significant differences between soil types by Tukey Kramer honestly significant difference (HSD) Test. The box plots summarize the distribution of C pool sizes for each soil type. The horizontal line in each box represents the median, the end of the box the 25th and 75th percentile and the lines extending from the box are the 10th and 90th percentile. Points outside of the interval are presented as dots. Please note the different scale for the fast C pool.

size estimates in deeper organic soils and a pool size of up to 90% in near-surface soils. The slow C pool was significantly smaller in the deep mineral soils compared to the organic or shallow mineral soils and was <10% of the total C pool for most of the deep mineral soils (Fig. 3b). The passive C pool was calculated as the total C pool minus the sum of the fast and slow C pool and because the fast C pool was so small the passive C pool showed the opposite pattern to the slow C pool (Fig. 3c). This means the largest passive C pool was found in deep mineral soils with up to 90% of passive C.

Pool-specific decay rates and MRT

Carbon pool turnover time or MRT is the inverse of the decay rate ($1/k$) and is expressed in years (Table 1). Turnover times are temperature sensitive, which is why we standardized results at 5 °C, as shown in Table 1. All soil types showed rather short turnover times for the fast C pool, with the average turnover time being less than 1 year. Variation in turnover time was large with little difference among the three soil types. Mean residence time for the slow C pool was also less than 10 years for all soil types, although when accounting for the high variation between soils it could be as high as 30 years. For all soils the decay rate of the passive C pool could not be constrained indicating that there was little information in the datasets about the decay of this pool (Table 1). CO_2 respiration rate at the end of every incubation study was still dominated by the slow C pool, which makes it impossible to estimate the true turnover time of this passive C pool because it contributes so little to measured fluxes. For the poorly constrained parameter $k_{passive}$ only a mean value could be calculated which spans the whole range of possible parameter values as determined in the prior parameter range. As we had *a priori* set the lower limit of this parameter to be 125 years in organic soils, and 2500 years in mineral soils (at 5 °C) the mean turnover time at 5 °C was >125 years in organic soils and >2500 years in mineral soils (Table 1).

Table 1 Mean residence times (±SD) at 5 °C for the fast, slow, and passive C pool grouped by soil type. Letters indicate significant differences by Tukey Kramer honestly significant difference (HSD) test

	MRT (years)		
	Fast C	Slow C	Passive C
Organic	0.41 ± 0.87^{b}	7.21 ± 4.32	>125
Mineral < 1 m	0.48 ± 0.51^{a}	8.76 ± 6.11	>2500
Mineral > 1 m	0.21 ± 0.17^{ab}	6.42 ± 4.99	>2500

Additional information on model performance (i.e., correlation between parameters, parameter uncertainty, and prediction uncertainty) is provided in the supplementary material (Table S4 and S5). Calculations of parameter correlations revealed that only the size of the slow C pool negatively correlated with its own decay rate (mean correlation over all soil samples was −0.68, Table S4) indicating that soil samples with larger amounts of slow C had a smaller decay rate.

One of our research questions had been to determine the factors that could predict the variation in C loss across soils. From all the variables that went into the final mixed effects regression model (%N, C : N, soil depth and vegetation) C : N showed a significant effect with each of the C pools ($P = 0.013$ for the fast C pool and $P < 0.001$ for the slow and passive C pool, Table 2). Total percentage C and soil type were predictors that

Table 2 Multiple regression results for estimated parameters† and C loss at three different time points of long-term incubations. Pool sizes were arcsine square root transformed and C loss was $\log_{10}$ transformed to meet the assumption of normality

Model	Coefficients	Estimate	SE	DF	*t* value	*P* value
C_{fast}	Intercept	−0.129	0.199	110	−0.646	0.519
	C : N	0.010	0.004	110	2.526	0.013*
	Depth	0.0002	0.0001	110	2.14	0.035*
	Tundra	−0.21	0.135	110	−1.575	0.118
C_{slow}	Intercept	0.374	0.100	111	3.729	<0.001**
	C : N	0.010	0.001	111	7.427	<0.0001***
	Tundra	−0.069	0.045	111	−1.539	0.127
$C_{passive}$	Intercept	1.174	0.100	111	11.753	<0.0001***
	C : N	−0.010	0.001	111	−7.517	<0.0001***
	Tundra	0.070	0.045	111	1.539	0.127
C loss, 1 year	Intercept	0.228	0.141	94	1.614	0.110
	C : N	0.015	0.003	94	5.246	<0.0001***
C loss, 10 years	Intercept	0.788	0.160	94	4.911	<0.0001***
	C : N	0.015	0.002	94	6.103	<0.0001***
C loss, 50 years	Intercept	0.936	0.147	93	6.348	<0.0001***
	C : N	0.013	0.002	93	5.937	<0.0001***
	N (%)	0.113	0.046	93	2.469	0.0154*

*P< 0.05; **P<0.001; ***P<0.0001.
†Results are only shown for parameters with significant predictors after model selection (see methods).

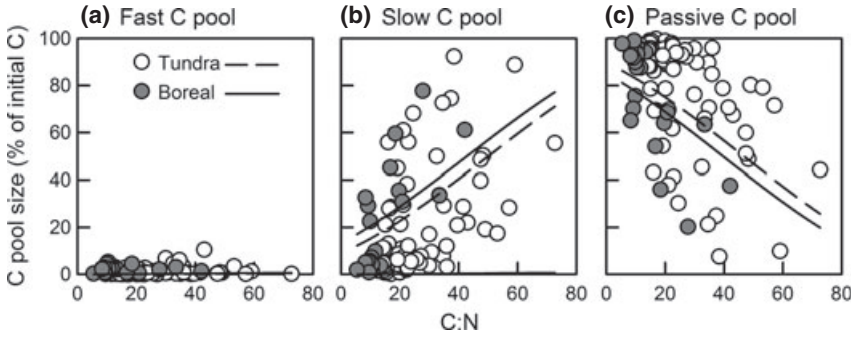

Fig. 4 Relationship between sizes of (a) the fast C pool, (b) the slow C pool and (c) the passive C pool and initial C : N of total soil C for tundra (white circles) and boreal (gray circles) separately. Lines show the predicted relationship of C pool sizes with initial C : N of total soil C for boreal soil samples (solid line) and tundra samples (dashed line).

had to be excluded from the final model because of high collinearity. The higher the C : N in a given soil was, the larger the slow C pool size was and consequently the smaller the passive C pool size (Fig. 4). The best regression model (based on lowest AIC) also included vegetation as a predictor although, it was not significant. Last, the correlation between the slow and passive C pool size to C : N was higher in boreal soils than that in tundra soils (Fig. 4).

C loss over time

Using the estimated C pool fractions and decay rates for each C pool, we projected potential C loss over a timeframe beyond the incubation period. For this extrapolation we assumed a constant incubation temperature of 5 °C and no input of new organic C. The 1 year time point (Fig. 5a) shows C loss within the actual incubation period whereas the 10 and 50 year time points extrapolate beyond the incubation time and therefore represent potential C loss (Fig. 5b and c). Within 1 year of incubation, organic soils respired on average 6% of their total initial C whereas mineral soils lost less than 5% (Fig. 5a). After 10 incubation years, organic soils showed a mean potential C loss of 25%, shallow mineral soils a potential C loss of 14% and 7% for deep mineral soils (Fig. 5b). The difference between soil types was significant at the level of $P < 0.0001$. The same significant difference in potential C loss between soil types was found at the 50 incubation year time point (Fig. 5c). Mean potential organic soil C loss was 40% of their initial C, with some soils being especially

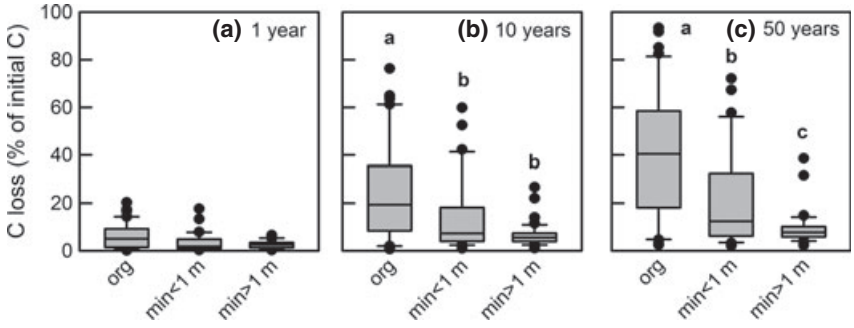

Fig. 5 C loss (in% of initial C) after (a) 1 year of incubation, (b) 10 years of incubation and (c) 50 years of incubation grouped by soil type with the following levels: organic (initial C > 20%), shallow mineral (initial C < 20% and depth < 1 m) and deep mineral (initial C < 20% and depth > 1 m). Incubation temperature was constant at 5 °C. Carbon loss beyond the incubation period of at least 1 year represents potential C loss. Different letters indicate significant differences between soil types by Tukey Kramer honestly significant difference (HSD) Test. The box plots summarize the distribution of C loss for each soil type. The horizontal line in each box represent the median, the end of the box the 25th and 75th percentile and the lines extending from the box are the 10th and 90th percentile. Points outside of the interval are presented as dots.

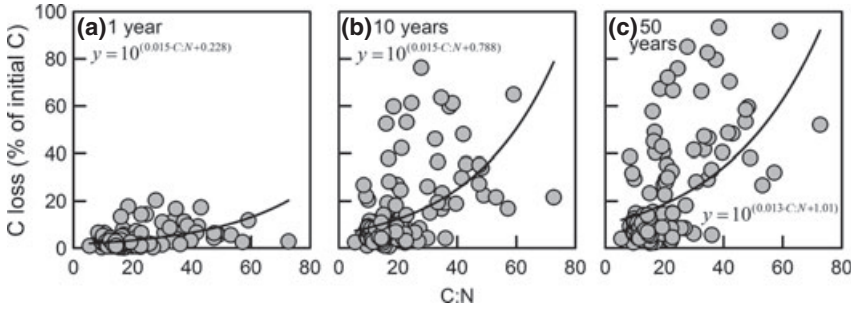

Fig. 6 C loss (in percentage of initial C) in relation to initial C : N of total soil C after (a) 1 year of incubation, (b) 10 years of incubation and (c) 50 years of incubation; all at a constant incubation temperature of 5 °C. C loss beyond the incubation period of at least 1 year represents potential C loss. Lines show the predicted relationship between C loss and initial C : N of total soil C. For plot c, the line shows the average predicted relationship between C loss and initial C : N of total soil C with N (%) as the second significant predictor kept at its mean value.

vulnerable, showing potential C losses of up to 90%, under constant incubation conditions. However, deeper organic soils were less likely to respire large amounts of C within the 50 year time frame. Shallow mineral soils were clearly distinguishable from deep mineral soils and showed an average potential C loss of 22% whereas the C loss in deep mineral soils was 9% (Fig. 5c). Carbon loss was highly correlated (R^2 = 0.93) with the slow C pool size showing that soils with a large fraction of slow C are more vulnerable to C decomposition than soils with a large passive C pool. Our calculations of potential C loss also included an uncertainty estimation (97.5% CI, Table S4) which increased over time and was larger with larger amounts of passive C. The 97.5% uncertainty interval for potential C loss after 50 years of incubation ranged from 13.3 to 37.3% over all soil samples.

Linear mixed effects regression results identified C : N as the strongest predictor of C loss at each of the 3 time points (Table 2; Fig. 6). The higher the C : N of a given soil, the higher the C loss, indicating greater vulnerability to C loss via decomposition. Initial C concentration and soil type dropped out of the model as they correlated too much with the other predictors. For the subset of soils that had bulk density, pH, MAT, and MAP data, we performed an additional linear mixed effects model to analyze correlations between C loss and those predictors. However, none of these variables were significant predictors of C loss, at least within this limited dataset. A sensitivity analysis using the upper and lower limit of the uncertainty interval of potential C loss showed that the relationship with C : N was robust (Table S6).

Discussion

Understanding the rate and form of C released to the atmosphere is essential to predict future losses of permafrost C and associated climate change (Schuur *et al.*, 2008). Our synthesis study illustrates how

long-term incubation studies with soils collected across the circum-polar region together with modeling can provide important insights into the factors controlling potential losses of C through the fast and slow C pools.

Rapidly declining respiration rates within the first few weeks of incubation (Fig. S1) were the result of a small C pool (<5% of total C) with a rapid turnover; this pattern was observed in both organic and mineral soils and confirms previous results (Dutta *et al.*, 2006; Shaver *et al.*, 2006; Lavoie *et al.*, 2011; Knoblauch *et al.*, 2013). This indicates that long-term permafrost C degradation will be dominated by slower degrading C, which was separated by the deconvolution analysis into a slow and a passive C pool. The passive C pool represents a C fraction that is not decomposable within years, decades or centuries and therefore persists in soils (Schmidt *et al.*, 2011). In contrast to spectroscopic, physical or chemical fractionation of permafrost C (Dai *et al.*, 2001; Dutta *et al.*, 2006; Shaver *et al.*, 2006; Wickland & Neff, 2008; Waldrop *et al.*, 2010), our three-pool C decomposition model divides the organic C into pools with similar turnover times that are not necessarily comprised of biochemically uniform molecules, but rather reflect inherent kinetics of the C compounds for their decomposition at given laboratory incubation conditions (Davidson & Janssens, 2006). Our results showed that organic soils have larger amounts of slow turning over C (mean = 29.3% ± 26.3) than mineral soils (mean = 10.7% ± 14.0), which strongly correlated with higher C loss. Inversely, passive C accounted on average for 69.2% (±26.9) of all C in organic soils and for 88.0% (±14.1) in mineral soils. Variations in the amounts of passive C in organic soils can be explained by different mechanisms underlying C incorporation into permafrost. Some of the C had been subject to microbial decomposition prior being incorporated into permafrost, leaving behind C of low quality (Schuur *et al.*, 2008). Furthermore, development of soil structures during permafrost formation may have physically disconnected organic matter and decomposers preventing some C from being decomposed (Schmidt *et al.*, 2011).

Short turnover times (mean of 0.35 years, ±0.6) observed in the initial stages of permafrost C mineralization indicate high decomposability of the fast C pool. Little information is available on how rapidly different C fractions turn over in permafrost soils, yet this is crucial information for modeling post thaw permafrost C vulnerability. A recent modeling approach by Knoblauch *et al.* (2013) using 26 incubated permafrost soil samples from Siberia estimated a 'labile' pool with a turnover time of 0.26 years (at 4 °C) and a 'stable pool' with an average turnover time of 170 years. We included the Knoblauch *et al.* (2013) data in our analysis, in addition to 95 other samples, and found that their labile pool estimate was comparable to our fast C pool within the larger dataset in both size and turnover time, suggesting these rate estimates are applicable across a broad region of the permafrost zone. Instead of separating less degradable C into a slow and passive C pool as we did, Knoblauch *et al.* (2013) pooled everything that was not easily decomposable into one large stable C pool and estimated an average turnover time of 170 years which in their model is the time after the pool is reduced to the fraction of 1/e. However, this approach assumes that all C from deep, mostly mineral soils is decomposable whereas we assume that some of the C in mineral soils is almost resistant to mineralization. By including a third pool with long turnover times in our model we allow one C pool to be protected from decomposition which constrains projections of C loss. Furthermore, recent improvements in our understanding of SOM dynamics suggests that a fraction of soil C persists in soils regardless of its molecular structure because of an interaction between substrate, microbial communities and abiotic factors (Kleber, 2010; Kleber *et al.*, 2011; Schmidt *et al.*, 2011; Dungait *et al.*, 2012; Schimel & Schaeffer, 2012).

Potential vulnerability of permafrost C

Recent thawing of permafrost (Osterkamp, 2007) is making large amounts of previously frozen C available to decomposition (Harden *et al.*, 2012). Depending on its decomposability, large amounts of C could be added to the atmosphere in the near future, which is one of the more likely positive feedbacks to climate change (Schuur *et al.*, 2008, 2013; Koven *et al.*, 2011; Schaefer *et al.*, 2011; MacDougall *et al.*, 2012; Schneider von Deimling *et al.*, 2012). Our extrapolations of C loss from permafrost showed that on average 23.1% (±23.1) of organic C measured in incubation studies could potentially be lost when projected over a 50 incubation year time period at a constant reference temperature of 5 °C. This calculation assumes that 12 months of the year the organic matter is exposed to 5 °C, and so should be viewed as a lab potential rather than an extrapolation to real-world conditions. Projecting C loss at a temperature of 1 °C (using a Q_{10} of 2.5), the average C loss from organic and mineral soils still accounts for 21.5% (±22.2) of total C lost over 50 incubation years, suggesting that incubation temperature, marginally above freezing, is less important than C quality. This is supported by Dutta *et al.* (2006) who incubated permafrost soils at 5, 10, and 15 °C and found that C fluxes later in the incubation correlated more with bulk soil C quality than with temperature. For the 50 incubation year extrapolation, the average potential C loss from organic soils accounted

for 40.0% (±26.0) of initial C compared to mineral soils (mean C loss of 13.8% ± 14.5) regardless of model assumptions. By using incubation data to upscale potential C loss we are using laboratory conditions for C decomposition as there is no input of fresh litter and no change in abiotic factors. However, despite the limitations of incubation studies, we can obtain knowledge of soil C turnover from incubation data and understand the effects of soil organic matter turnover as a whole. Knoblauch *et al.* (2013) estimated the average aerobic C loss from Siberian permafrost to be 15% of the initial C over 100 year projections at 4 °C for mineral soils, assuming soils would only be thawed for 4 months a year. Comparisons with an equivalent number of thaw months in our study gave 13% C loss for our mineral soils with the small discrepancies likely being caused by the larger dataset used in our synthesis and our three-pool model approach instead of a two-pool model.

There are large amounts of organic C stored in thick organic layers in permafrost which reside in the upper permafrost and are most susceptible to thaw (Harden *et al.*, 2012). Therefore, an average C loss of 40% in organic soils after 50 incubation years of decomposition (in the absence of new organic material) suggests that very large quantities of C could be released to the atmosphere from organic horizons alone. However, high C concentration in soils does not translate to greater decomposability of the C; it only indicates that a large quantity of C is present and could potentially be decomposed. This is an important distinction as the absolute C release of a soil tells a different story than the relative C release expressed as percentage of initial C. With the latter approach, we can estimate the relative C loss from each soil independent of its quantity, which represents the qualitative nature of the stored C. Despite different C concentrations in mineral vs. organic soils they can both have a similar proportional C loss, indicating that both soil types can be equally vulnerable to C loss. As illustrated in Fig. 5, organic soils showed higher mean% of initial C loss than both types of mineral soils, but there was considerable potential C loss in some of the deep mineral soils. The differences in C release within permafrost soil types can be explained by different mechanisms of how C was incorporated into permafrost (Schuur *et al.*, 2008).

C loss upscaling

A recent study by Harden *et al.* (2012) estimated that by 2050 between 147 (RCP4.5) to 208 (RCP8.5) Pg C from permafrost could become thawed using a range of warming scenarios (RCP: Representative Concentration Pathway of 4.5 or 8.5 W m^{-2} by 2100). We combined the estimated amounts of thawed C by 2050 from Harden *et al.* (2012) with an average aerobic C loss of 16.6% for the same timeframe (assuming soils would be thawed for only 4 months per year for the next 40 years till 2050 and then stay at a constant temperature of 5 °C) for a rough upscaling of potential C loss across the permafrost zone. Within the next four decades, between 24.4 Pg C to 34.5 Pg C could potentially be released to the atmosphere when using RCP4.5 and RCP8.5. These potential C losses likely overestimate the carbon loss that can be expected under natural conditions but they indicate the large amount of C from the permafrost zone that could be added to the atmosphere.

C : N as scaling parameter

A primary objective of this synthesis study was to identify whether any commonly measured environmental or soil factor could be used as a metric to represent permafrost C quality and vulnerability across soil types. In this analysis, we show that C : N was the strongest predictor of C loss over time, explaining more variation in C loss across samples than did C or N concentration alone. In the early stages of litter decomposition, C : N of organic matter is negatively related to decomposition rates due to the high nutrient demand of decomposers (Enríquez *et al.*, 1993). However, over time with continued decomposition, C : N ratios decrease due to losses in C and retention and recycling of N (Malmer & Holm, 1984; Chapin *et al.*, 2002). As a result, C : N in our soils decreased with depth, indicating a higher degree of historical decomposition as has been shown by many previous studies (Kuhry & Vitt, 1996; Dutta *et al.*, 2006; Callesen *et al.*, 2007). In permafrost ecosystems, partially decomposed vegetation (with an incomplete history of decomposition) was buried into permafrost and stayed frozen for thousands of years leaving behind organic matter with lower C : N (Schirrmeister *et al.*, 2011). In this case, positive relationships between C : N and C losses (Fig. 6) may reflect long-term permafrost history and the fact that N does not leave the system and becomes incorporated into chemical structures that have low decomposability such as aromatic rings (Chapin *et al.*, 2002).

Some very deep soils in Siberia, known as Yedoma soils, have been described as relatively rich in easily decomposable C as extensive areas of organic-rich loess accumulated during the Pleistocene (Zimov *et al.*, 2006a). However, projected C loss over the 50 incubation year period was smallest (mean of 9%) in deep soils, as most C was attributed to the passive C pool. Nevertheless, deep soils store very large quantities of C and are vulnerable to thaw, so a small relative emission rate can still promote large absolute emissions. In addition, deep C can become exposed to the soil surface

through various disturbance processes such as thermal erosion (Grosse *et al.*, 2011) that are not considered in models that project active layer thickening (e.g. Harden *et al.*, 2012) suggesting that exploring the consequences for abrupt thaw mechanisms in promoting C loss from deep permafrost soils still needs further work.

Boreal soils exhibited a slightly higher correlation with the slow C pool size and C : N than tundra soils, however, this variable was not significant at $P = 0.05$, showing that the C quality in boreal and tundra soils is similar. In addition to % initial C and C : N, other soil predictors might also be important to predict future C loss from permafrost soils. Nevertheless, various multiple regression analyses with a subset of soils reporting MAT, MAP, pH, and bulk density did not reveal any significant relationships with any of the variables. Depth, at which soil samples were taken, was included in the main regression analysis but was not significant and seems to be a rather unreliable measure of C quality as depth was differently reported and means different things at different sites. However, the dataset used in this study is still of limited nature and we do not rule out that other variables are important, however, we could not detect them here.

Permafrost thaw will not only increase aerobic C decomposition but also anaerobic C release in the form of methane (CH_4) if local drainage conditions are anoxic. Two recent incubation studies have looked at aerobic and anaerobic C mineralization from permafrost-affected soils and found that although CH_4 has the higher global warming potential (Shindell *et al.*, 2009) than CO_2 the total C release under anaerobic conditions is substantially reduced (Lee *et al.*, 2012; Knoblauch *et al.*, 2013).

This synthesis study focused on the vulnerability of permafrost C to decomposition by estimating C pool sizes and turnover times of thawed permafrost. The vulnerability of C ranges from 40% loss in organic soils to 16% in shallow mineral soils and 9% in deep mineral soils over 50 years of incubation at a given temperature of 5 °C. Our results show that across the permafrost zone organic and mineral soils with high C : N are the most vulnerable soils to C loss in the near future. The C : N in permafrost soils reflects the stage of decomposition when organic matter was incorporated into permafrost thousands of years ago. High C : N ratios therefore mean large amounts of easily decomposable C that result in higher C loss. The C : N metric can be used to scale C quality across landscapes and soil maps as it best describes C pool sizes and potential C loss from permafrost. Furthermore, we suggest including C : N into ecosystem models to account for varying C pool sizes and vulnerability of permafrost C across the arctic.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Observed and modeled respiration rates for five randomly selected soil samples (a–e). The samples are the same as in Table S3.
Table S1. Soil sample parameters for each individual soil core.
Table S2. Prior parameter range for C pool partitioning coefficients (f_i) and decay rates (k_i).
Table S3. Comparison of data-model fit and C loss for three time frames using a 2-pool and a 3-pool model for five randomly selected soil samples.
Table S4. Correlations between model parameters.
Table S5. MLE (97.5% CI) for all parameters and potential C loss for 1, 10, and 50 incubations years for all 121 soil samples.
Table S6. Multiple regression results for estimated parameters and C loss (MLE, upper and lower limit of 97.5% CI) for 50 incubation years at 5 °C.