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Carbon loss from northern circumpolar permafrost soils amplified by rhizosphere
 priming

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As global temperatures continue to rise, a key uncertainty of climate projections is the 45 microbial decomposition of vast organic carbon stocks in thawing permafrost soils. 46 47 Decomposition rates can accelerate up to four-fold in the presence of plant roots and this mechanism – termed the rhizosphere priming effect – may be especially relevant to 48 49 thawing permafrost soils as rising temperatures also stimulate plant productivity in the Arctic. However, priming is currently not explicitly included in any model projections of 50 future carbon losses from the permafrost area. Here we combine high-resolution spatial 51 and depth-resolved datasets of key plant and permafrost properties with empirical 52 53 relations of priming effects from living plants on microbial respiration. We show that 54 rhizosphere priming amplifies overall soil respiration in permafrost-affected ecosystems 55 by ~12 %, which translates to a priming-induced absolute loss of ~40 Pg soil carbon from the northern permafrost area by 2100. Our findings highlight the need to include 56 57 fine-scale ecological interactions in order to accurately predict large-scale greenhouse 58 gas emissions, and suggest even tighter restrictions on the estimated 200 Pg 59 anthropogenic carbon emission budget to keep global warming below 1.5°C.

Rapidly rising temperatures spark a biotic awakening of the Arctic that accelerates carbon 60 cycling and may induce a positive feedback to global warming¹⁻³. Deepening of the 61 seasonally-thawed surface active layer of permafrost soils is expected to promote the 62 microbial degradation of previously frozen soil organic matter (SOM) to CO₂ or CH₄. At the 63 same time, large areas across the northern permafrost region already show enhanced plant 64 65 gross primary production (GPP) as a result of rising temperatures and atmospheric CO₂ fertilization⁴. However, existing estimates of broad-scale CO₂ emissions from permafrost soils 66 67 do not consider interactions between plants and soil microorganisms (Fig. 1a).

Plants can accelerate SOM degradation by a mechanism termed the rhizosphere priming 68 69 effect (RPE; Fig. 1b). The RPE is defined as a change in the microbial respiration of soil organic carbon (SOC) affected by plant roots compared to soil without roots, and is the 70 71 composite effect of enhanced microbial activity by increased carbon availability from root 72 exudates and litter, altered pH values, soil aggregation, and microbial community composition⁵⁻⁹. Recent reviews show a stimulation of SOC respiration by up to 380% in 73 experiments with intact plants and by up to 1200% in *in vitro* experiments that simulate the 74 input of plant compounds^{5,10}. Both experimental¹¹ and observational^{12–14} evidence suggest 75 persistence of the priming effect over long time frames. Since Arctic soils are vulnerable to 76 the RPE^{12,15–20}, this raises concern about underestimating future greenhouse gas emissions 77 from permafrost soils in a greening Arctic (Fig 1c). 78

79

80 Quantifying priming-induced carbon losses

Here, we present the first estimate of RPE-induced SOC losses across the northern circumpolar permafrost area under baseline (2010) and future climatic conditions (2100, representative concentration pathways [RCP] 4.5 and 8.5). The aim of this study is two-fold, to provide a robust estimate for the magnitude of RPE including uncertainty analyses, and to

identify key knowledge gaps that should be targeted by future experimental work. The novel 85 PrimeSCale model integrates plant root and microbial activities with soil physico-chemical 86 properties at high spatial (5 x 5 km^2) and depth resolution (5 cm intervals down to a max. 87 depth of 3 m). To that end, we combined two meta-analyses of empirical data on the 88 magnitude of the RPE relative to basal and root respiration (Fig. 1d) and on root depth 89 distribution in tundra and boreal ecosystems (Extended Data Fig. 2-4) with databases and 90 model outputs of SOC storage²¹, SOM composition $(C/N)^{22}$, GPP^{23,24}, active layer thickness 91 $(ALT)^{24}$, basal SOC respiration rates²⁴ and vegetation type²⁵ in the northern circumpolar 92 permafrost area. The combined uncertainties are accounted for using Markov chain Monte 93 94 Carlo simulations (see Methods as well as Extended Data Fig. 1 and Supplementary Table 1 for details of model setup and input data). 95

96 The impact of plant roots on SOC respiration was quantified based on a meta-analysis of 97 experimental studies that specifically measured RPE induced by intact plants (n = 65; Supplementary Table 2). Our meta-analysis showed that SOC respiration from plant-98 99 affected soil was on average higher than from unaffected soil by a factor of 1.54 ± 0.54 (mean \pm standard deviation; "RPE ratio"). This range is in line with *in vitro* experiments on 100 101 permafrost soils that substitute intact plants by addition of plant-derived organic compounds¹⁶. The meta-analysis further revealed a significant, positive relationship between 102 the RPE ratio and root respiration, as a proxy for root activity (Fig. 1d). We applied this 103 104 relationship in the *PrimeSCale* model to derive RPE ratios for individual vegetated grid cells and soil depth increments (Fig. 2), with root respiration for each grid cell estimated from GPP 105 and proportionally assigned to individual soil depth increments using rooting-depth 106 107 distribution functions. In a second meta-analysis (n = 66; Supplementary Table 3) we generated separate ALT-dependent rooting-depth distribution functions for erect-shrub, 108 prostrate-shrub, wetland and graminoid tundra and boreal forest, all within the northern 109

permafrost domain (Extended Data Fig. 2). These functions account for denser plant rooting 110 111 in the shallow soil and an increase in plant rooting depth with active layer deepening 112 (Extended Data Fig. 2-4). Under current conditions, 90% of roots are in the top 1.1 m in boreal forest and 0.7 m in tundra. Due to shifts in vegetation and active layer deepening these 113 values are projected to increase by 2100 to 1.2 m and 0.8 m in the RCP 4.5 scenario, and to 114 115 1.4 m and 1.1 m in the RCP 8.5 scenario (Fig. 2b). Finally, spatial and depth-explicit basal SOC respiration rates (Supplementary Table 4) derived from the Community Land Model²⁴ 116 117 were combined with RPE ratios for each grid cell and depth increment, to calculate absolute 118 rates of additional SOC respiration induced by the RPE (Fig. 2c-e).

119

120 Rhizosphere priming amplifies permafrost soil carbon loss

121 By accounting for interactions between spatial and depth distributions of seasonally unfrozen 122 SOC and roots, and the spatial distribution of GPP, the *PrimeSCale* model permits a first 123 broad-scale assessment of the magnitude of the RPE in natural ecosystems. Across the study area, we estimate that the RPE induces additional SOC respiration of 0.40 Pg yr⁻¹ (10 – 90%) 124 CI, 0.06 - 0.79Pg yr⁻¹) under 2010 conditions, and of 0.43 Pg yr⁻¹ (0.07 - 0.87 Pg yr⁻¹; RCP 125 4.5) and 0.49 Pg yr⁻¹ (0.07 – 0.99 Pg yr⁻¹; RCP 8.5) in 2100 (Table 1, Fig. 3d-f). At present, 126 RPE-induced SOC respiration is strongly dominated by the shallow soil with 84% from layers 127 128 less than 20 cm deep (>95% from layers less than 40 cm deep). Although RPE depth is projected to increase until 2100 due to increasing ALT and consequently deeper rooting, 69% 129 130 of RPE-induced SOC respiration still derives from soil layers less than 20 cm deep (89% from layers less than 40 cm deep; RCP 8.5) (Fig. 2). The absolute increase over time for both RCPs 131 results from a general increase in SOC respiration rates due to climate warming. The relative 132 133 importance of the RPE remains largely stable over time from an average RPE-ratio of 1.14 in 2010, to 1.13 (RCP 4.5) or 1.11 (RCP 8.5) by 2100 (Fig. 3a-c). Overall, we estimate that the 134

135 RPE will provoke the cumulative absolute loss of 38 Pg SOC (5.9 –75 Pg; RCP 4.5) or 40 Pg

136 SOC (6.0 – 80 Pg; RCP 8.5) to the atmosphere between 2010 and 2100 (Fig. 3d-f; Table 1).

137 Since the occurrence of the RPE might depend on the quality of SOM, and in particular on a limitation of soil microorganisms by low C availability^{7,16,26}, we performed a sensitivity 138 analysis under the assumption that only SOM with a C/N ratio below 20 is susceptible to the 139 RPE (Supplementary Table 5). This sensitivity analysis resulted in lower but still substantial 140 estimates of RPE-induced SOC loss of 27 Pg (4.3 - 55 Pg, RCP 4.5) and 28 Pg (4.2 - 60 Pg, RCP 4.5)141 RCP 8.5) between 2010 and 2100 (Fig. 3g-i; Table 1). Although the theory behind the 142 assumption of a microbial C limitation requirement matches many experimental findings, we 143 emphasize that individual studies observed priming also at high C/N (organic soils) $^{27-29}$. We 144 therefore consider this a sensitivity analysis and highlight the need to target priming at high 145 C/N in experimental studies. 146

Estimated RPE-induced SOC-respiration showed high spatial variability across the northern 147 circumpolar permafrost region (Fig. 3, Extended Data Fig. 6). Regression analysis revealed 148 soil and vegetation characteristics as primary drivers of this variation ($R^2 = 0.10-0.70$) as 149 150 opposed to climate and topography, with maxima in areas with high SOC stocks and change 151 in GPP. In the no C/N threshold scenario, RPE-induced SOC-respiration was strongly correlated to occurrence of peat soils (Histels; $R^2 = 0.33$) owing to the high SOC density in 152 this soil type. Assuming that microbial C limitation is a requirement for priming (threshold 153 154 scenario) reduced the importance of peat soils (which typically have high C/N) but revealed a 155 strong correlation with the occurrence of cryoturbation that also promotes high SOC storage (Turbels, $R^2 = 0.37$) (Supplementary Table 6). Overall, we identify hot spots of RPE losses 156 in lowlands within the boreal forest biome, including the Hudson Bay, Mackenzie and West 157 158 Siberian Lowlands, as well as large areas across eastern Siberia (Fig. 3).

159

160 Reducing uncertainties of priming-induced carbon losses

While the PrimeSCale model is based on our current understanding of the RPE and 161 162 permafrost soils, it also highlights knowledge gaps for which a paucity of empirical data for meta-analysis or inconclusive relations prevent their robust incorporation into broad-scale 163 models: (i) Low temperatures and frequent anoxia in permafrost soils might affect the 164 magnitude of the RPE³⁰, and geochemical and mineral changes related to permafrost thaw 165 might further affect mineral protection of SOC, and in turn the $RPE^{5,9,31}$. (ii) Our model does 166 not consider leaching of dissolved organic carbon to the deeper soil. Given also the strong 167 priming potential of deep mineral soil horizons observed in *in vitro* experiments¹⁶, leaching of 168 169 easily available substrate could induce a priming effect that is not restricted to the vicinity of roots³². (iii) We assumed that rooting patterns follow an ALT-dependent dose-response 170 curve³³, which strongly constrains the influence of roots on deeper soil layers. Recent field 171 172 experiments suggest, however, that permafrost thaw might promote deeper rooting of some plant species³⁴⁻³⁶ to exploit plant-available nutrients at the permafrost thaw-front^{35,37,38}. 173 Further, (iv) while we included spatial variation in GPP and differences in rooting patterns 174 between different tundra vegetation types and boreal forest as well as future changes in 175 vegetation distribution³⁹, we did not incorporate potential changes in the relative allocation of 176 GPP to roots³⁵ or different mycorrhizal type associations. While many studies suggest a role 177 of mycorrhiza in priming^{13,14,40,41} and spatial products for mycorrhizal type distribution 178 exist⁴², mycorrhizal type is not considered in our model since mycorrhizal type effects on soil 179 C-sequestration are highly context dependent⁴³. Lastly, (v) potential future change in 180 functional microbial diversity is not addressed, although recent literature shows that microbial 181 communities in newly thawed permafrost soils differ from those in active layer soils^{44,45} and 182 upon thaw are vulnerable to change in both community composition^{45,46} and likely 183

184 functioning^{46–48}. Given the large potential impact of RPE on global permafrost SOC losses,

these current uncertainties should urgently be targeted by experimental studies.

186

187 Implications for the global carbon budget

188 Our results demonstrate the importance of the rhizosphere priming effect for future carbon releases from permafrost-affected soils to the atmosphere. The estimated RPE-induced ~40 Pg 189 190 SOC loss from the northern permafrost area until 2100 (RCP 8.5) is additional to permafrost carbon losses due to active layer deepening and increasing soil temperatures, currently 191 estimated at 57 Pg C (range 28-113 Pg; RCP 8.5)³ over the same period. Moreover, the 192 193 magnitude of RPE-induced greenhouse gas emissions is in the same range or even exceeds those from other key processes in the northern permafrost region, e.g. from abrupt permafrost 194 collapse⁴⁹ or methane release from lakes, ponds⁵⁰ and the Arctic Ocean⁵¹ (Supplementary 195 196 Table 7). Remaining knowledge gaps emphasize the need for further studies of plant-microbe 197 interactions in permafrost-affected soils. The RPE-induced permafrost carbon release to the 198 atmosphere is currently unaccounted for in global emission scenarios and implies that the remaining anthropogenic carbon budget to keep warming below 1.5 or 2°C, currently 199 estimated at 200 and 430 Pg C, respectively⁵², may need to be even more constrained. 200

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- F.K. and E.D. conceived the idea. F.K., B.W. and E.D. led the conceptual model development
- in collaboration with M.K., C.B., G.B.-W., S.F., K.G., G.G., G.H., E.K., P.K., S.M., A.R and
- J.W. The model was implemented by M.K. and M.J., and C.B., N.G., G.H., C.K., and P.K.
- 346 provided additional data. M.K., G.H., C.K., J.W. and E.D. performed additional statistical
- analyses. F.K. and B.W. wrote the manuscript with contribution of all authors.

Competing interests

349 The authors declare no competing interests.

350 **Figure captions**

351 Fig. 1. The rhizosphere priming effect (RPE). (a) Permafrost soil organic carbon (SOC) 352 respiration without RPE; (b) SOC respiration including the RPE under present conditions; (c) 353 Future scenario considering climate warming: faster growing plants; deeper active layer; 354 deeper rooting depth. (d) The RPE ratio (SOC respiration from plant-affected over not plantaffected soils) vs root respiration, an indicator for plant root activity. Data are from meta-355 356 analysis of studies quantifying RPE in experiments with intact plants, representing 65 individual treatment combinations. The dotted line indicates an RPE ratio of 1, i.e. no RPE, 357 358 with observed positive RPE above and negative RPE below.

359

Fig. 2. Depth distribution of soil and root properties, and the RPE. Averages across (b-d) or summed over (a, e) the northern circumpolar permafrost region, of (a) total SOC stock and SOC stocks above the ALT in 2010 and 2100 (RCP 8.5); (b) plant root percentage and cumulative percentage in 2010 and 2100; (c) soil respiration without the RPE; (d) RPE ratios (SOC respiration from plant-affected over not plant-affected soils) in seasonally unfrozen and vegetated soils and (e) absolute annual RPE-induced SOC losses in 2010 and 2100. Uncertainty ranges are included for c-e. See Extended Data Fig. 1 for model structure.

367

Fig. 3. Spatial distribution of the RPE across the northern circumpolar permafrost region in 2010 and 2100 (RCP 4.5 and 8.5). (**a-c**) Distribution of the RPE ratio and (**d-i**) of the absolute annual RPE-induced SOC loss (in Mg C km⁻² yr⁻¹), assuming that (**d-f**) all plant-affected SOC is susceptible to the RPE (no C/N threshold scenario) or that (**g-i**) microbial carbon limitation is required (C/N threshold scenario). See **Extended Data Fig. 6** for coefficients of variation.

373 Tables

Table 1. Annual and cumulative RPE-induced SOC respiration from the northern circumpolar permafrost area in 2010 and 2100 (RCP 4.5 and 8.5). The RPE-induced SOC respiration was calculated in two scenarios, assuming that all plant-affected SOC is susceptible to the RPE (no C/N threshold scenario) or that microbial carbon limitation is required (C/N threshold scenario). Values are means for Monte Carlo (N = 1000) simulations (10% - 90% confidence intervals).

	2010	2100	2100								
		[RCP 4.5]	[RCP 8.5]								
Annual RPE-induced SOC respiration ($Pg yr^{-1}$)											
No C/N threshold scenario	0.40 (0.06 - 0.79)	0.43 (0.07 - 0.87)	0.49 (0.07 - 0.99)								
C/N Threshold scenario	0.28 (0.05 - 0.60)	0.31 (0.05 - 0.61)	$0.34\ (0.05 - 0.74)$								
Cumulative RPE-induced SOC respiration (Pg)											
No C/N threshold scenario	38 (5.9 - 75)	40 (6.0 - 80)									
C/N Threshold scenario		27 (4.3 – 55)	28 (4.2 - 60)								

374

375 Methods

376 Overview of the PrimeSCale model

377 The PrimeSCale model was developed to quantify soil organic carbon (SOC) respiration 378 induced by the rhizosphere priming effect (RPE) on large spatial scales and with high depth resolution, while accounting for interactions between spatial and depth distributions of plant-379 380 carbon inputs and SOC content and quality. The model represents current peer-reviewed RPE knowledge only, i.e. potential mechanisms for which evidence is inconclusive or where data 381 382 are too scarce for meaningful meta-analysis are not included. The model thus reveals 383 knowledge gaps, which are discussed in the manuscript section 'Reducing uncertainties of 384 priming-induced carbon losses'. The relatively simple model structure allows for rapid integration of new data when available (Extended Data Fig. 1). 385

386 The current study focuses on the terrestrial northern circumpolar permafrost area, defined by 387 the overlapping extent of permafrost terrain in the Circum-Arctic Map of Permafrost and Ground-Ice Conditions⁵³ and the Northern Circumpolar Soil Carbon Database^{54,55}. After 388 389 masking out all non-vegetated areas, i.e. barren land, rocklands, land ice (glaciers and icesheets), and freshwater, the study area covers 14 million km², around 12% of the global ice-390 free land area. The model's spatial resolution is 5 km x 5 km, and the study area includes 391 561,956 active grid cells. We considered only the top 3 m of the soil, where the vast majority 392 of plant roots is located³³. The 0-3 m soil column was divided into 5 cm thick layers, resulting 393 394 in 60 soil layers. We thus modelled the RPE in 33.7 million grid cubes with a dimension of 5 395 km x 5 km x 5 cm. Results were reported either as global values, as averages over soil layers for each grid cell to derive maps, or as averages over grid cells for each soil layer to derive 396 depth profile figures. 397

We estimated current (year 2010), future (year 2100) and cumulative (2010 - 2100) RPEinduced SOC losses under the representative concentration pathway (RCP) scenarios 4.5 and

400 8.5, considering projected changes in active layer thickness (ALT), gross primary production 401 (GPP), vegetation distribution and growing season length based on existing models. To 402 estimate the cumulative RPE-induced SOC losses, we assumed linear changes in ALT, 403 vegetation distribution and GPP per growing season day for each grid cell until 2100. An 404 overview of all input data and model parameters is given in **Supplementary Table 1**. The 405 PrimeSCale model is structured in three modules: Soil, Plant and Soil Respiration. The model 406 setup is outlined in **Extended Data Fig. 1**.

407

408 Soil Module

409 Soil organic C stocks of the northern permafrost area

Data on SOC stocks were derived from the Northern Circumpolar Soil Carbon 410 Database^{21,54,55}, at a spatial resolution of 5 km x 5 km and a depth resolution of 5 cm, to a 411 maximum depth of 3 m. We used data from all three Gelisol suborders (Histels, Orthels, 412 Turbels), and distinguished three soil horizon types: organic, cryoturbated and mineral²². Note 413 that the discontinuity in SOC stocks at 1 m (Fig. 2a) is due to a potential sampling bias in the 414 Northern Circumpolar Soil Carbon Database^{21,55}. For each of the soil horizon types, SOC was 415 summed over the three Gelisol suborders. Soil organic carbon stocks are stable over time in 416 our model, creating a $\sim 3\%$ overestimation of the entire carbon pool by 2100 as estimated from 417 CLM projections of SOC changes⁵⁶. The SOC stocks for the three soil horizon types are 418 419 presented in Extended Data Fig. 7.

420

421 *Active layer depth*

The thickness of the seasonally thawed active layer at the surface of permafrost soils (ALT; active layer thickness) was calculated based on CLM4.5 simulations²⁴. The suitability of 424 CLM for this purpose has been previously described and confirmed⁵⁷. We used 11-year 425 average ALT values for the years 2010 (2006-2016) and 2100 (2095-2105) under the RCP4.5

426 and RCP8.5 scenarios (Extended Data Fig. 7).

427

428 Soil organic matter C/N ratios

Previous studies in permafrost and other soils suggest that C limitation of soil microorganisms 429 might be a requirement for the RPE^{15,16,26,58}. We therefore calculated RPE-induced SOC 430 respiration for two scenarios: (i) in the "no threshold scenario", we assumed that RPE is 431 independent of microbial C limitation; (ii) in the "threshold scenario", we assumed that 432 433 microbial C limitation is required for the RPE. Microbial C limitation has been suggested to occur where the C/N ratio of SOM is below a Threshold Elemental Ratio, that is estimated to 434 fall between 20 and 27 (mol/mol)⁵⁹⁻⁶¹. For the threshold scenario, we thus used a threshold 435 436 C/N ratio of 20 which is at the lower end of the suggested range, i.e. more conservative, and 437 assumed that SOM with a C/N ratio above this threshold is not susceptible to the RPE (RPE 438 ratio = 1). The threshold scenario serves as a sensitivity analysis; presented data refer to the 439 no threshold scenario unless specified otherwise. We estimated the fraction of soil horizons that fall above or below this threshold based on observational data (N = 472) compiled from 440 previous studies^{22,62} and extensive unpublished data from G. Hugelius and P. Kuhry. The 441 442 observational data were grouped by soil horizon type and depth in the soil column to extract the fraction of observations that fell above the C/N threshold of 20 (Supplementary Table 443 5). 444

445

446 <u>Plant Module</u>

447 *RPE ratio function*

The RPE is driven by the transfer of fresh organic compounds from plants to the soil, and is 448 449 consequently expected to show a positive relationship to plant root activity. To describe this 450 relationship, we conducted a meta-analysis of published studies (retrieved from the Web of Science, 10.10.2016) that report on experiments with intact, potted plants that were 451 continuously labelled with ¹³C-depleted CO₂. In such an experimental setup, the ¹³C-depleted 452 453 part of respired CO₂ is derived from the plants themselves or plant-associated microorganisms that thrive on plant root exudates or litter (further termed plant-associated respiration), 454 455 whereas non-depleted CO₂ comes from SOC decomposition (further termed SOC respiration). 456 Our meta-analysis included only studies where (a) plants were grown in natural soils, (b) plants were continuously labelled with ¹³C-depleted CO₂, and in which (c) SOC respiration 457 from planted pots, (d) SOC respiration from unplanted control pots, and (e) either total or 458 belowground plant-associated respiration were published or could be obtained from the 459 460 authors.

461 We refrained from including studies that were not based on experiments with isotopically 462 labelled living plants, but instead simulate plant-soil C transfer by adding one or few isotopically labelled organic substrates to the soil. While such a reduced experimental setup is 463 a prerequisite for dissecting the mechanisms underlying RPE¹⁰, only experiments using living 464 465 plants capture the full natural range of soil modifications by plants (continuous exudation of a wide range of chemical compounds released by plants, changes in nutrient and water 466 availability, pH, soil aggregation, and microbial community composition)^{63,64}, and allow us to 467 468 link the magnitude of RPE to estimates of root activity.

The dataset used for meta-analysis consisted of 12 studies on intact plants and comprised 65 individual treatment combinations (i.e., combinations of soil, plant species, and growth conditions, **Supplementary Table 2**). All studies reported total or belowground plant associated respiration, which we converted into root respiration (See **Supplementary**

Methods). All soils were mineral soils, most soils and plant species were derived from 473 temperate ecosystems, and temperatures during experiments were in the range of 15-20°C 474 475 (night) and 25-28°C (day). No studies were available that included arctic or subarctic soils or plants. To minimize potential biases introduced by differences between temperate and arctic 476 477 systems, we normalized RPE by calculating RPE ratios, as (unlabelled) SOC respiration in planted pots divided by SOC respiration in unplanted control pots. We thus aimed to reduce 478 effects of parameters such as temperature, organic matter quantity or quality that drive 479 480 differences in absolute SOC respiration between systems.

The RPE ratios in our meta-analysis ranged from 0.39 to 3.15 (note that RPE-ratio values below 1 represent negative priming), with a mean value of 1.54 (\pm 0.54 standard deviation). These values fall well in line with other recent global meta-analyses of RPE in intact plant experiments (mean 1.59)⁵ and substrate addition experiments (mean 1.27)¹⁰, and, importantly, with RPE ratios measured in 119 arctic permafrost soils after substrate addition (cellulose addition: mean 1.21; protein addition: mean 1.81)¹⁶.

Our meta-analysis showed a positive relationship between RPE ratio and root respiration (mg 487 $C \text{ kg}^{-1}$ soil d⁻¹) across all studies which we described with a saturating (Michaelis-Menten) 488 function fit with Markov chain Monte Carlo methods assuming gamma priors on both fitted 489 parameters, and Normal distributed errors (Extended Data Fig. 8). Since we assumed neither 490 positive nor negative priming at root respiration = 0 we fixed the intercept at 1. The 491 492 Michaelis-Menten fit showed a lower root mean square error than a linear model implying 493 better in-sample prediction performance, and is additionally supported by previous substrate 494 addition experiments where a similar relationship was observed between the amount of substrate added and their utilization by the microbial community^{65,66}. The posterior medians 495 496 of the two fitted parameters yielded the following empirical relationship between RPE and root respiration: 497

498
$$RPE\text{-ratio} = 1 + \frac{2.47 \text{*root respiration}}{13.01 + root respiration}$$
 (1)

This RPE ratio function was applied in the *PrimeSCale* model to calculate RPE ratios for each grid cube, using root respiration estimates derived from GPP that were spread over the soil column employing the root depth distribution functions.

502

503 Gross primary production

Current annual GPP across the northern permafrost area was derived from ref.²³ at a 504 resolution of 0.5°. Future GPP in the year 2100 was estimated for RCP 4.5 and RCP 8.5 505 scenarios, by applying the relative change in GPP CLM 4.5^{24} as a result of rising temperatures 506 and atmospheric CO₂ fertilization to the current GPP estimate, thus preserving the higher 507 spatial resolution of ref.²³. Annual GPP values^{23,24} were converted into daily GPP values for 508 the growing season by dividing annual GPP values by growing season length⁶⁷. For details on 509 510 calculation of future GPP and conversion to daily values see Supplementary Methods. The final GPP maps are presented in Extended Data Fig. 7. 511

512

513 *Root respiration*

514 Root respiration was used as a proxy for plant belowground C allocation in order to estimate 515 RPE and calculated both (1) for grid cells of the model area, based on GPP data (Extended 516 Data Fig. 5), and (2) as a common output unit for studies used in the RPE ratio meta-analysis, 517 based on total plant-associated respiration (respiration by whole plants and root associated microorganisms) or belowground plant-associated respiration (respiration by roots and root 518 associated microorganisms) depending on which was reported in the respective study 519 520 (Extended Data Fig. 8; Supplementary Table 2). We derived conversion factors from previously published extensive meta-analyses on different aspects of plant C allocation, 521

including GPP⁶⁸, total and belowground plant-associated respiration⁶⁹, as well as root 522 respiration⁷⁰. Overall, we estimated root respiration as 3.6% of GPP, 7.4% of total plant-523 524 associated respiration, and 48% of belowground plant-associated respiration. Starting from 525 current and future GPP data, we thus approximated root activity in each grid cell of the study area, which we spread over depth using soil bulk density data (See Supplementary Methods: 526 527 Supplementary Table 8) and root distribution functions (below). Via the RPE ratio function we calculated, for each grid cube, the expected RPE ratio at its root activity. For further 528 529 details on calculation of root respiration and application in the PrimeSCale model see 530 Supplementary Methods.

531

532 *Root depth distribution functions*

533 Root density, and consequently the potential for RPE, decrease with soil depth in natural 534 ecosystems. Root depth distribution functions were therefore applied in the PrimeSCale 535 model to proportionally spread root respiration estimates (see Supplementary Methods) over 536 the soil depth profile. We derived root depth distribution functions for five vegetation types 537 within the northern permafrost area by a meta-analysis of studies on root depth distribution in natural arctic and subarctic tundra systems, as well as in boreal forests, all on permafrost soils. 538 We included only studies where root data from at least three soil depths were reported, where 539 540 information on active layer thickness could be retrieved, and where roots from either the 541 entire vegetation or from all individual species at the site were analysed; in the latter case, 542 individual species data were summed to retrieve combined root profiles for the respective site. Following Schenk and Jackson³³ we fitted logistic dose-response functions for each profile: 543

544
$$r(D) = \frac{100}{1 + \left(\frac{D}{D_{50}}\right)^c}$$
 (2)

where r(D) is the observed cumulative percentage of roots above depth D, and D50 (representing the depth above which we find 50% of the roots), and c (a dimensionless shapeparameter) are estimated from the data. Given that rooting depth is limited by ALT in permafrost soils³³, we expressed D (and D50) as a fraction of ALT; this allows adjustment of maximum rooting depth according to variations in ALT (spatial variation between the grid cells or changes in ALT between 2010 and 2100).

551 For a small number of root profile datasets the non-linear regression routine did not converge, usually because of insufficient data points. These profiles were excluded from subsequent 552 analyses resulting in a total of 66 root profiles from 25 individual studies (Supplementary 553 554 Table 3). This meta-analysis represents to our knowledge the first on boreal forests specifically on permafrost, as well as an almost tripling of tundra root profile observations 555 from 20 to 54 profiles compared to a previous study³³. Subsequently, tundra root profiles were 556 assigned to tundra types (graminoid tundra, erect-shrub tundra, prostrate-shrub tundra and 557 tundra wetland) based on the site description in the original publications and the criteria 558 defined in the Circumpolar Arctic Vegetation Map²⁵. Means as well as uncertainty ranges of 559 D50 and c were calculated for each vegetation type: boreal forest (mean D50 = 0.19, mean c = 560 -2.32, n = 12 profiles), graminoid tundra (D50 = 0.28, c = -2.51, n = 20), erect-shrub tundra 561 (D50 = 0.26, c = -2.92, n = 8), prostrate-shrub tundra (D50 = 0.29, c = -2.75, n = 8) and 562 tundra wetlands (D50 = 0.25, c = -3.20, n = 18). 563

Equation (2) was then used to spread root respiration (equation S1, **Supplementary Methods**) proportionally across the soil depth profile in each vegetation class (**Extended Data Fig. 2-5**), using the corresponding ALT for each grid cell. Vegetation distribution for the tundra biome was based on the present Circumpolar Arctic Vegetation Map²⁵ and its future projections³⁹, and the remaining northern permafrost area was classified as boreal forest (**Extended Data Fig. 9**). 570

571 Soil Respiration Module

572 Basal SOC respiration

Basal SOC respiration without the RPE was calculated for the northern permafrost area using 573 output from the CLM4.5²⁴, which does not include any explicit RPE terms or dependency of 574 SOM decomposition rates on plant productivity or other biotic factors. In addition, the CLM 575 has been shown to systematically underestimate soil turnover rates in cold biomes²⁴, 576 potentially, among other factors, due to lack of RPE. The CLM has, however, a relatively 577 coarse spatial resolution and the absolute values of GPP and SOC at any given site are less 578 579 realistic than those available in the data-based products used in the *PrimeSCale* model (e.g. 580 the CLM model has no peatlands). We therefore calculated basal SOC respiration as a 581 function of GPP, using GPP as a proxy for climatic conditions that favour both GPP and basal SOC respiration^{71–73}. We extracted a relationship between GPP and the fraction of total active 582 583 layer SOC that is heterotrophically respired (Rh/SOC) from permafrost-affected grid cells in 584 the CLM model, and applied this to the high resolution SOC and GPP data used in the PrimeSCale model to generate basal SOC respiration values for each individual gridcell. To 585 avoid an overestimation of basal SOC respiration by CO₂-fertilization of GPP in the future 586 (which is independent from the climatic conditions driving respiration), we used GPP data 587 from a CLM simulation without CO₂-fertilization²⁴ for this purpose. We used quantile 588 regression to fit a model for the median and 10th and 90th percentiles (for uncertainty analysis, 589 see below) of simulated Rh/SOC as a function of simulated GPP, assuming an exponential 590 relationship: 591

$$592 \qquad \frac{Rh}{SOC} = A * GPP^B \tag{3}$$

where A and B are model parameters to be estimated. Because of the wide range of individual grid cell-level SOC values predicted by the CLM4.5, we performed an outlier selection to first remove all zero-productivity grid cells and then use only the 10th-90th percentiles of the grid cells as ranked by their initial SOC stocks. Soil respiration (Rh-fraction * SOC) per grid cell was spread over depth using an ALT-dependent depth function extracted from the CLM model (**Extended Data Fig. 10**).

599

600 Plant-affected SOC respiration

Plant-affected SOC respiration (i.e., SOC respiration considering the RPE) was calculated by 601 602 combining RPE ratios (Plant Module) with basal SOC respiration rates (Soil Respiration 603 Module). For grid cubes that were identified as primeable (i.e. seasonally thawed; GPP > 0; 604 and in the case of the microbial C limitation scenario below a C/N threshold of 20), we 605 calculated plant-affected SOC respiration by multiplying their basal SOC respiration estimate 606 with the RPE ratio. For grid cells identified as not primeable, we set the RPE ratio to 1 (i.e., 607 no RPE) so plant-affected SOC respiration equalled basal SOC respiration (i.e. no increase in 608 SOC respiration).

609

610 <u>Uncertainty estimates</u>

We used Monte Carlo simulations (n = 1000) to analyse model uncertainties (Extended Data
Fig. 6), considering the parameters listed in Supplementary Table 9 and assuming normal
distribution for all parameters except SOC and soil bulk density, for which a truncated normal
distribution with range [0 - 2*mean] was used to avoid negative values. Confidence intervals
(CI) in the main text refer to Monte Carlo Confidence Intervals⁷⁴.

616

617 <u>Analysis of spatial patterns</u>

618 We used linear regression to analyse the relationship of the spatial variation in RPE-induced 619 SOC respiration (2100, RCP 8.5) and RPE ratio of both C/N threshold and no threshold 620 scenarios to the spatial variation of 15 potential drivers: characteristics of the vegetation (GPP 621 in 2100; relative change in GPP until 2100), soil (SOC stock in active layer; SOC stock in 622 upper 3 m; distribution of three Gelisol suborders: Histels, Turbels, Orthels), climate (ALT in 623 2100; change in ALT until 2100; 1970-2000 mean annual average temperature, mean annual precipitation, as well as annual temperature range as a measure of continentality⁷⁵), and 624 terrain (distance to large rivers, distance to lakes, topography⁷⁶⁻⁷⁸) (Supplementary Table 6). 625

626

627 <u>Data availability</u>

All datasets generated and/or analysed for this study are freely available. References to published data can be found in **Supplementary Table 1** (PrimeSCale model), **Supplementary Table 2** (meta-analysis of priming studies) and **Supplementary Table 3** (meta-analysis of root depth profiles for tundra and boreal), as well as in the main text. Other supporting files are available in the Bolin Centre Database (https://bolin.su.se/data/keuperwild-2020) and include: a) Input data for the PrimeSCale model (.mat); b) Intermediate output data of the PrimeSCale model (.xls); c) Output (Geotiff) and metadata.

635

636 <u>Code availability</u>

The custom code for the PrimeSCale 1.0 model, including model script and complementary
function script, is available from the authors upon request, as well as from the Bolin Centre
code repository: https://git.bolin.su.se/bolin/keuper-wild-2020.

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702













PRESENT



























20% Root percentage [%]

30%

0%

10%

20%

30%

0%

10%

20%

30%

10%

10%

0%

20%

30%

10%

20%

30%

0%

0%

PRESENT









1.35 ≤ 0.7







