

1 **Carbon loss from northern circumpolar permafrost soils amplified by rhizosphere**
2 **priming**

3

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45 As global temperatures continue to rise, a key uncertainty of climate projections is the
46 microbial decomposition of vast organic carbon stocks in thawing permafrost soils.
47 Decomposition rates can accelerate up to four-fold in the presence of plant roots and this
48 mechanism – termed the rhizosphere priming effect – may be especially relevant to
49 thawing permafrost soils as rising temperatures also stimulate plant productivity in the
50 Arctic. However, priming is currently not explicitly included in any model projections of
51 future carbon losses from the permafrost area. Here we combine high-resolution spatial
52 and depth-resolved datasets of key plant and permafrost properties with empirical
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
56 from the northern permafrost area by 2100. Our findings highlight the need to include
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.

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

68 Plants can accelerate SOM degradation by a mechanism termed the rhizosphere priming
69 effect (RPE; **Fig. 1b**). The RPE is defined as a change in the microbial respiration of soil
70 organic carbon (SOC) affected by plant roots compared to soil without roots, and is the
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
73 composition⁵⁻⁹. Recent reviews show a stimulation of SOC respiration by up to 380% in
74 experiments with intact plants and by up to 1200% in *in vitro* experiments that simulate the
75 input of plant compounds^{5,10}. Both experimental¹¹ and observational¹²⁻¹⁴ evidence suggest
76 persistence of the priming effect over long time frames. Since Arctic soils are vulnerable to
77 the RPE^{12,15-20}, this raises concern about underestimating future greenhouse gas emissions
78 from permafrost soils in a greening Arctic (**Fig 1c**).

79

80 **Quantifying priming-induced carbon losses**

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

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

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

110 permafrost domain (**Extended Data Fig. 2**). These functions account for denser plant rooting
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
113 boreal forest and 0.7 m in tundra. Due to shifts in vegetation and active layer deepening these
114 values are projected to increase by 2100 to 1.2 m and 0.8 m in the RCP 4.5 scenario, and to
115 1.4 m and 1.1 m in the RCP 8.5 scenario (**Fig. 2b**). Finally, spatial and depth-explicit basal
116 SOC respiration rates (**Supplementary Table 4**) derived from the Community Land Model²⁴
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
124 area, we estimate that the RPE induces additional SOC respiration of 0.40 Pg yr⁻¹ (10 – 90%
125 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
126 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,
127 RPE-induced SOC respiration is strongly dominated by the shallow soil with 84% from layers
128 less than 20 cm deep (>95% from layers less than 40 cm deep). Although RPE depth is
129 projected to increase until 2100 due to increasing ALT and consequently deeper rooting, 69%
130 of RPE-induced SOC respiration still derives from soil layers less than 20 cm deep (89% from
131 layers less than 40 cm deep; RCP 8.5) (**Fig. 2**). The absolute increase over time for both RCPs
132 results from a general increase in SOC respiration rates due to climate warming. The relative
133 importance of the RPE remains largely stable over time from an average RPE-ratio of 1.14 in
134 2010, to 1.13 (RCP 4.5) or 1.11 (RCP 8.5) by 2100 (**Fig. 3a-c**). Overall, we estimate that the

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

147 Estimated RPE-induced SOC-respiration showed high spatial variability across the northern
148 circumpolar permafrost region (**Fig. 3, Extended Data Fig. 6**). Regression analysis revealed
149 soil and vegetation characteristics as primary drivers of this variation ($R^2 = 0.10-0.70$) as
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
152 correlated to occurrence of peat soils (Histels; $R^2 = 0.33$) owing to the high SOC density in
153 this soil type. Assuming that microbial C limitation is a requirement for priming (threshold
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
156 (Turbels, $R^2 = 0.37$) (**Supplementary Table 6**). Overall, we identify hot spots of RPE losses
157 in lowlands within the boreal forest biome, including the Hudson Bay, Mackenzie and West
158 Siberian Lowlands, as well as large areas across eastern Siberia (**Fig. 3**).

159

160 **Reducing uncertainties of priming-induced carbon losses**

161 While the *PrimeScale* model is based on our current understanding of the RPE and
162 permafrost soils, it also highlights knowledge gaps for which a paucity of empirical data for
163 meta-analysis or inconclusive relations prevent their robust incorporation into broad-scale
164 models: (i) Low temperatures and frequent anoxia in permafrost soils might affect the
165 magnitude of the RPE³⁰, and geochemical and mineral changes related to permafrost thaw
166 might further affect mineral protection of SOC, and in turn the RPE^{5,9,31}. (ii) Our model does
167 not consider leaching of dissolved organic carbon to the deeper soil. Given also the strong
168 priming potential of deep mineral soil horizons observed in *in vitro* experiments¹⁶, leaching of
169 easily available substrate could induce a priming effect that is not restricted to the vicinity of
170 roots³². (iii) We assumed that rooting patterns follow an ALT-dependent dose-response
171 curve³³, which strongly constrains the influence of roots on deeper soil layers. Recent field
172 experiments suggest, however, that permafrost thaw might promote deeper rooting of some
173 plant species^{34–36} to exploit plant-available nutrients at the permafrost thaw-front^{35,37,38}.
174 Further, (iv) while we included spatial variation in GPP and differences in rooting patterns
175 between different tundra vegetation types and boreal forest as well as future changes in
176 vegetation distribution³⁹, we did not incorporate potential changes in the relative allocation of
177 GPP to roots³⁵ or different mycorrhizal type associations. While many studies suggest a role
178 of mycorrhiza in priming^{13,14,40,41} and spatial products for mycorrhizal type distribution
179 exist⁴², mycorrhizal type is not considered in our model since mycorrhizal type effects on soil
180 C-sequestration are highly context dependent⁴³. Lastly, (v) potential future change in
181 functional microbial diversity is not addressed, although recent literature shows that microbial
182 communities in newly thawed permafrost soils differ from those in active layer soils^{44,45} and
183 upon thaw are vulnerable to change in both community composition^{45,46} and likely

184 functioning⁴⁶⁻⁴⁸. Given the large potential impact of RPE on global permafrost SOC losses,
185 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
189 releases from permafrost-affected soils to the atmosphere. The estimated RPE-induced ~40 Pg
190 SOC loss from the northern permafrost area until 2100 (RCP 8.5) is additional to permafrost
191 carbon losses due to active layer deepening and increasing soil temperatures, currently
192 estimated at 57 Pg C (range 28-113 Pg; RCP 8.5)³ over the same period. Moreover, the
193 magnitude of RPE-induced greenhouse gas emissions is in the same range or even exceeds
194 those from other key processes in the northern permafrost region, e.g. from abrupt permafrost
195 collapse⁴⁹ or methane release from lakes, ponds⁵⁰ and the Arctic Ocean⁵¹ (**Supplementary**
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
199 remaining anthropogenic carbon budget to keep warming below 1.5 or 2°C, currently
200 estimated at 200 and 430 Pg C, respectively⁵², may need to be even more constrained.

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342 **Author contributions**

343 F.K. and E.D. conceived the idea. F.K., B.W. and E.D. led the conceptual model development
344 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
345 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
347 analyses. F.K. and B.W. wrote the manuscript with contribution of all authors.

348 **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 plant-
355 affected soils) vs root respiration, an indicator for plant root activity. Data are from meta-
356 analysis of studies quantifying RPE in experiments with intact plants, representing 65
357 individual treatment combinations. The dotted line indicates an RPE ratio of 1, i.e. no RPE,
358 with observed positive RPE above and negative RPE below.

359

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

367

368 **Fig. 3.** Spatial distribution of the RPE across the northern circumpolar permafrost region in
369 2010 and 2100 (RCP 4.5 and 8.5). **(a-c)** Distribution of the RPE ratio and **(d-i)** of the absolute
370 annual RPE-induced SOC loss (in Mg C km⁻² yr⁻¹), assuming that **(d-f)** all plant-affected SOC
371 is susceptible to the RPE (no C/N threshold scenario) or that **(g-i)** microbial carbon limitation
372 is required (C/N threshold scenario). See **Extended Data Fig. 6** for coefficients of variation.

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 [RCP 4.5]	2100 [RCP 8.5]
<i>Annual RPE-induced SOC respiration (Pg yr⁻¹)</i>			
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)
<i>Cumulative RPE-induced SOC respiration (Pg)</i>			
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)

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
379 resolution, while accounting for interactions between spatial and depth distributions of plant-
380 carbon inputs and SOC content and quality. The model represents current peer-reviewed RPE
381 knowledge only, i.e. potential mechanisms for which evidence is inconclusive or where data
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
385 integration of new data when available (**Extended Data Fig. 1**).

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
388 Ground-Ice Conditions⁵³ and the Northern Circumpolar Soil Carbon Database^{54,55}. After
389 masking out all non-vegetated areas, i.e. barren land, rocklands, land ice (glaciers and ice-
390 sheets), and freshwater, the study area covers 14 million km², around 12% of the global ice-
391 free land area. The model’s spatial resolution is 5 km x 5 km, and the study area includes
392 561,956 active grid cells. We considered only the top 3 m of the soil, where the vast majority
393 of plant roots is located³³. The 0-3 m soil column was divided into 5 cm thick layers, resulting
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
396 for each grid cell to derive maps, or as averages over grid cells for each soil layer to derive
397 depth profile figures.

398 We estimated current (year 2010), future (year 2100) and cumulative (2010 – 2100) RPE-
399 induced 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*

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

420

421 *Active layer depth*

422 The thickness of the seasonally thawed active layer at the surface of permafrost soils (ALT;
423 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*

429 Previous studies in permafrost and other soils suggest that C limitation of soil microorganisms
430 might be a requirement for the RPE^{15,16,26,58}. We therefore calculated RPE-induced SOC
431 respiration for two scenarios: (i) in the “no threshold scenario”, we assumed that RPE is
432 independent of microbial C limitation; (ii) in the “threshold scenario”, we assumed that
433 microbial C limitation is required for the RPE. Microbial C limitation has been suggested to
434 occur where the C/N ratio of SOM is below a Threshold Elemental Ratio, that is estimated to
435 fall between 20 and 27 (mol/mol)⁵⁹⁻⁶¹. For the threshold scenario, we thus used a threshold
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
440 that fall above or below this threshold based on observational data ($N = 472$) compiled from
441 previous studies^{22,62} and extensive unpublished data from G. Hugelius and P. Kuhry. The
442 observational data were grouped by soil horizon type and depth in the soil column to extract
443 the fraction of observations that fell above the C/N threshold of 20 (**Supplementary Table**
444 **5**).

445

446 Plant Module

447 *RPE ratio function*

448 The RPE is driven by the transfer of fresh organic compounds from plants to the soil, and is
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
451 Science, 10.10.2016) that report on experiments with intact, potted plants that were
452 continuously labelled with ^{13}C -depleted CO_2 . In such an experimental setup, the ^{13}C -depleted
453 part of respired CO_2 is derived from the plants themselves or plant-associated microorganisms
454 that thrive on plant root exudates or litter (further termed plant-associated respiration),
455 whereas non-depleted CO_2 comes from SOC decomposition (further termed SOC respiration).
456 Our meta-analysis included only studies where (a) plants were grown in natural soils, (b)
457 plants were continuously labelled with ^{13}C -depleted CO_2 , and in which (c) SOC respiration
458 from planted pots, (d) SOC respiration from unplanted control pots, and (e) either total or
459 belowground plant-associated respiration were published or could be obtained from the
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
463 isotopically labelled organic substrates to the soil. While such a reduced experimental setup is
464 a prerequisite for dissecting the mechanisms underlying RPE¹⁰, only experiments using living
465 plants capture the full natural range of soil modifications by plants (continuous exudation of a
466 wide range of chemical compounds released by plants, changes in nutrient and water
467 availability, pH, soil aggregation, and microbial community composition)^{63,64}, and allow us to
468 link the magnitude of RPE to estimates of root activity.

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

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

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

487 Our meta-analysis showed a positive relationship between RPE ratio and root respiration (mg
488 C kg⁻¹ soil d⁻¹) across all studies which we described with a saturating (Michaelis-Menten)
489 function fit with Markov chain Monte Carlo methods assuming gamma priors on both fitted
490 parameters, and Normal distributed errors (**Extended Data Fig. 8**). Since we assumed neither
491 positive nor negative priming at root respiration = 0 we fixed the intercept at 1. The
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
495 substrate added and their utilization by the microbial community^{65,66}. The posterior medians
496 of the two fitted parameters yielded the following empirical relationship between RPE and
497 root respiration:

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

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

502

503 *Gross primary production*

504 Current annual GPP across the northern permafrost area was derived from ref.²³ at a
505 resolution of 0.5°. Future GPP in the year 2100 was estimated for RCP 4.5 and RCP 8.5
506 scenarios, by applying the relative change in GPP CLM4.5²⁴ as a result of rising temperatures
507 and atmospheric CO₂ fertilization to the current GPP estimate, thus preserving the higher
508 spatial resolution of ref.²³. Annual GPP values^{23,24} were converted into daily GPP values for
509 the growing season by dividing annual GPP values by growing season length⁶⁷. For details on
510 calculation of future GPP and conversion to daily values see **Supplementary Methods**. The
511 final GPP maps are presented in **Extended Data Fig. 7**.

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
518 microorganisms) or belowground plant-associated respiration (respiration by roots and root
519 associated microorganisms) depending on which was reported in the respective study
520 (**Extended Data Fig. 8; Supplementary Table 2**). We derived conversion factors from
521 previously published extensive meta-analyses on different aspects of plant C allocation,

522 including GPP⁶⁸, total and belowground plant-associated respiration⁶⁹, as well as root
523 respiration⁷⁰. Overall, we estimated root respiration as 3.6% of GPP, 7.4% of total plant-
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
526 area, which we spread over depth using soil bulk density data (See **Supplementary Methods**;
527 **Supplementary Table 8**) and root distribution functions (below). Via the RPE ratio function
528 we calculated, for each grid cube, the expected RPE ratio at its root activity. For further
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
538 natural arctic and subarctic tundra systems, as well as in boreal forests, all on permafrost soils.
539 We included only studies where root data from at least three soil depths were reported, where
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.
543 Following Schenk and Jackson³³ we fitted logistic dose-response functions for each profile:

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

545 where $r(D)$ is the observed cumulative percentage of roots above depth D , and $D50$
546 (representing the depth above which we find 50% of the roots), and c (a dimensionless shape-
547 parameter) are estimated from the data. Given that rooting depth is limited by ALT in
548 permafrost soils³³, we expressed D (and $D50$) as a fraction of ALT; this allows adjustment of
549 maximum rooting depth according to variations in ALT (spatial variation between the grid
550 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,
552 usually because of insufficient data points. These profiles were excluded from subsequent
553 analyses resulting in a total of 66 root profiles from 25 individual studies (**Supplementary**
554 **Table 3**). This meta-analysis represents to our knowledge the first on boreal forests
555 specifically on permafrost, as well as an almost tripling of tundra root profile observations
556 from 20 to 54 profiles compared to a previous study³³. Subsequently, tundra root profiles were
557 assigned to tundra types (graminoid tundra, erect-shrub tundra, prostrate-shrub tundra and
558 tundra wetland) based on the site description in the original publications and the criteria
559 defined in the Circumpolar Arctic Vegetation Map²⁵. Means as well as uncertainty ranges of
560 $D50$ and c were calculated for each vegetation type: boreal forest (mean $D50 = 0.19$, mean $c =$
561 -2.32 , $n = 12$ profiles), graminoid tundra ($D50 = 0.28$, $c = -2.51$, $n = 20$), erect-shrub tundra
562 ($D50 = 0.26$, $c = -2.92$, $n = 8$), prostrate-shrub tundra ($D50 = 0.29$, $c = -2.75$, $n = 8$) and
563 tundra wetlands ($D50 = 0.25$, $c = -3.20$, $n = 18$).

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

570

571 Soil Respiration Module

572 *Basal SOC respiration*

573 Basal SOC respiration without the RPE was calculated for the northern permafrost area using
574 output from the CLM4.5²⁴, which does not include any explicit RPE terms or dependency of
575 SOM decomposition rates on plant productivity or other biotic factors. In addition, the CLM
576 has been shown to systematically underestimate soil turnover rates in cold biomes²⁴,
577 potentially, among other factors, due to lack of RPE. The CLM has, however, a relatively
578 coarse spatial resolution and the absolute values of GPP and SOC at any given site are less
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
582 SOC respiration⁷¹⁻⁷³. We extracted a relationship between GPP and the fraction of total active
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
585 *PrimeScale* model to generate basal SOC respiration values for each individual gridcell. To
586 avoid an overestimation of basal SOC respiration by CO₂-fertilization of GPP in the future
587 (which is independent from the climatic conditions driving respiration), we used GPP data
588 from a CLM simulation without CO₂-fertilization²⁴ for this purpose. We used quantile
589 regression to fit a model for the median and 10th and 90th percentiles (for uncertainty analysis,
590 see below) of simulated Rh/SOC as a function of simulated GPP, assuming an exponential
591 relationship:

592
$$\frac{Rh}{SOC} = A * GPP^B \quad (3)$$

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

599

600 *Plant-affected SOC respiration*

601 Plant-affected SOC respiration (i.e., SOC respiration considering the RPE) was calculated by
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 Uncertainty estimates

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

616

617 Analysis of spatial patterns

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
624 precipitation, as well as annual temperature range as a measure of continentality⁷⁵), and
625 terrain (distance to large rivers, distance to lakes, topography⁷⁶⁻⁷⁸) (**Supplementary Table 6**).

626

627 Data availability

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

635

636 Code availability

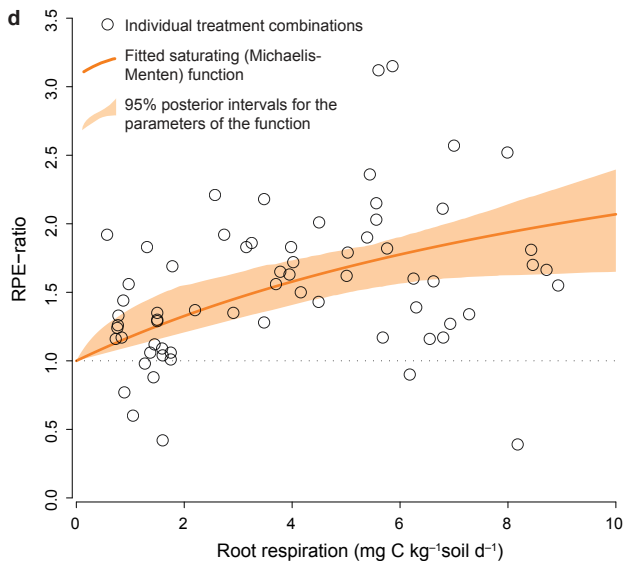
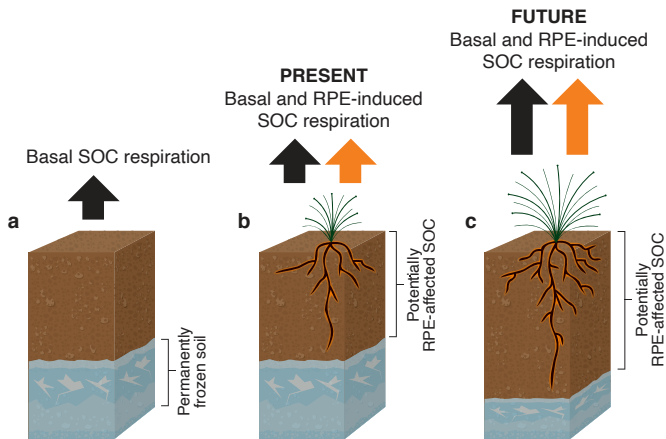
637 The custom code for the PrimeScale 1.0 model, including model script and complementary
638 function script, is available from the authors upon request, as well as from the Bolin Centre
639 code repository: <https://git.bolin.su.se/bolin/keuper-wild-2020>.

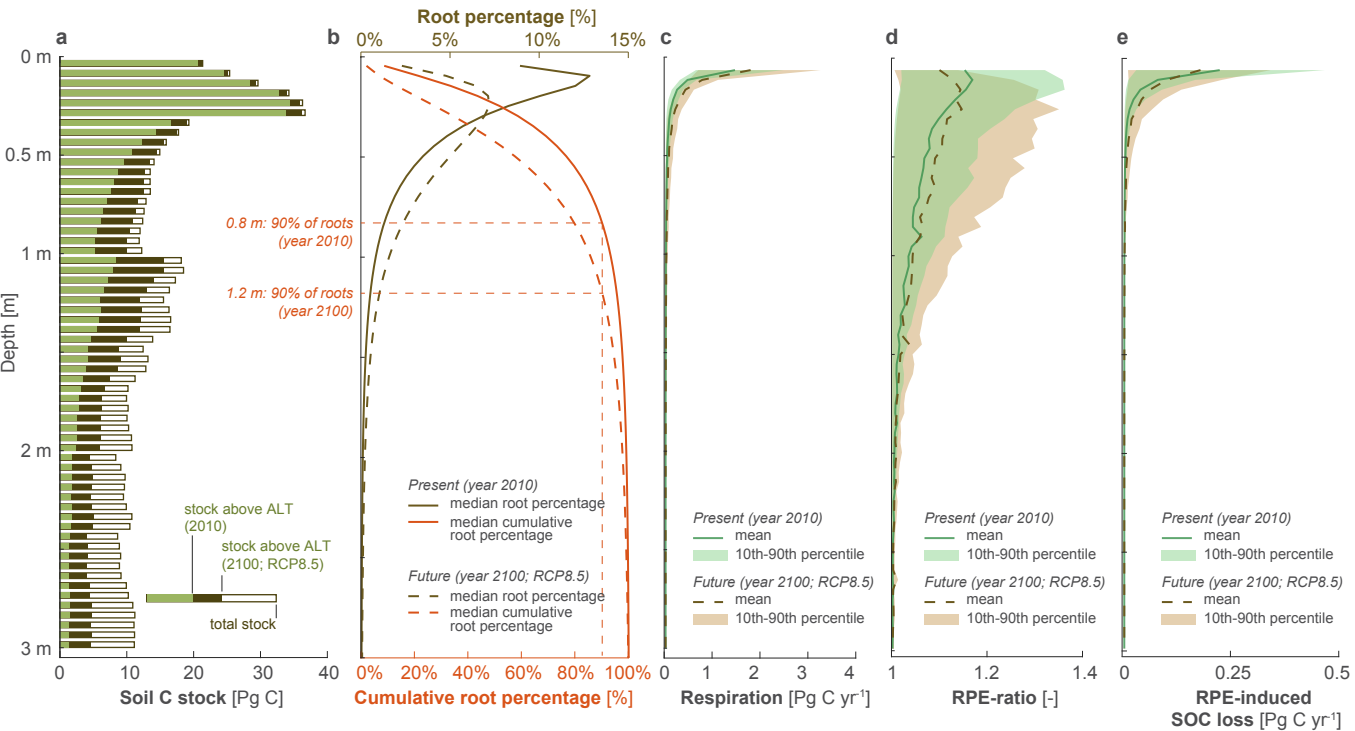
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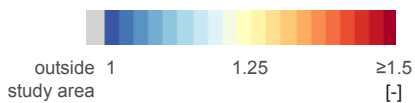
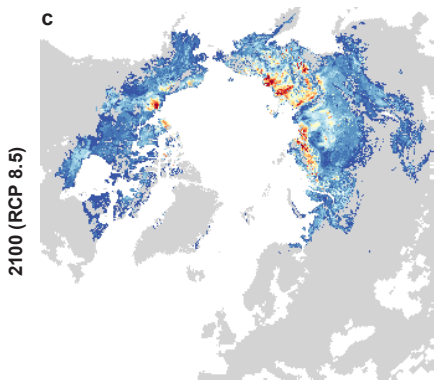
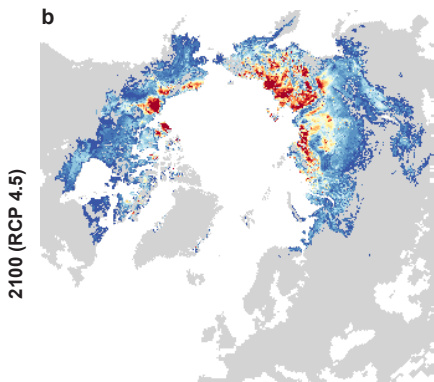
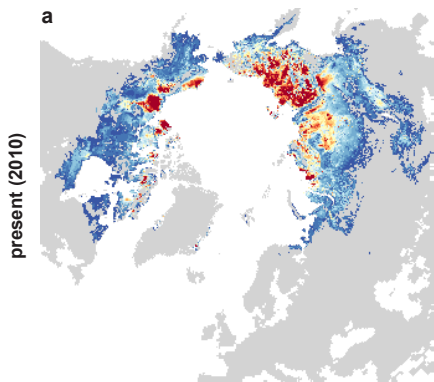
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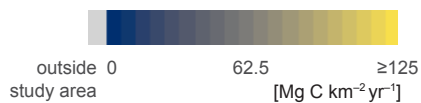
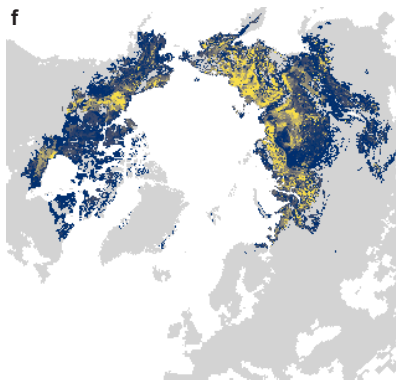
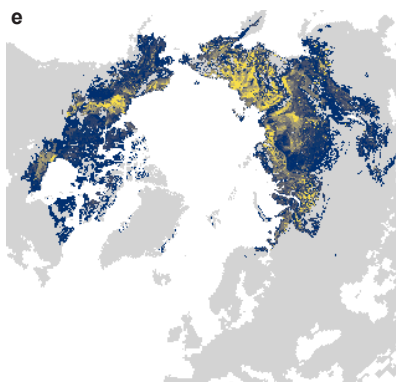
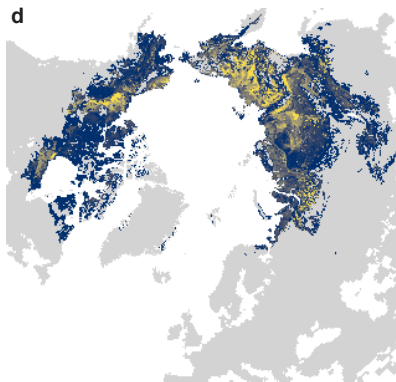




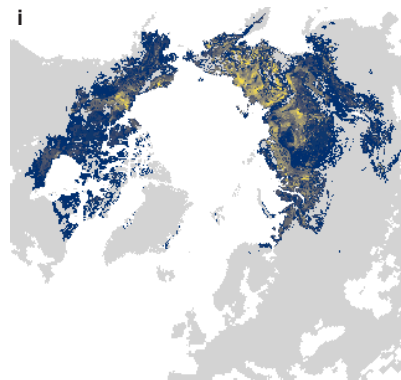
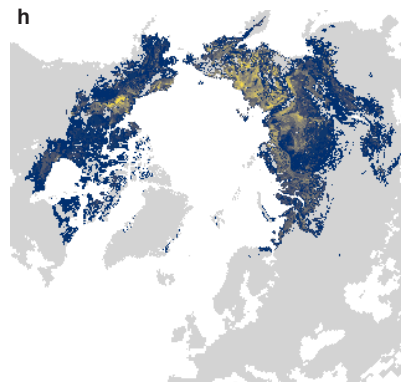
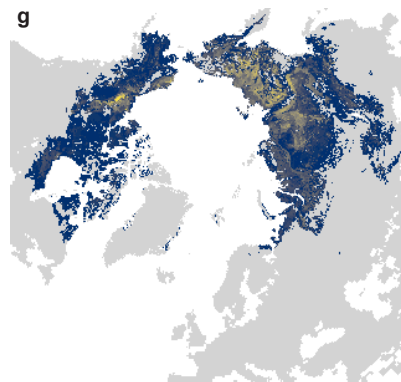
RPE ratio
Mean (n = 1000)

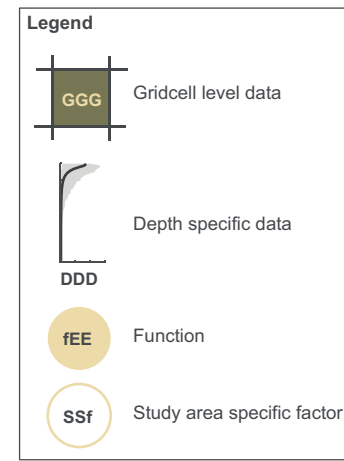
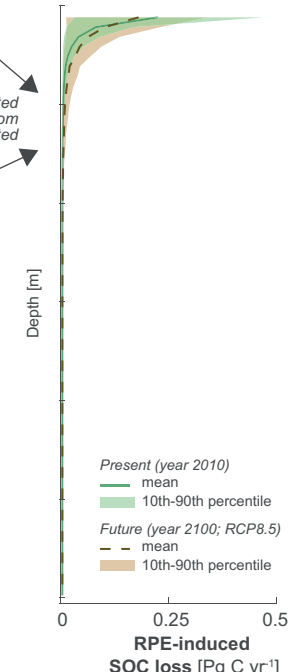
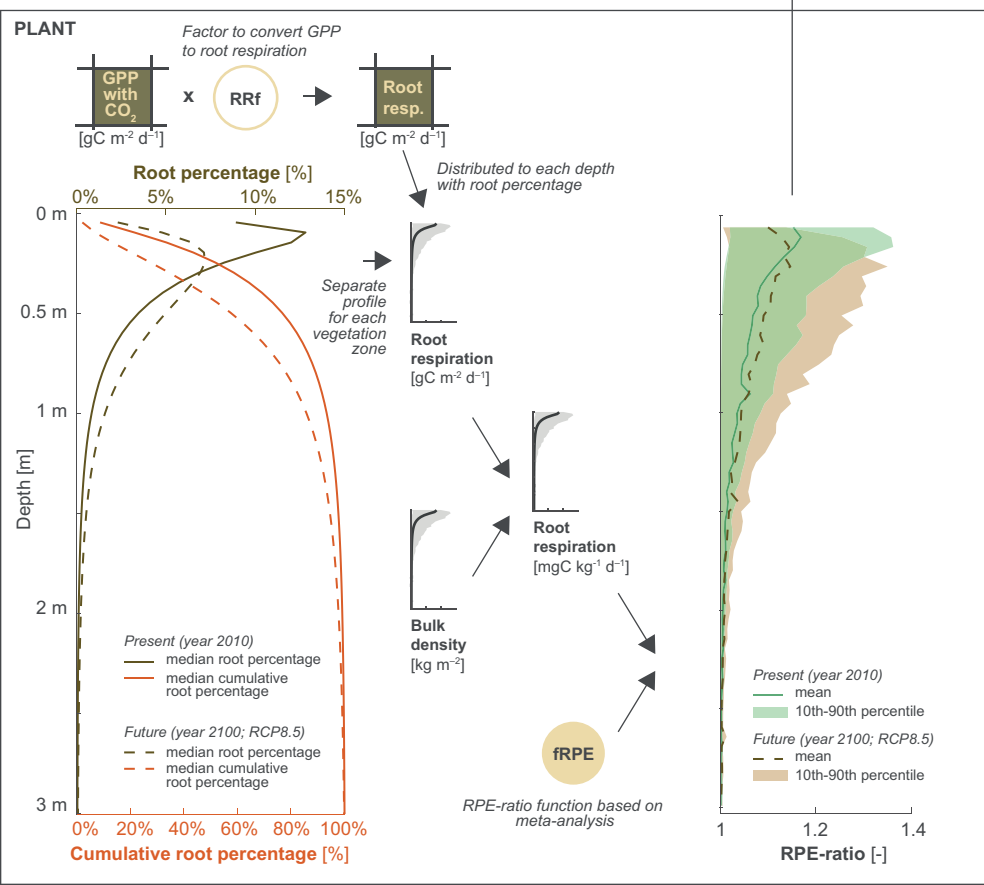
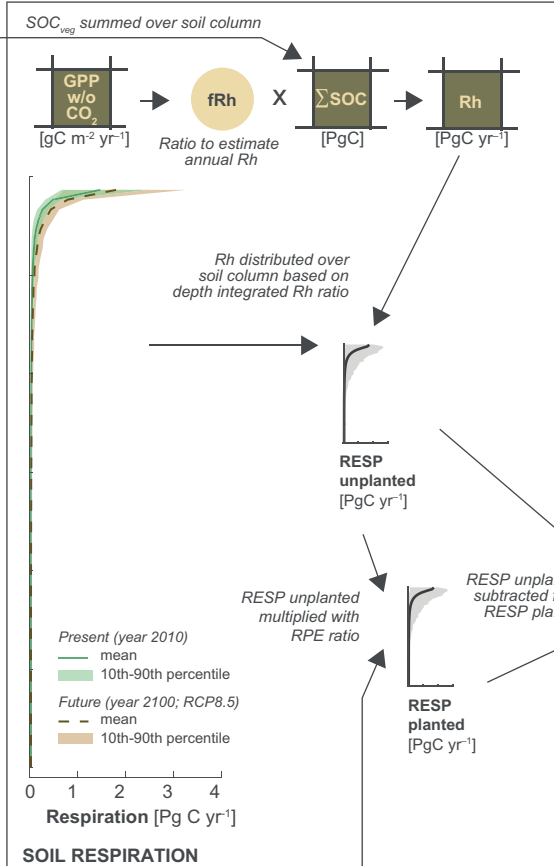
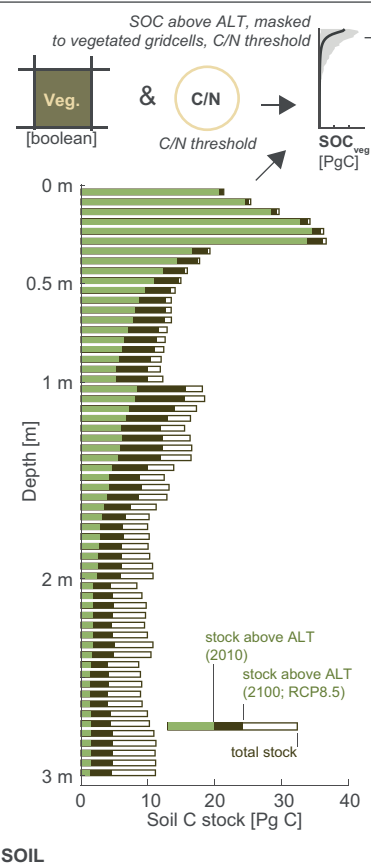


**RPE-induced SOC loss
no C/N threshold**
Mean (n = 1000)

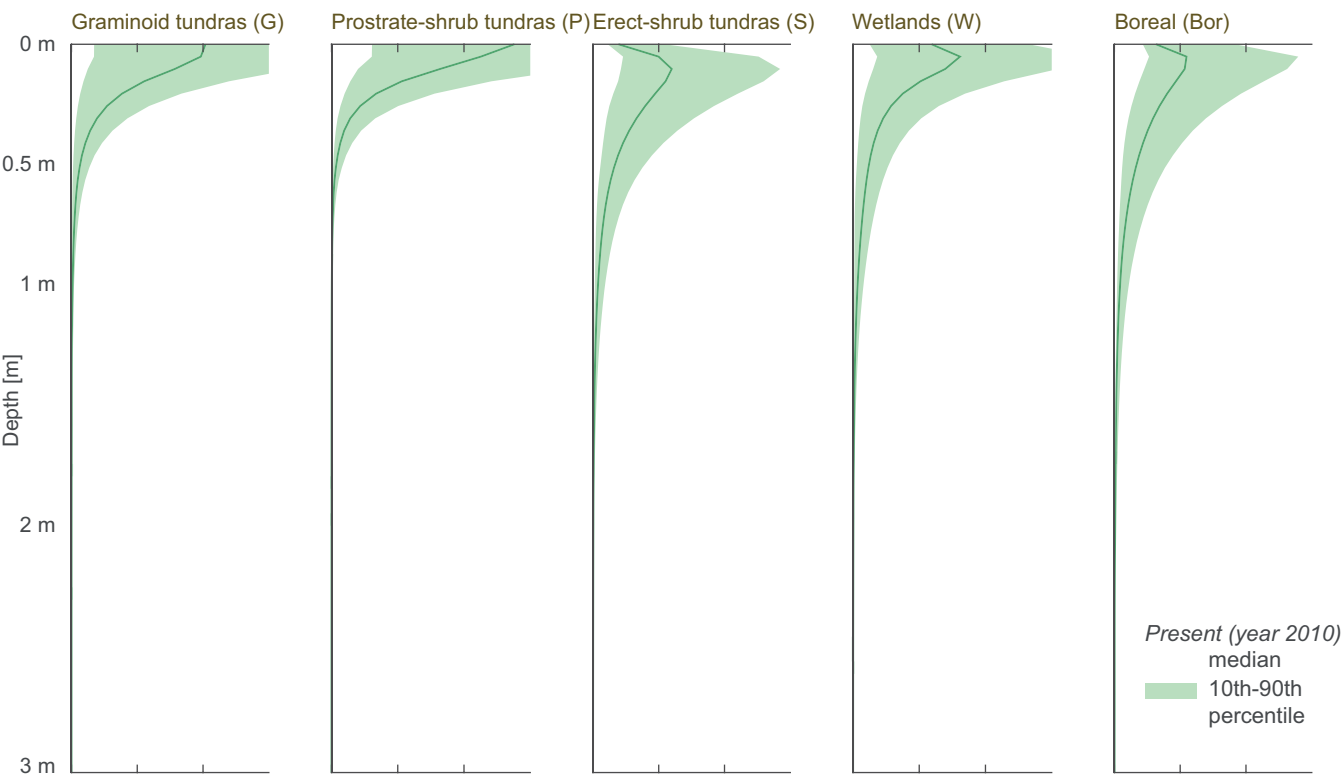


**RPE-induced SOC loss
C/N threshold**
Mean (n = 1000)

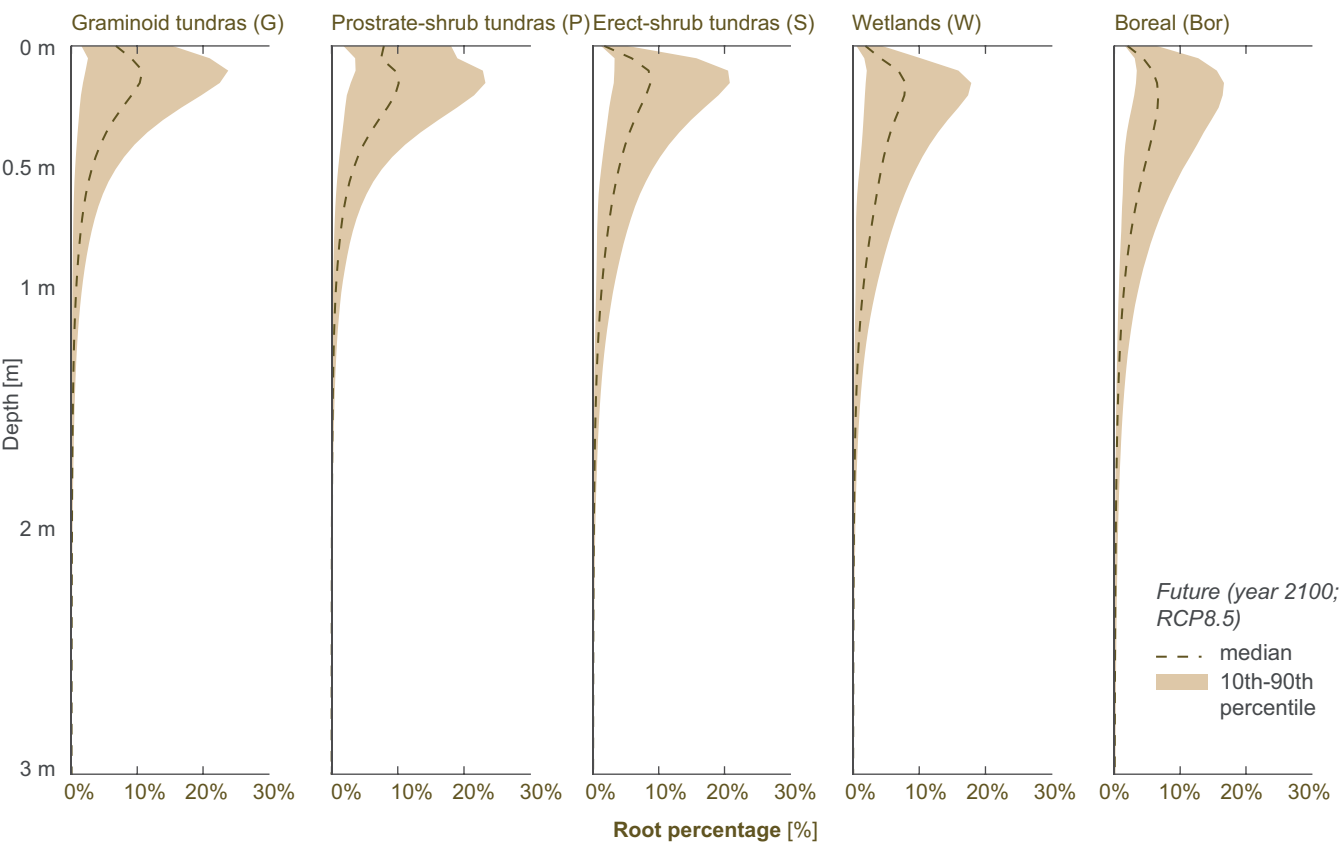




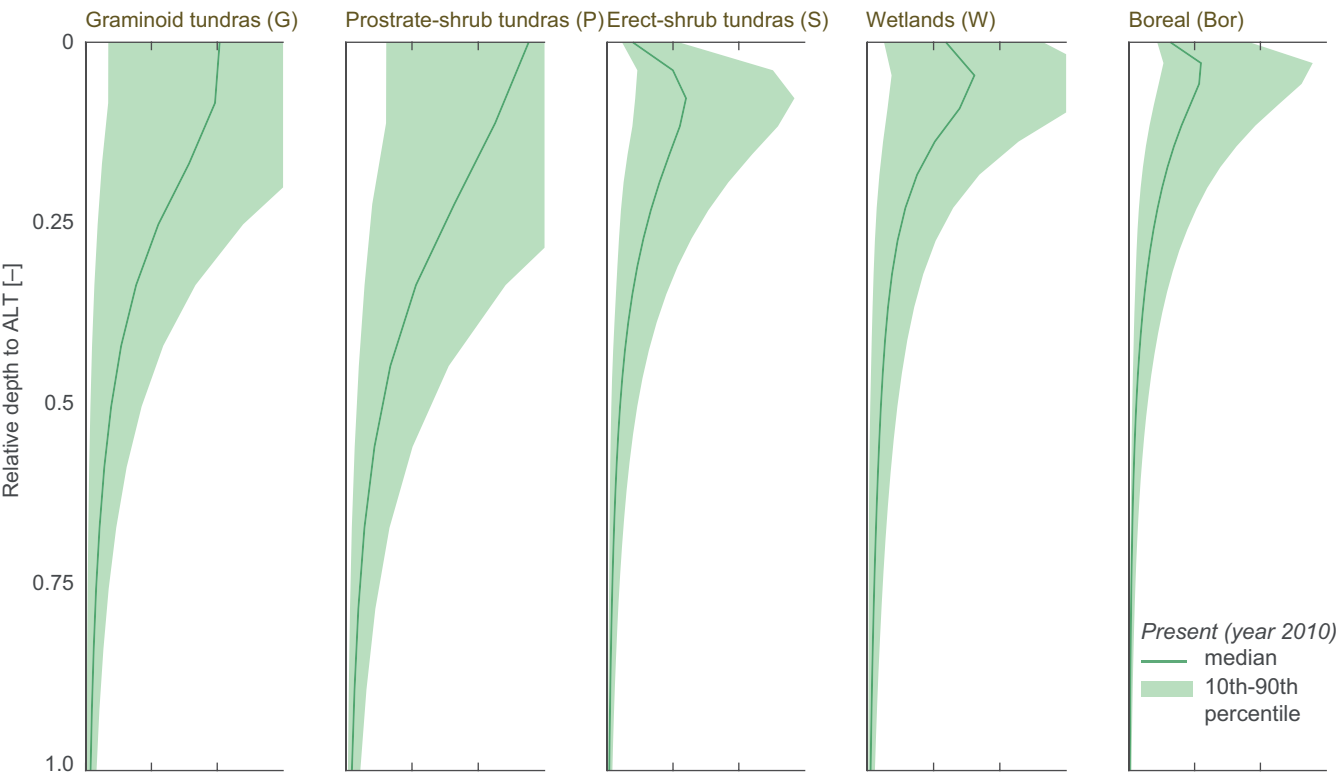
PRESENT



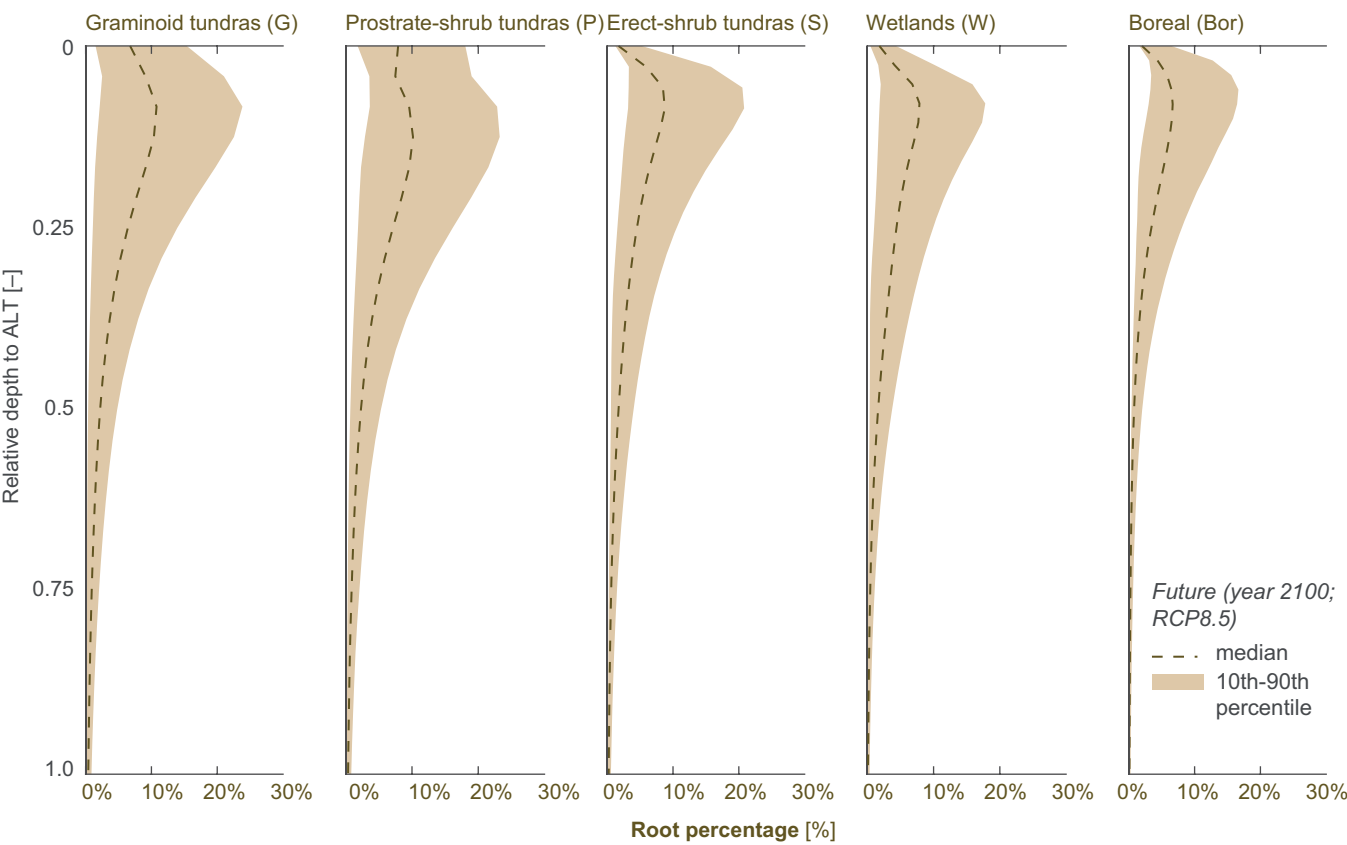
FUTURE (RCP8.5)

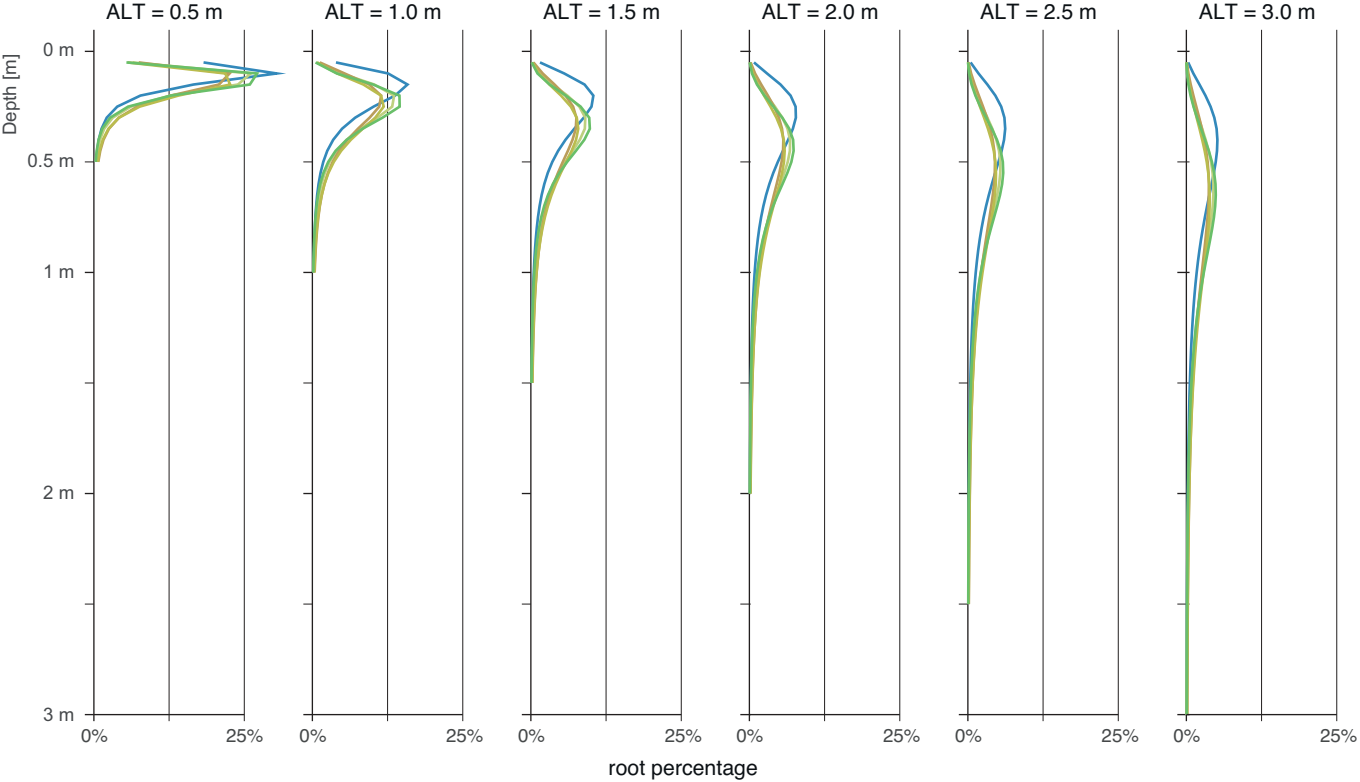


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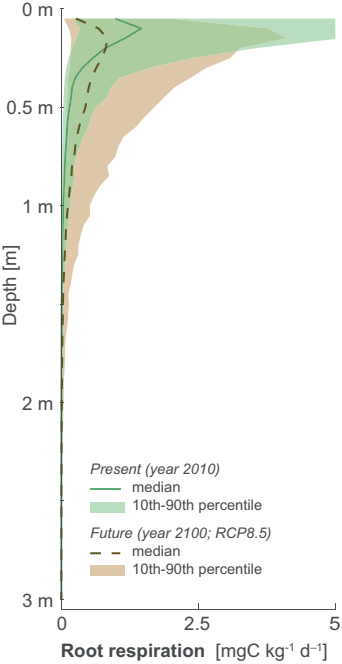
FUTURE (RCP8.5)



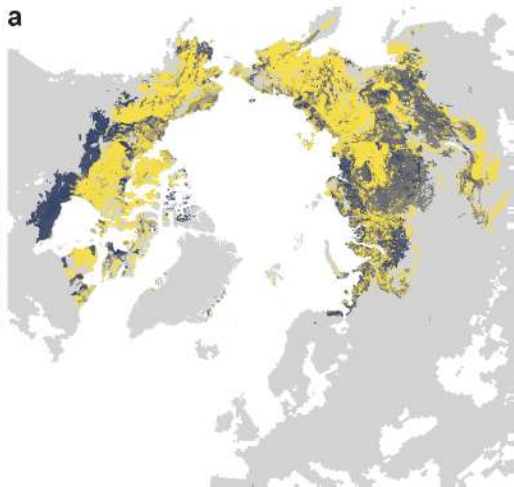


Vegetation zones

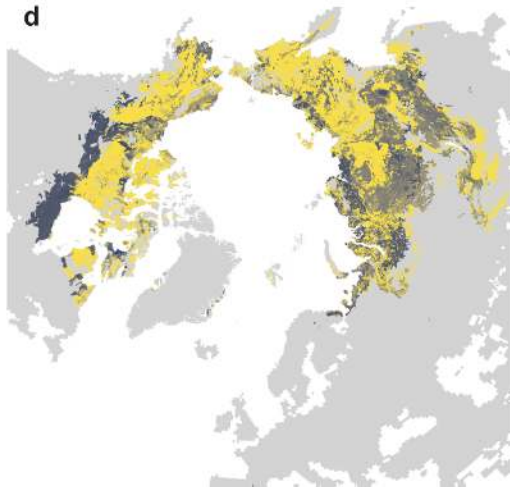
- Boreal (Bor)
- Erect-shrub tundras (S)
- Graminoid tundras (G)
- Prostrate-shrub tundras (P)
- Wetlands (W)



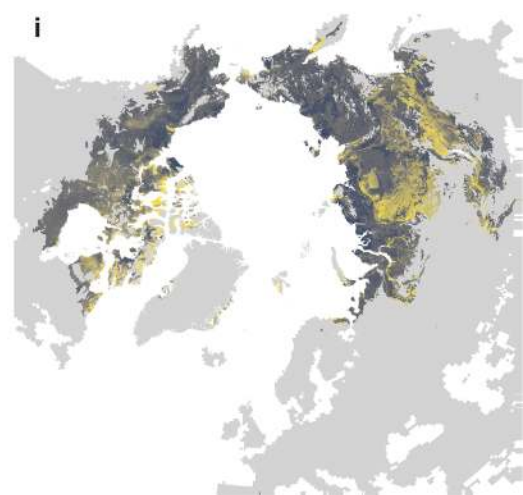
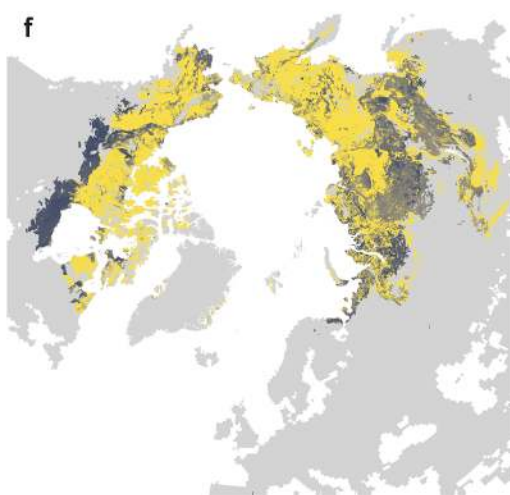
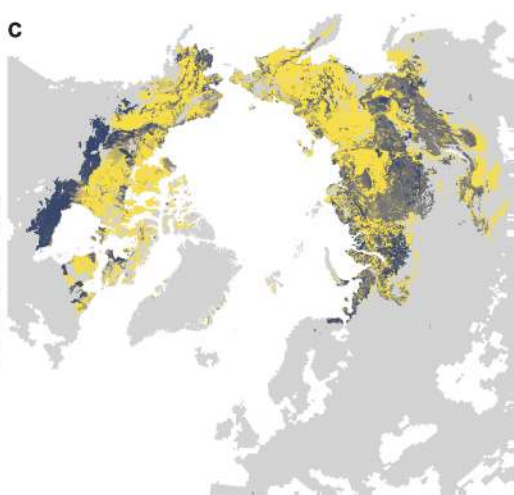
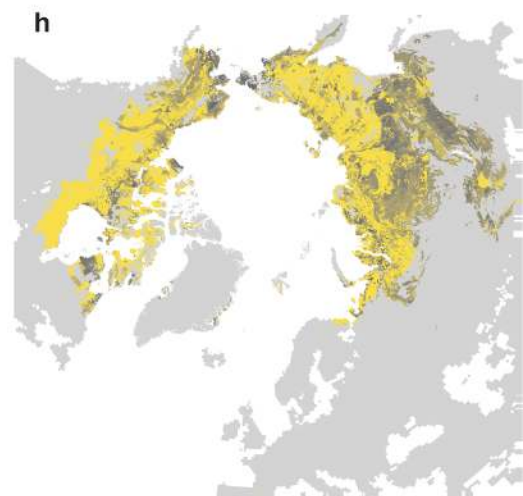
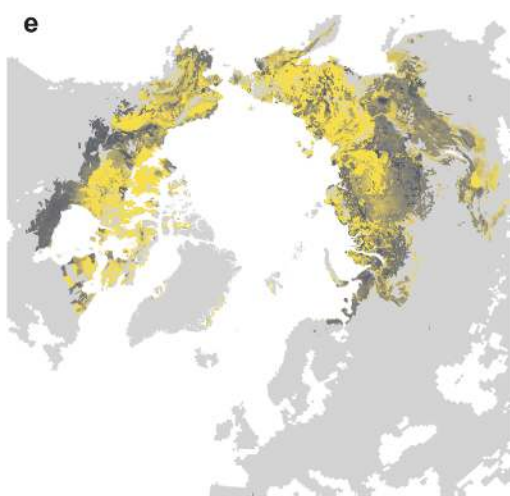
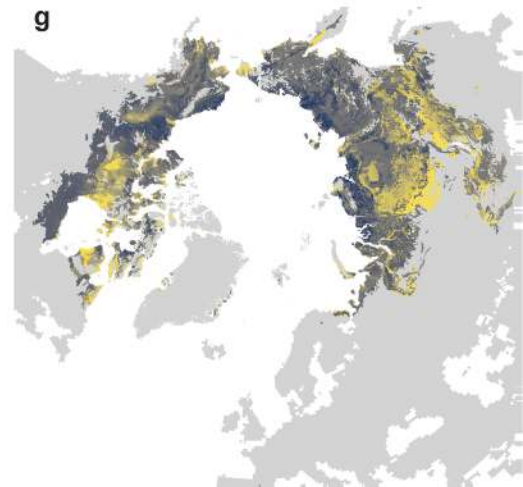
CV for RPE ratio
Mean (n = 1000)

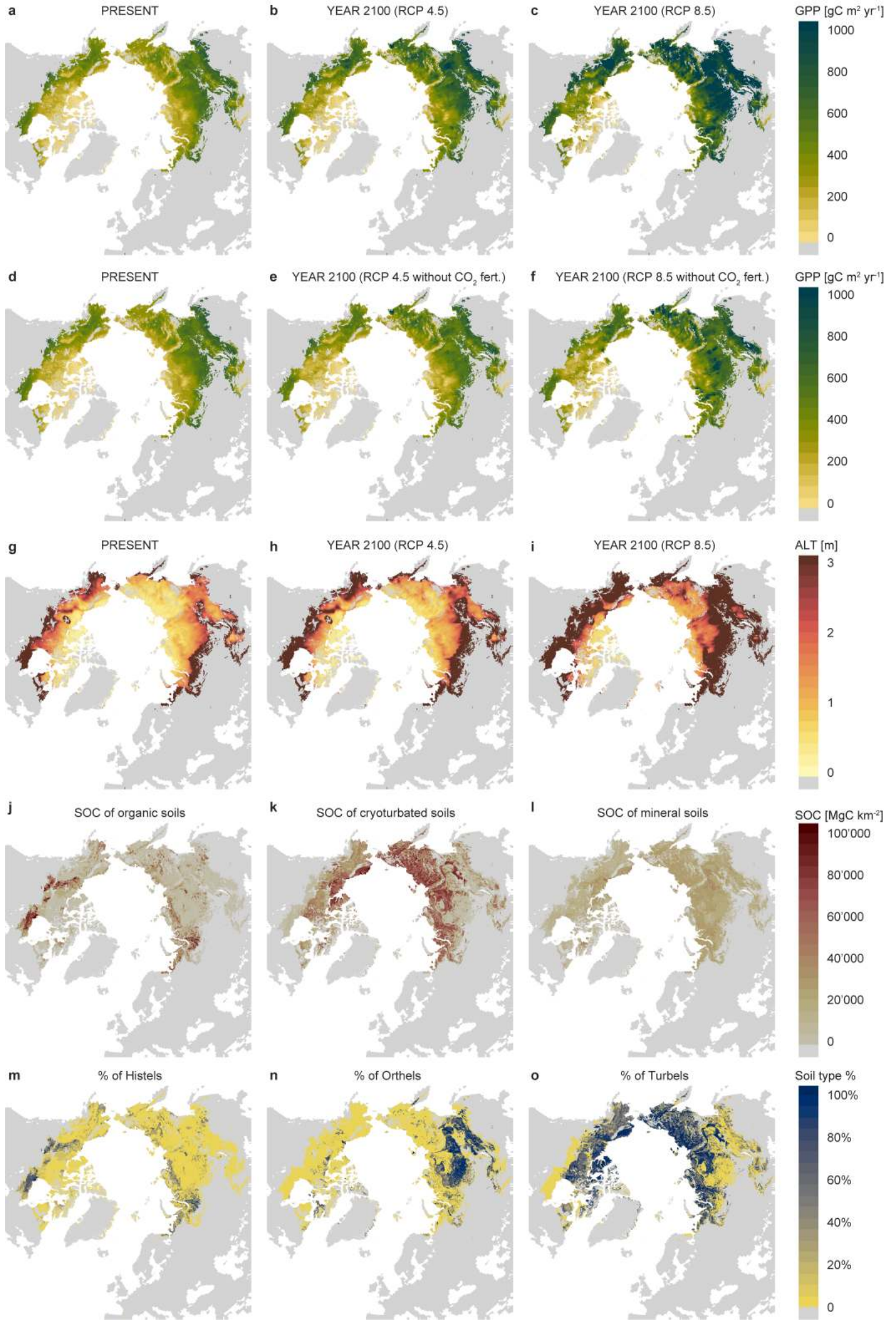


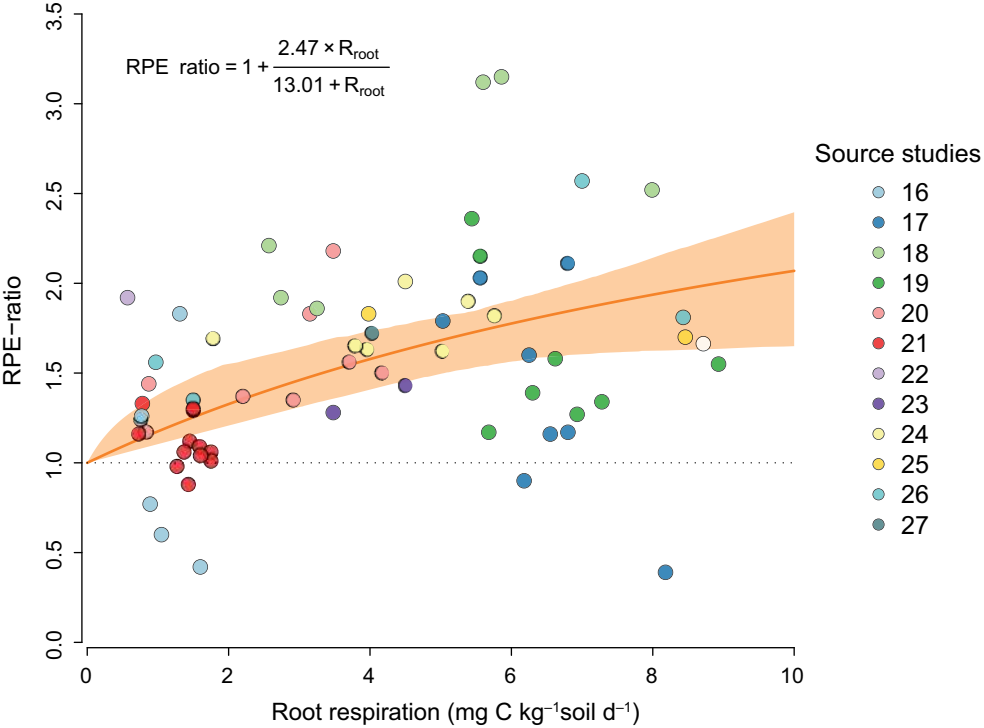
CV for RPE-induced SOC loss
no C/N threshold
Mean (n = 1000)

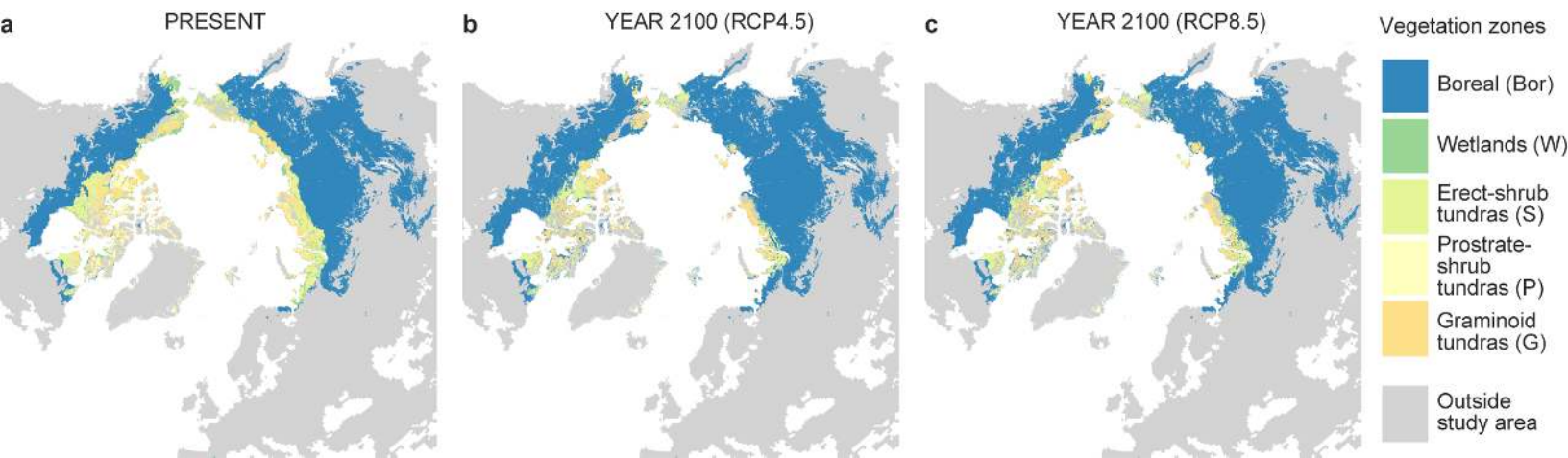


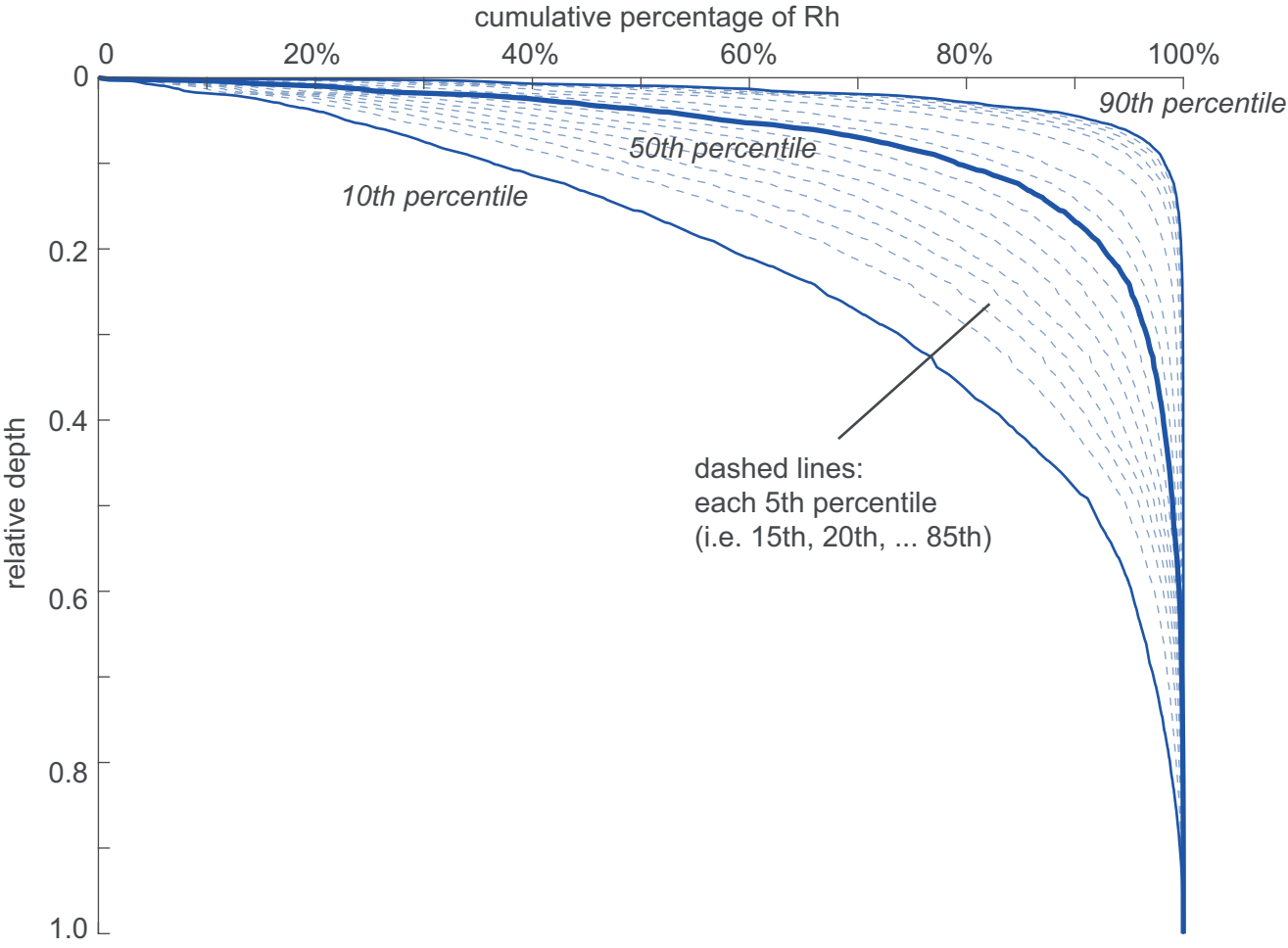
CV for RPE-induced SOC loss
C/N threshold
Mean (n = 1000)

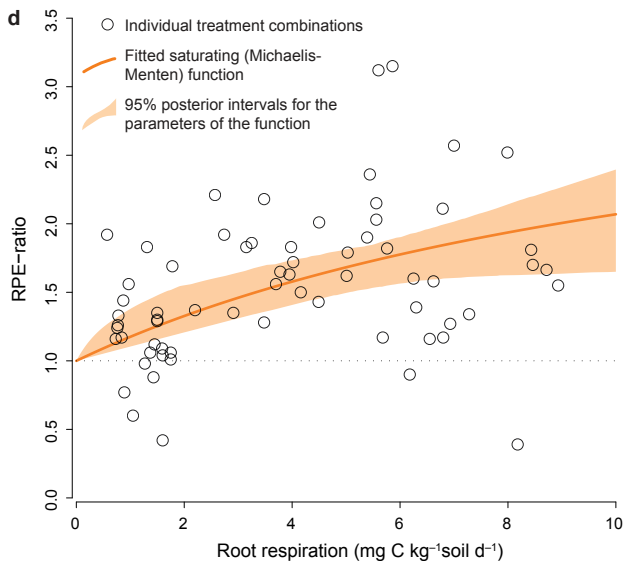
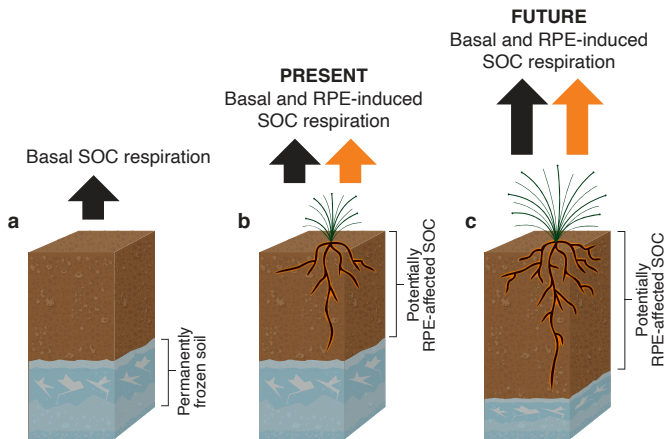


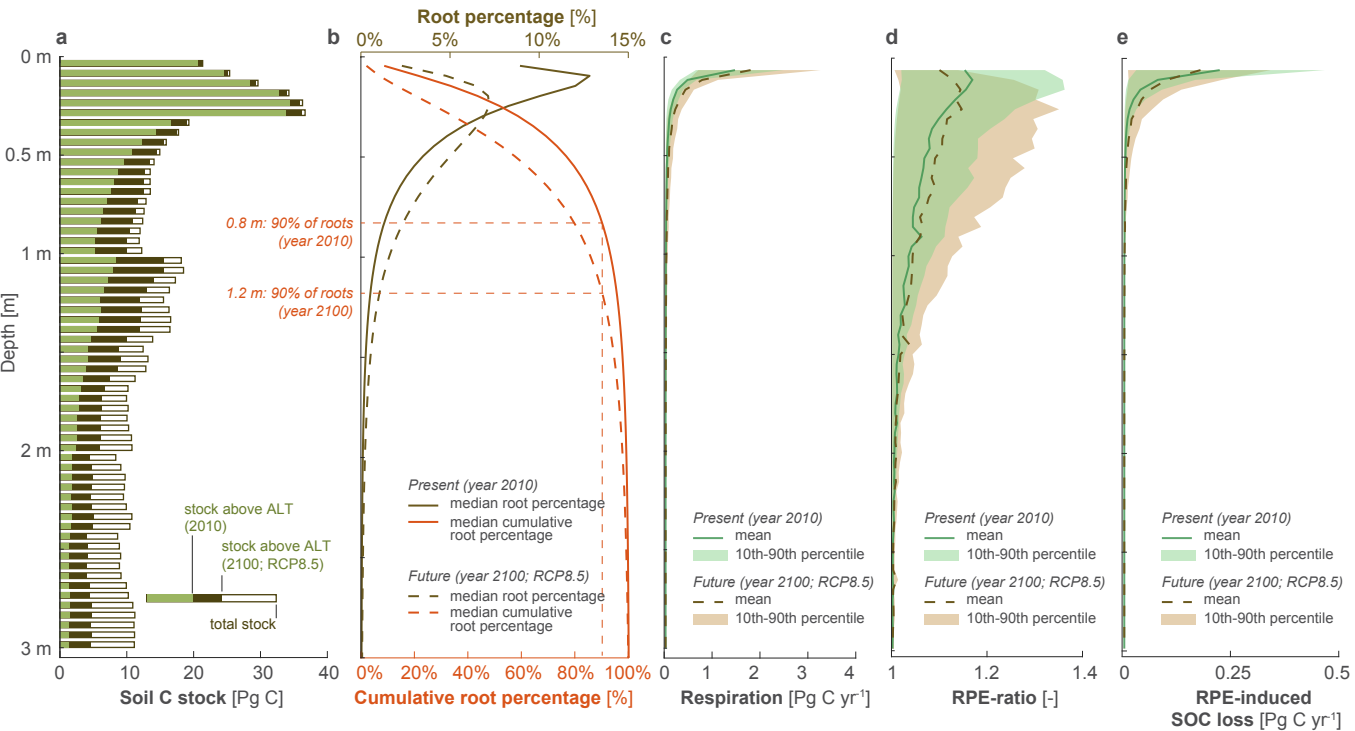




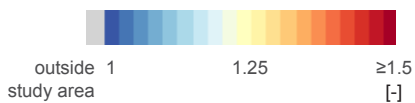
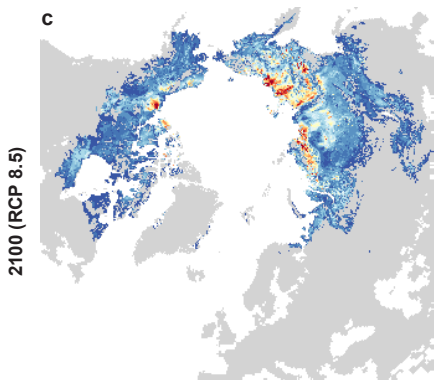
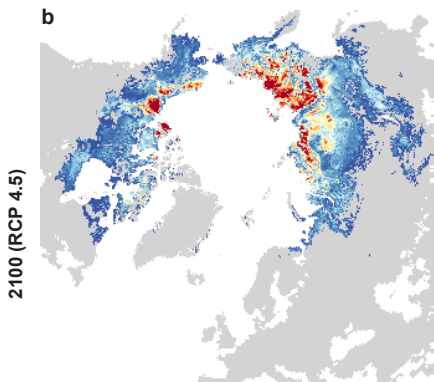
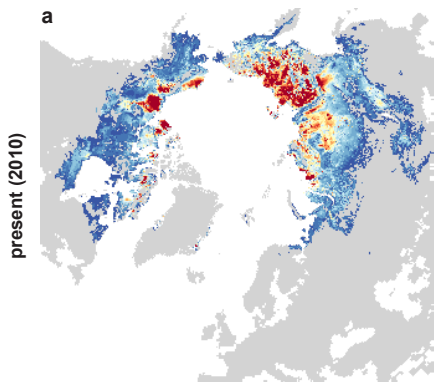




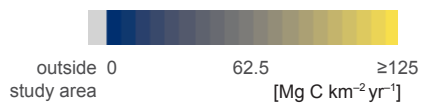
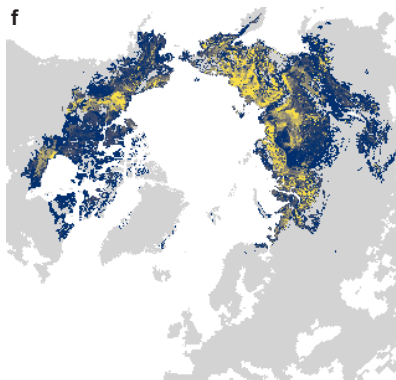
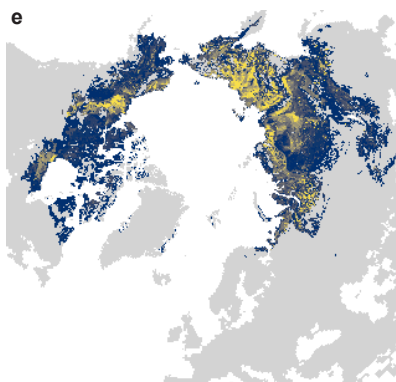
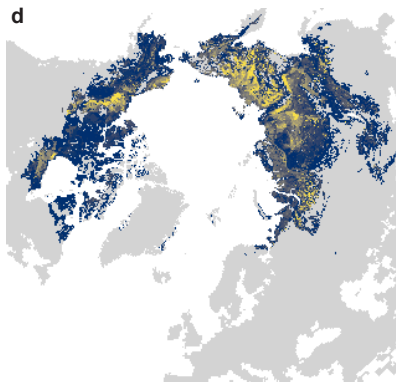




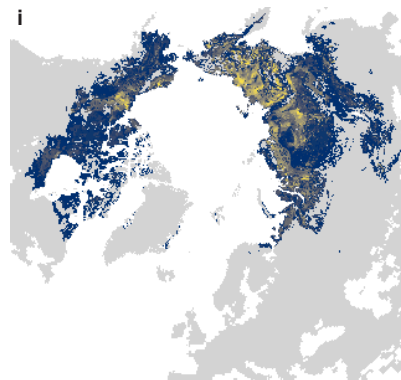
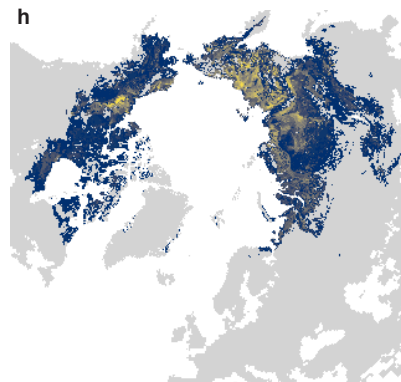
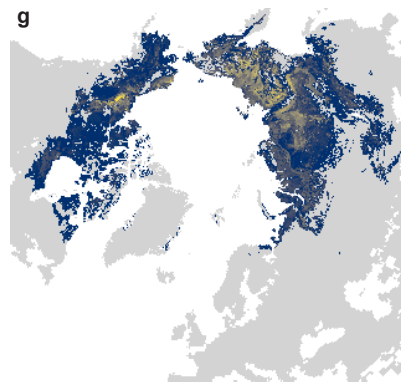
RPE ratio
Mean (n = 1000)

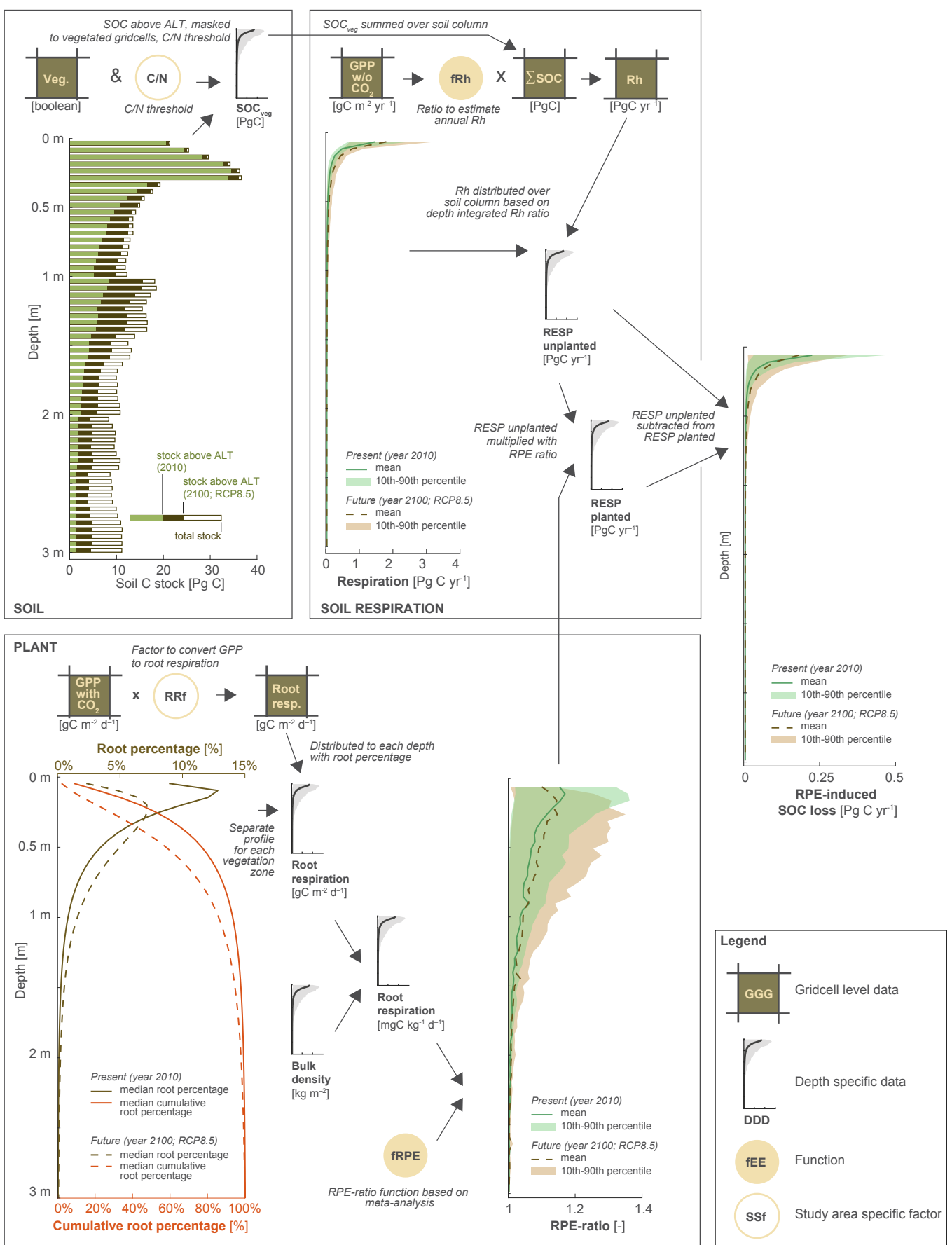


**RPE-induced SOC loss
no C/N threshold**
Mean (n = 1000)

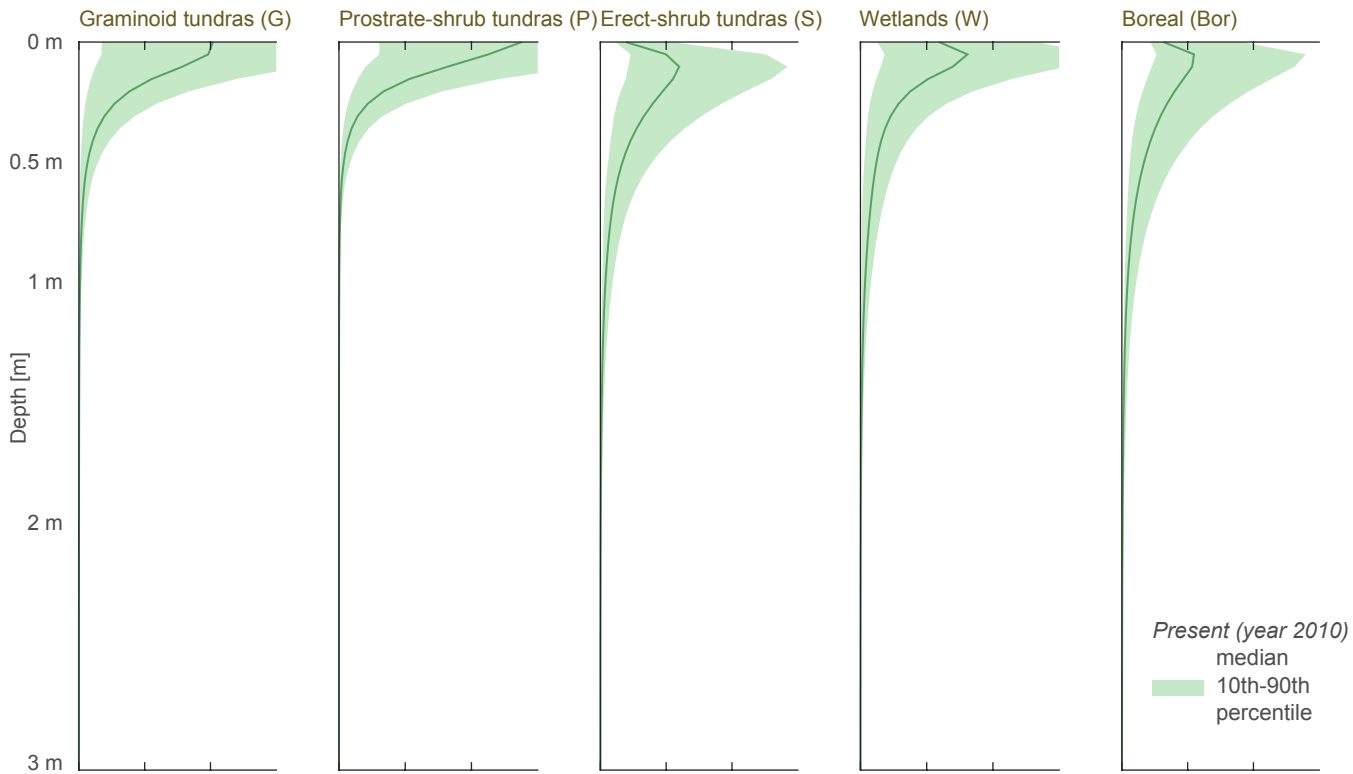


**RPE-induced SOC loss
C/N threshold**
Mean (n = 1000)

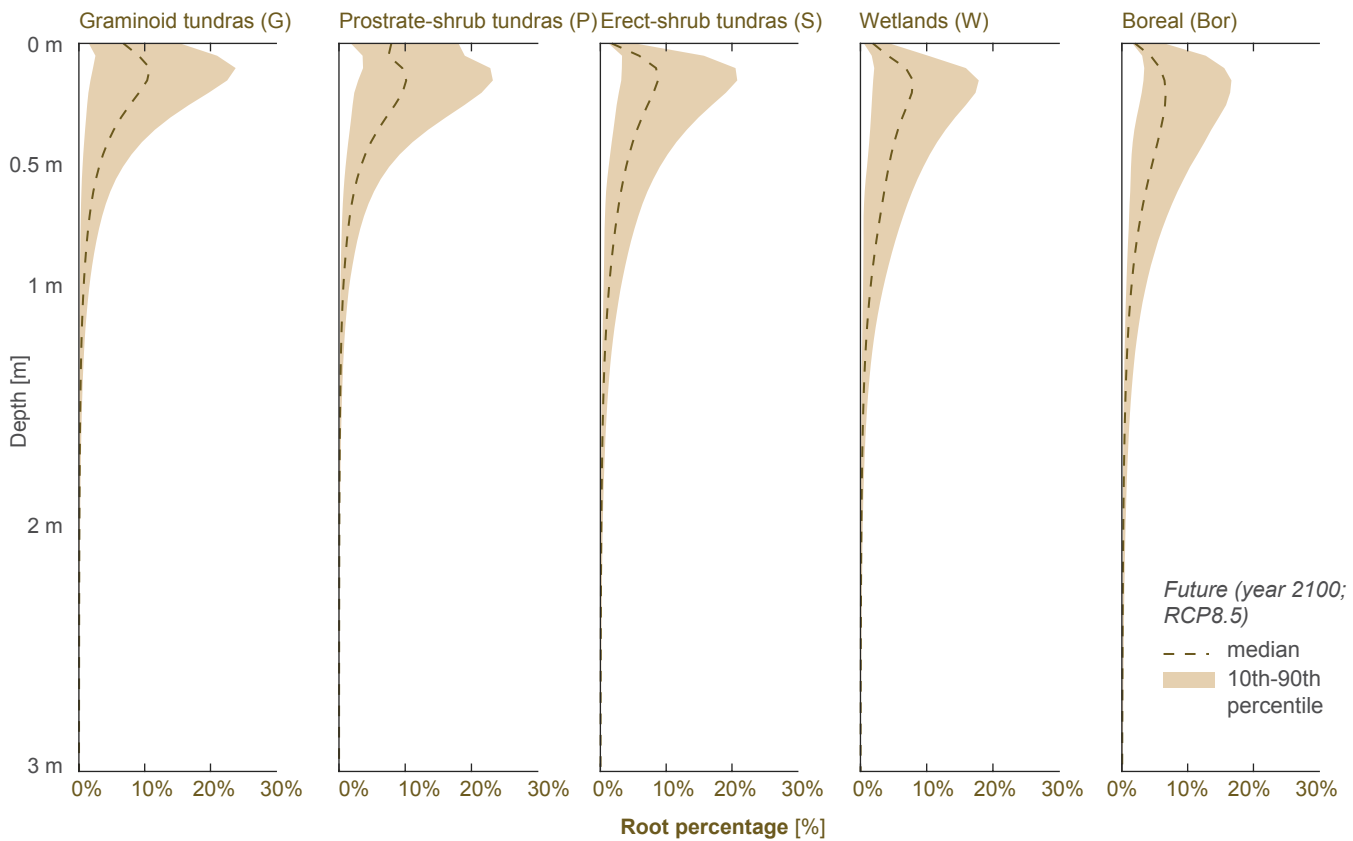




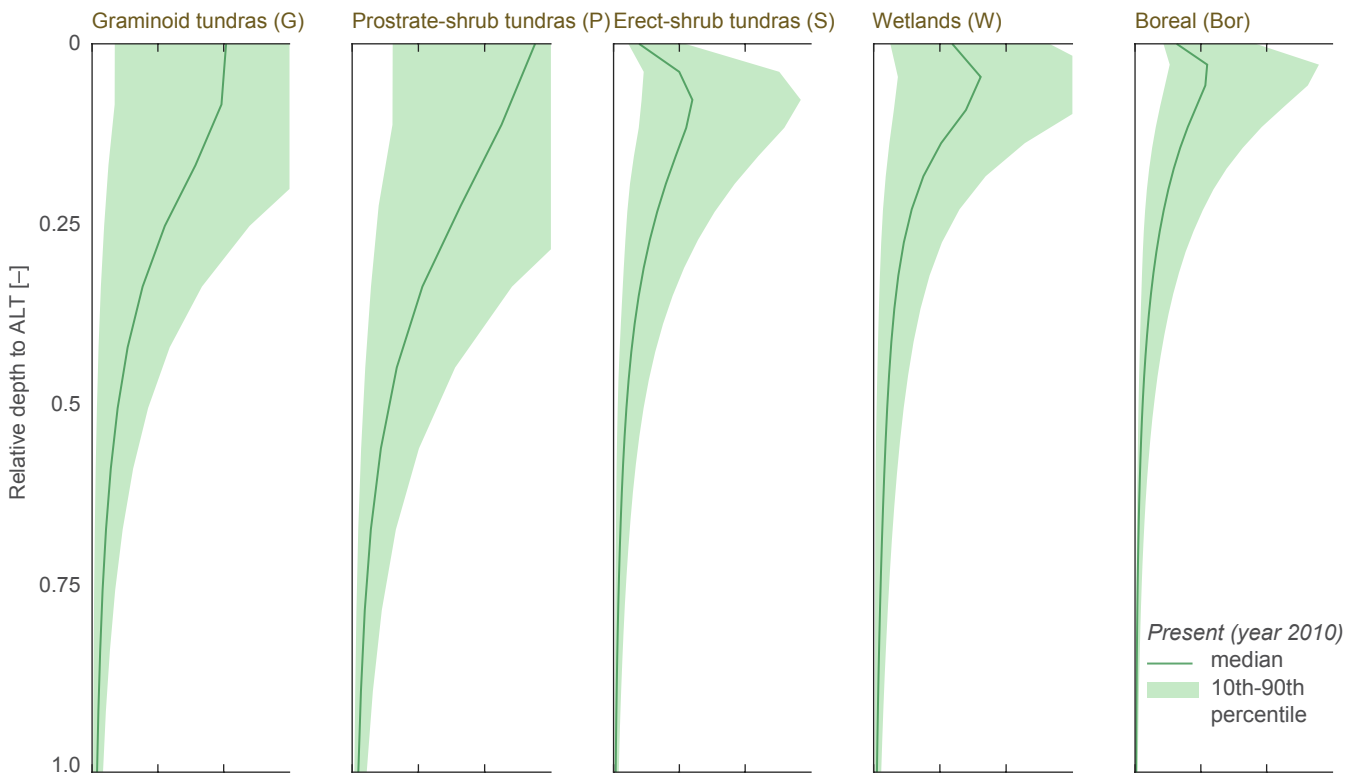
PRESENT



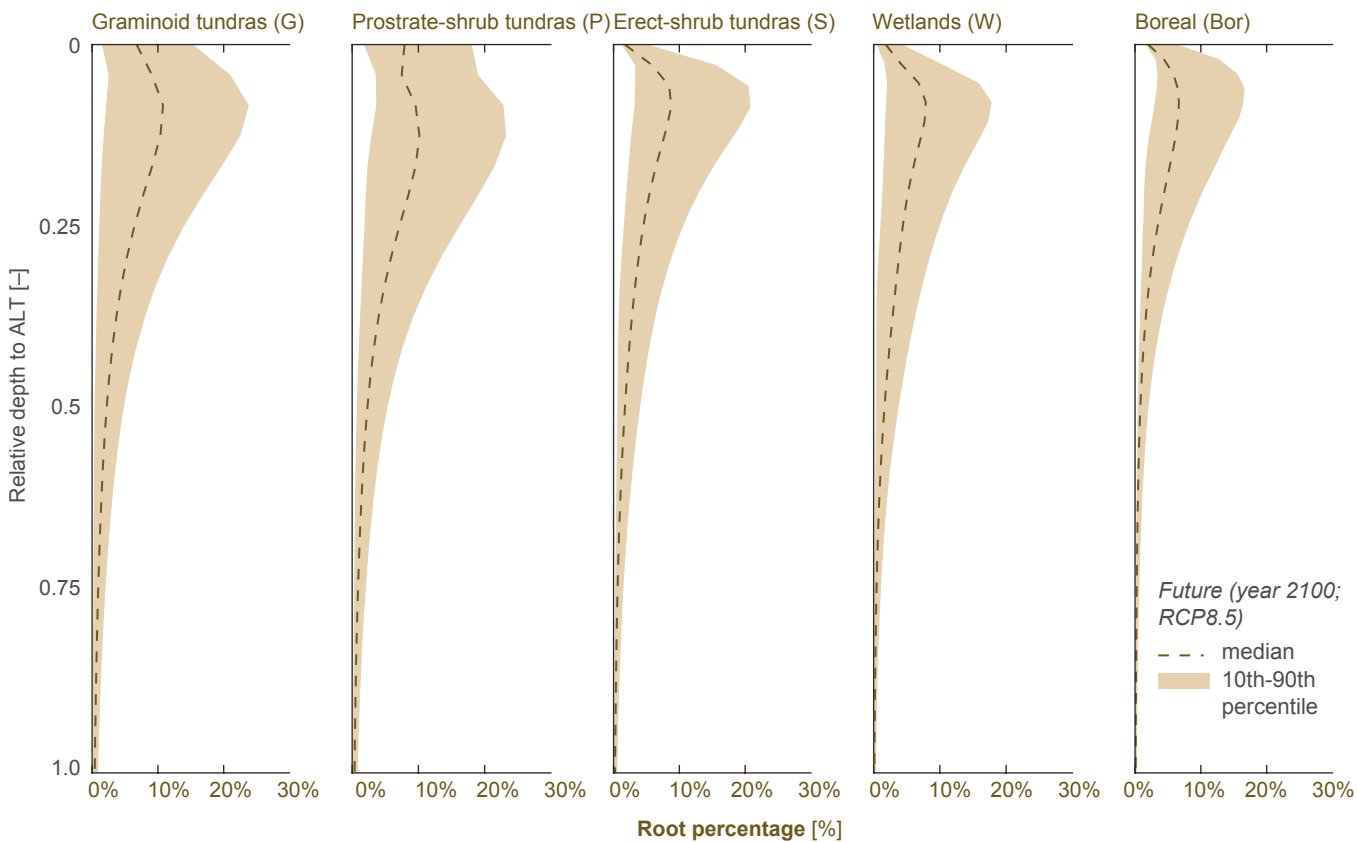
FUTURE (RCP8.5)

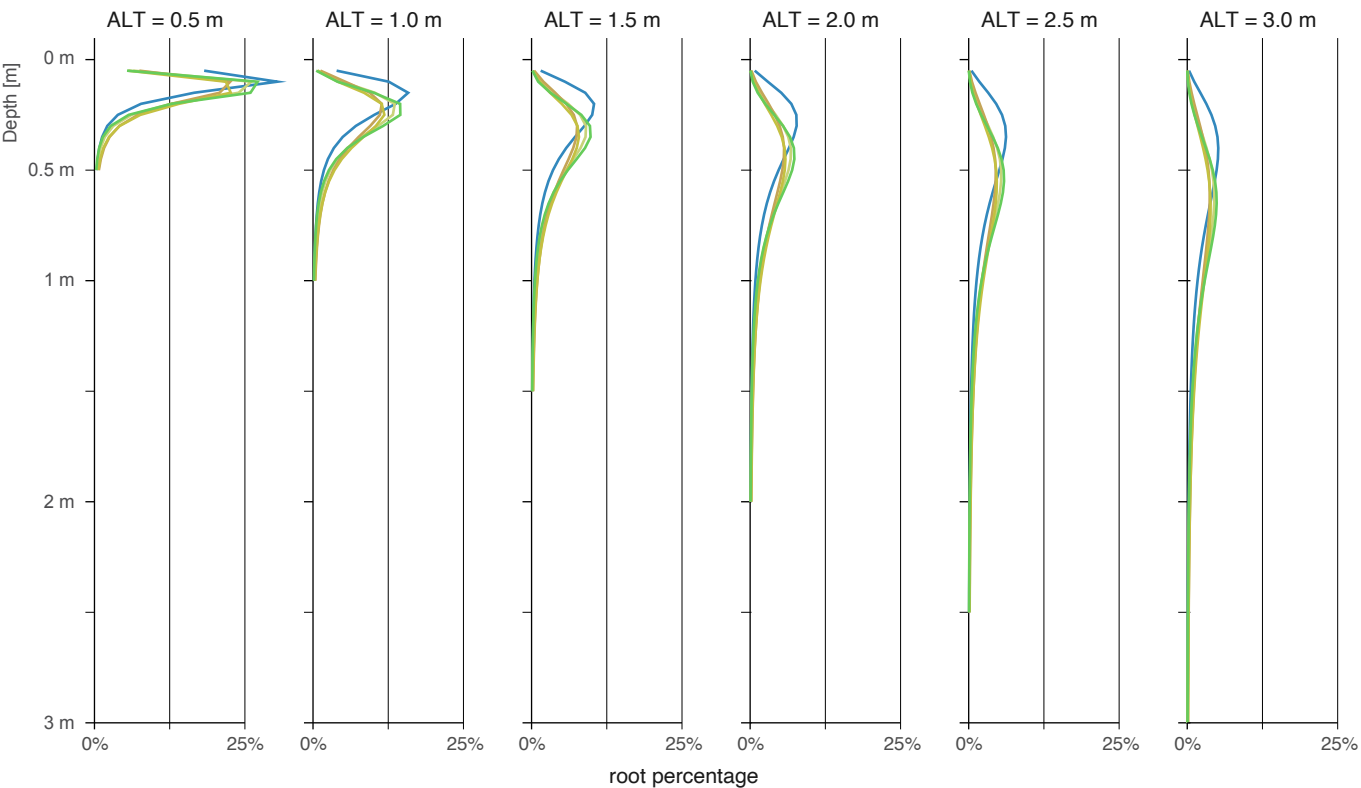


PRESENT



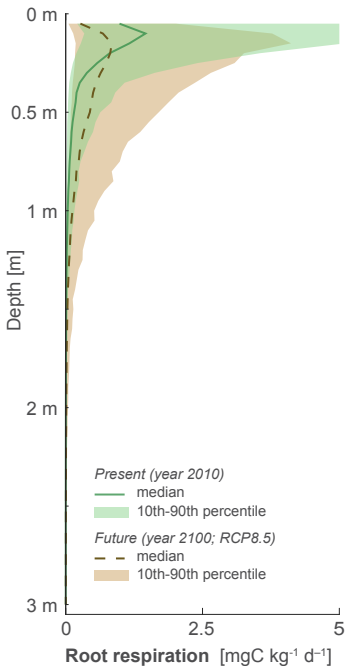
FUTURE (RCP8.5)





Vegetation zones

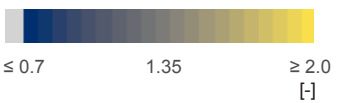
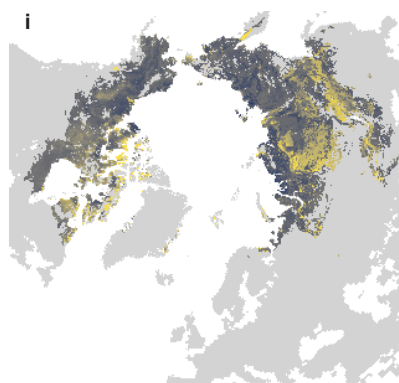
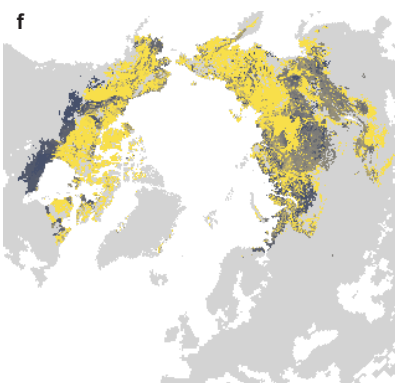
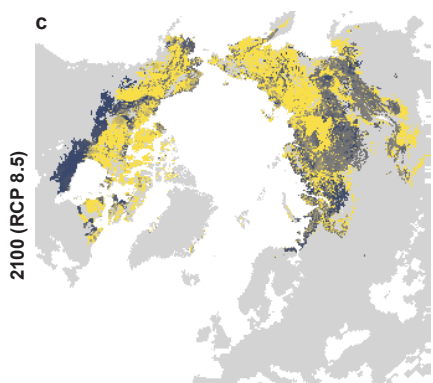
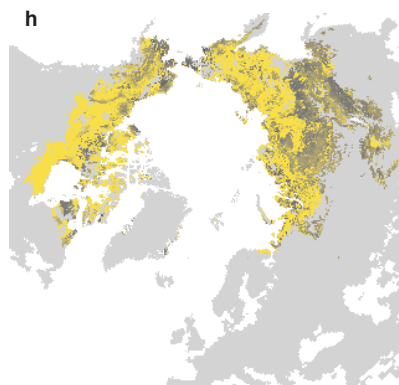
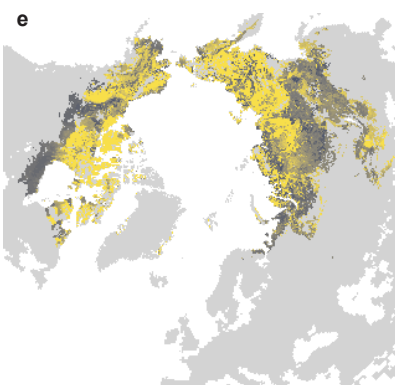
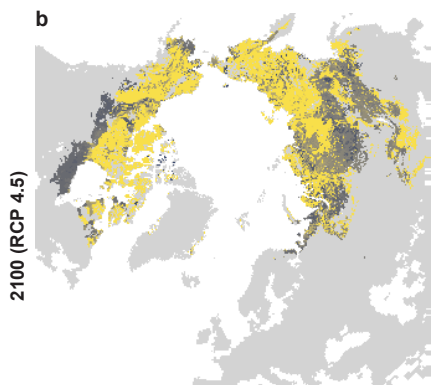
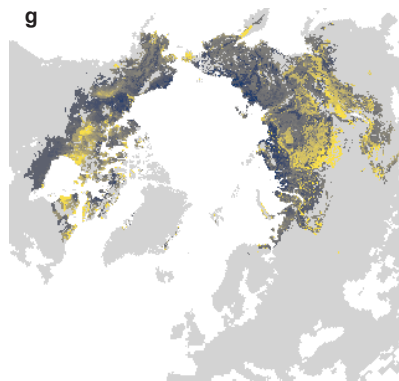
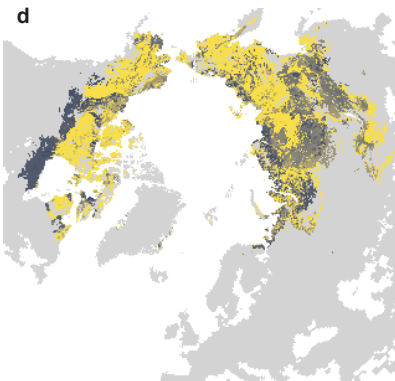
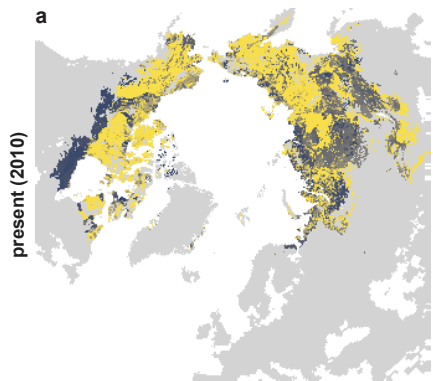
- Boreal (Bor)
- Erect-shrub tundras (S)
- Graminoid tundras (G)
- Prostrate-shrub tundras (P)
- Wetlands (W)

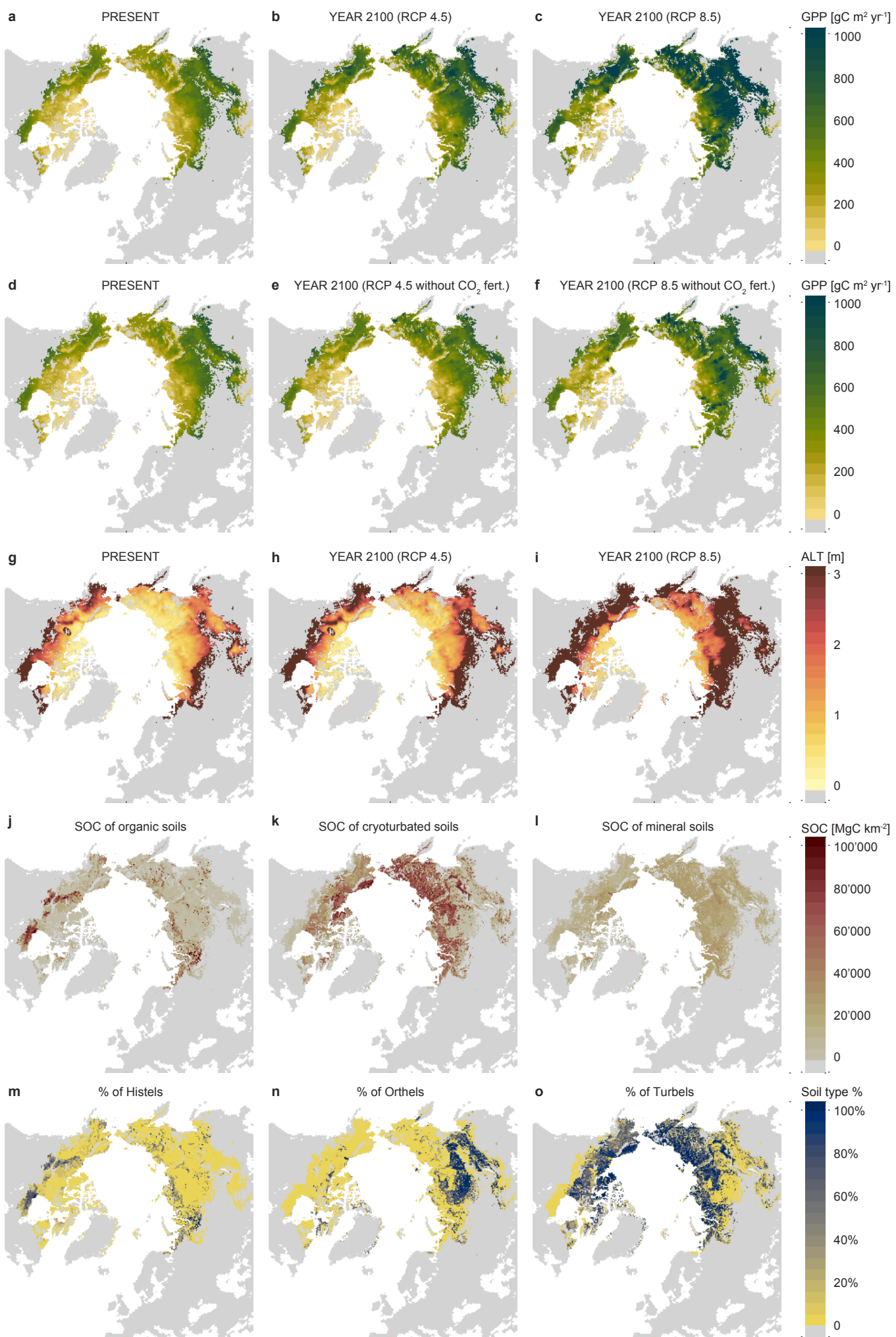


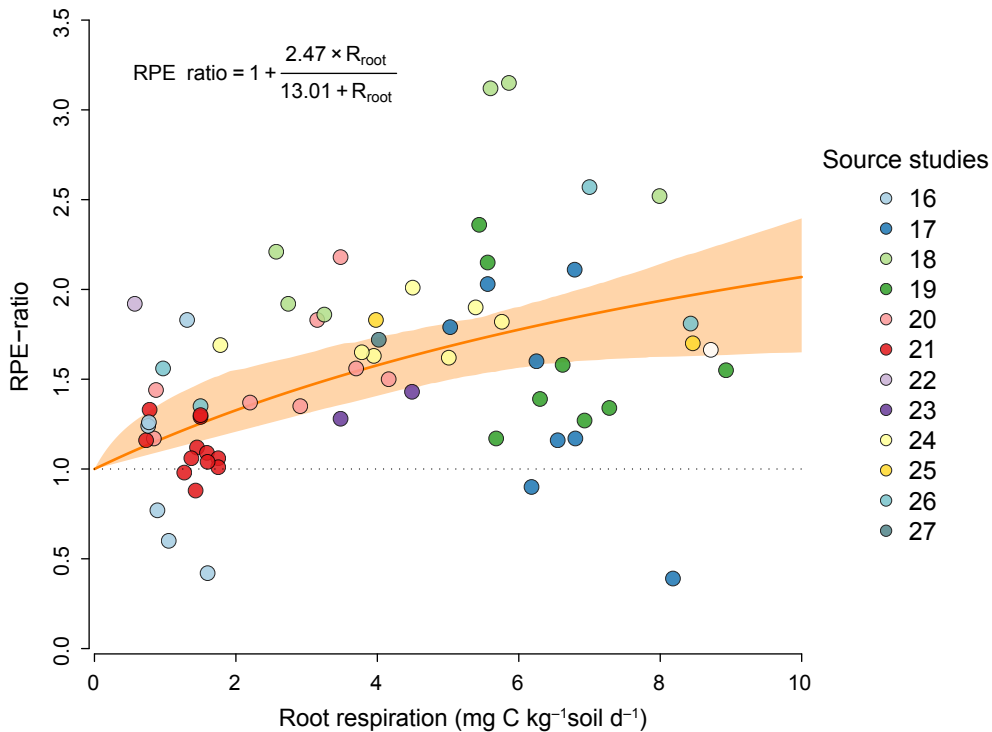
CV for RPE ratio
Mean (n = 1000)

CV for RPE-induced SOC loss
no C/N threshold
Mean (n = 1000)

CV for RPE-induced SOC loss
C/N threshold
Mean (n = 1000)







a

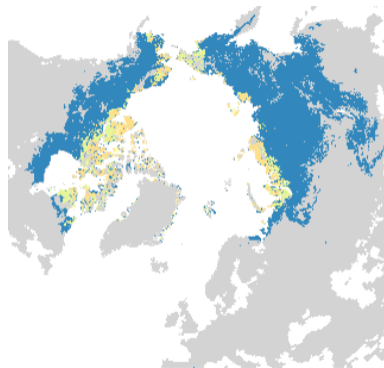
PRESENT

**b**

YEAR 2100 (RCP4.5)

**c**

YEAR 2100 (RCP8.5)



Vegetation zones



