

1 **Title: Continental-scale relationships of fine root and soil carbon stocks hold in grasslands but not**  
2 **forests**

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45  
46 **Keywords (4 to 6)**

47 roots, soil carbon, priming, forest, grassland, NEON

## 48 Abstract

49 Increasing root carbon inputs into soils has been proposed as a solution to increasing soil organic carbon  
50 (SOC). However, while fine root carbon (FRC) inputs can increase SOC accrual in soils, FRC can also  
51 enhance SOC loss by stimulating microbial respiration and cause a net loss of SOC through priming. It  
52 remains unclear how SOC varies as a function of FRC at broad spatial scales and across ecosystems and  
53 depths. Here, we tested the relationship of SOC and FRC using data from 43 sites across the US National  
54 Ecological Observatory Network (NEON). We found that total stocks of SOC and FRC in the top 2  
55 meters of soil were positively related with an across-ecosystem slope of  $7 \pm 3$  kg SOC m<sup>-2</sup> per kg FRC m<sup>-2</sup>.  
56 However, grassland sites primarily drove this relationship. Grasslands had  $15 \pm 2$  kg SOC m<sup>-2</sup> per kg  
57 FRC m<sup>-2</sup>, which is double the across-ecosystem slope. We used deviations from the standardized 1:1  
58 relationship between FRC and SOC to infer whether ecosystems were net priming (indicated by observed  
59 SOC being lower than the 1:1 line) or SOC accruing (higher SOC than the 1:1 line). Grassland soils and  
60 especially their deep soil layers (>30 cm) showed primarily SOC accrual with increasing fine root  
61 abundance. Meanwhile, forest soils had high variability in whether increasing fine roots were associated  
62 with net SOC priming or accrual across both shallow and deeper soil layers. We found that in grasslands,  
63 FRC inputs are strongly related to SOC accrual, especially at depth and at sites with high moisture and  
64 clay content. In contrast, SOC-FRC relationships in forests remain difficult to characterize. Nevertheless,  
65 deep grassland soils may serve as optimal environments in which increasing FRC could lead to  
66 meaningful increases in SOC stocks.

## 67 Introduction

68 Increasing and deepening root inputs into soils is proposed as a mechanism to increase soil organic carbon  
69 (SOC) but it remains unclear to what extent and under which environmental conditions this will be an  
70 effective strategy<sup>1,2</sup>. Fine roots (typically defined as roots with <2 mm diameter) are a key input to SOC  
71 and contribute disproportionately to SOC formation<sup>3-5</sup>. However, experimental evidence suggests that  
72 fine roots can either stabilize or destabilize SOC<sup>6-9</sup>. On one hand, labile compounds released by  
73 rhizodeposits or root litter may increase microbial biomass (and more critically, microbial necromass)  
74 thus increasing soil organic matter (SOM) if this necromass is stabilized by minerals<sup>4,10,11</sup>. On the other  
75 hand, the release of labile compounds from roots may cause a net loss of SOC (priming) by the  
76 breakdown of chemical associations between organic compounds and reactive soil minerals<sup>12</sup>, and by  
77 stimulating microbial respiration of detrital carbon (C)<sup>13-15</sup>.

78  
79 Whether fine root C inputs drive SOC accrual or priming is expected to vary by ecosystem and vegetation  
80 type, soil moisture, SOC stock and its distribution between particulate and mineral-associated pools, the  
81 amount and reactivity of soil minerals, and macro and micro soil nutrients<sup>6-8</sup>. Since these factors vary  
82 throughout the organic and mineral layers of soils, we also expect soil depth and horizons to be important  
83 predictors of the relationship between fine root C and SOC. Ecosystem types with different dominant  
84 vegetation could also vary in their accrual and priming behaviors due to differences in belowground  
85 allocation, rooting depth and other root traits<sup>16-18</sup>. One emerging hypothesis is that SOC accrual is highest  
86 in soils with high reactivity minerals and in high moisture conditions, where plant productivity, SOM  
87 transport through the profile, and SOM stabilization to mineral surfaces are also high<sup>13,19,20</sup>. However, this  
88 hypothesis remains untested with regard to root-derived organic matter inputs. Quantifying the long-term  
89 stabilization of fine root C into SOC requires repeat measurements over multiple decades. Given the lack

90 of such datasets<sup>21–23</sup>, natural gradients spanning variation in soil and ecosystem types, and containing soil  
91 and root measurements across depths, provide one means of testing the long-term, steady-state  
92 relationship between fine root C and SOC.

93  
94 Here, we used a natural gradient with varying fine root biomass carbon stocks (hereafter, FRC) to explore  
95 the relationship between FRC and SOC stocks. We also tested how the FRC-SOC relationship varies by  
96 ecosystem type, soil depth and soil horizon (organic or mineral), and how the relationship is influenced by  
97 climate, mineralogy, and soil nutrients. We expected grassland ecosystem types to have stronger FRC-  
98 SOC relationships than forests because of the high below:aboveground biomass ratio in grasslands<sup>17,18</sup>.  
99 We also expected that mineral horizons would have a stronger relationship between FRC and SOC than  
100 organic horizons because the latter are likely more influenced by aboveground litter inputs<sup>24</sup>.  
101 Additionally, in mineral horizons where SOC stabilization can proceed via organo-mineral interactions,  
102 FRC is likely linked to net SOC to a greater extent than in organic horizons, where SOC may be less  
103 protected from microbial attack and microbial population abundances tend to be higher<sup>5</sup>.

104  
105 Furthermore, by comparing our observed FRC-SOC relationships with a theoretical one-to-one  
106 relationship between FRC input and SOC stock, we inferred net SOC accrual versus priming across the  
107 gradient. Specifically, we assumed that sites with observed SOC above the 1:1 line of standardized SOC  
108 and FRC data indicate the potential for net SOC accrual (hereafter, SOC accrual), whereas sites with SOC  
109 below the 1:1 FRC-SOC line indicate the potential for net priming (hereafter, priming). We hypothesized  
110 that SOC accrual would be highest in ecosystems with high moisture and clay content where plant  
111 production and mineral stabilization of fine root litter would be optimized<sup>13,19</sup>. Conversely, priming would  
112 be more likely in ecosystems with lower moisture and clay content, where SOC would have a lower  
113 probability of interacting with soil minerals. We also hypothesized that SOC accrual would be greater at  
114 depth due to higher concentrations of reactive minerals and/or metals and lower microbial  
115 abundance/activity than in surface soils<sup>25,26</sup>.

116  
117 We used the continental gradient provided by the National Ecological Observatory Network (NEON;  
118 Figure 1a) where coupled FRC and SOC measurements to 2-m depth have been conducted at 43 sites  
119 across the USA (see Table S1 for data sources). NEON sites represent a range of climates, with mean  
120 annual temperatures ranging from -12 to 25 °C and mean annual precipitation ranging from 100 to 2500  
121 mm year<sup>-1</sup>. The sites also capture a variety of ecosystem types, though we focus our analyses primarily on  
122 grasslands and forests, which are the most abundant ecosystems across the network. Although it is  
123 difficult to leverage observational data collected at a continental spatial scale to probe processes such as  
124 microbial priming and mechanisms of SOC persistence that can occur at the micron scale, our work  
125 illuminates broad spatial patterns in SOC stocks that may be driven by these underlying processes.

126

127

## 128 **Results**

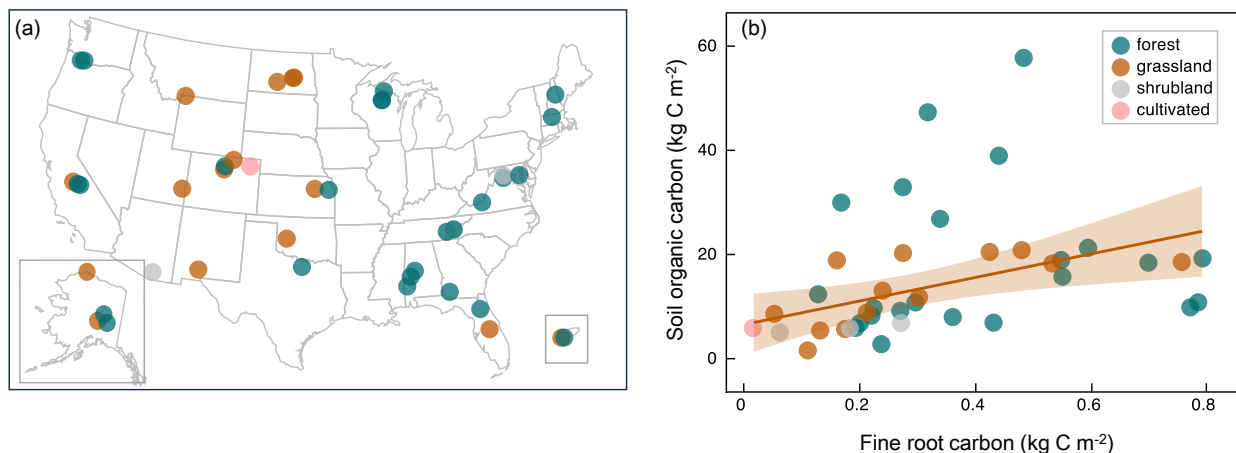
### 129 ***Grasslands drive broad-scale fine root and soil carbon relationships***

130 As hypothesized, FRC and SOC were related across sites, but these trends were primarily driven by  
131 grasslands (Figure 1b). Combining C stocks across the entire soil profile (to a maximum 2-m depth; Table

132 S2), we found that FRC and SOC were positively related across our continental USA spatial gradient. The  
133 total SOC stock in a soil profile was positively related to whole-profile FRC (Figure S1a; adj  $r^2= 0.39$ ,  $p <$   
134  $0.001$ ,  $n = 43$ ) and was best predicted by FRC, mean annual temperature (MAT), clay content, and land  
135 cover type (Table S3). For a one  $\text{kg m}^{-2}$  increase in FRC, there was a  $7 \pm 3 \text{ kg m}^{-2}$  increase in SOC (Figure  
136 S1a). Within grasslands, for every one  $\text{kg m}^{-2}$  increase in FRC, there was a  $15 \pm 2 \text{ kg m}^{-2}$  ( $p < 0.0001$  in a  
137 linear regression) increase in SOC (or  $23 \pm 7 \text{ kg m}^{-2}$  increase in SOC if the two highest FRC outliers are  
138 excluded;  $p = 0.0114$ ). This grassland-only estimate is more than double the value across all ecosystems  
139 (cross-ecosystem estimate:  $7 \pm 3 \text{ kg SOC m}^{-2}$  per  $\text{kg FRC m}^{-2}$ ; Figure S1) due to the lack of a FRC-SOC  
140 relationship in forests. Our analyses suggest that aridity (MAP standardized by MAT; see methods),  
141 micronutrients, and aboveground litter input may be important in explaining forest SOC, but the  
142 relationships were not statistically significant (Figure S2).

143  
144 When separated into organic and mineral horizons, FRC and SOC remained positively related across  
145 ecosystems, and ecosystem type was a significant predictor across most statistical models (Table S4a-b).  
146 However, the slope and best predictors of the relationship differed between soil horizons (Figure S1b).  
147 The only significant predictor of SOC in the organic horizon was FRC (adj  $r^2= 0.41$ ,  $p = 0.03$ ,  $n = 17$  out of  
148 which 2 were grasslands and rest were forests; Table S4a). Conversely, in the mineral horizon other  
149 factors such as MAT and percent clay were also important (adj  $r^2= 0.30$ ,  $p = 0.003$ ,  $n = 43$ ; Table S4b).  
150 Interestingly, three high latitude sites had more than twice as much root biomass than the others: NEON  
151 site codes WREF (cold and wet coniferous forest), BARR (tundra), and HEAL (tundra) (See Table S2 for  
152 details corresponding to site codes). Excluding these three sites, a model with root biomass, MAT, clay,  
153 and land cover still resulted in significant relationships, albeit weaker (adj  $r^2 = 0.19$ ,  $p < 0.001$ ,  $n = 40$ ).  
154 Thus, contrary to our hypotheses, our cross-ecosystem analysis suggests that in organic horizons, FRC is  
155 a primary predictor of SOC, while in mineral horizons, MAT and clay content are also important. MAT  
156 likely is a proxy for temperature limitations on plant productivity and decomposition of SOM while clay  
157 content represents the potential for mineral-associated organic matter formation.

158

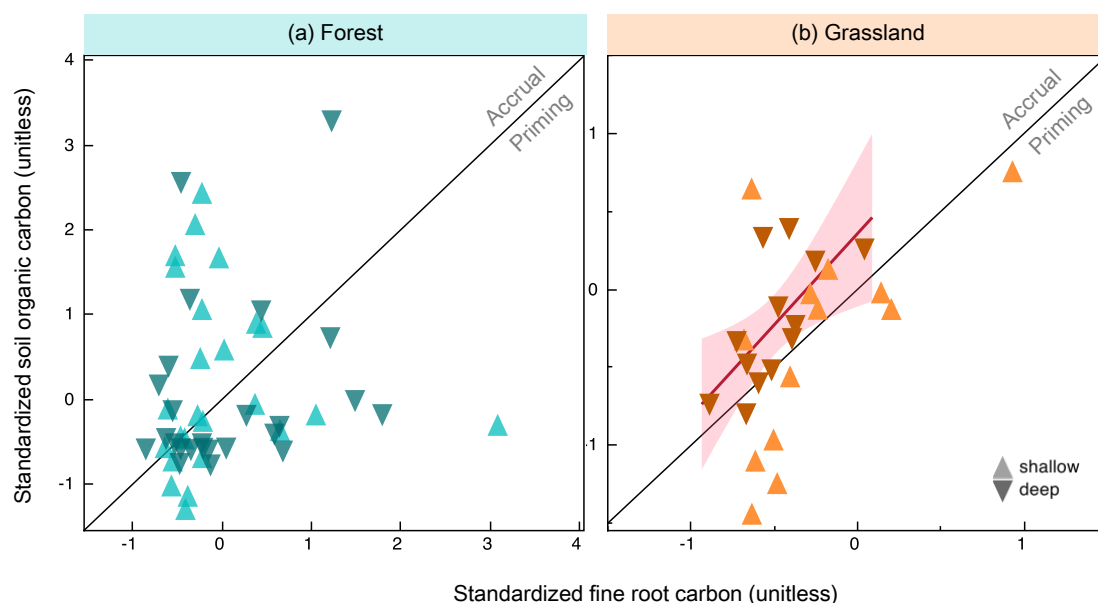


159  
160 Figure 1. Site locations and relationships between fine root carbon and soil organic carbon stocks. (a)  
161 NEON site distribution by ecosystem type. Alaska and Puerto Rico are shown as insets. (b) The overall  
162 relationship between FRC and SOC (in Figure S1a) is driven by grasslands. Grasslands ( $n = 15$ ) have a  
163 significant relationship between FRC and SOC ( $r^2= 0.80$ ,  $F_{1,13}=53.14$ ,  $p < 0.0001$ ;  $y = 8.5 + 15.5x$ ). For

164 ease of visualization, we have removed the three highest FRC sites here, but these tundra sites are  
165 included in Figure S1a and Table S2. Removing these outliers decreases the  $r^2$  to 0.46 but increases the  
166 slope to 22.6 kg SOC FRC<sup>-1</sup> m<sup>-2</sup>. Forest FRC and SOC are unrelated (n = 25). Shrubland (n= 3) and  
167 cultivated (n= 1) ecosystem types do not have adequate sample sizes to analyze FRC-SOC relationships.  
168 Table S2 also provides information on depth of sampling, typically 2 m.

### 169 ***Strong positive FRC-SOC relationships in deep grassland soils***

170 Similar to the relationships between total FRC and SOC summed across the soil profile, we found that  
171 depth distributions of FRC and SOC stocks (quantified using an exponential decay function fit; Figure  
172 S3) were related in grasslands but not in forests (Figure S3-S5, Tables S5a and S5b). Furthermore, we  
173 investigated how shallow (< 30 cm soil depth) and deep (> 30 cm soil depth) FRC influence shallow and  
174 deep SOC. Specifically, we tested whether the slope of the standardized FRC-SOC relationship in deep  
175 soil layers is higher than the slope of the FRC-SOC relationship in shallow layers. This observation would  
176 suggest a more effective SOC accrual per unit FRC at depth. We found that in deep soils, SOC increased  
177 more with increasing FRC than in shallow soils in grasslands (Figure S7 and Figure 2b) but not in forests  
178 (Figure S8 and Figure 2a). Our results thus support the hypothesis that deep FRC increases deep SOC  
179 more than shallow FRC increases shallow SOC, but only in grasslands. Furthermore, in grasslands, while  
180 a unit increase in standardized deep FRC increases deep SOC by  $1.23 \pm 0.42$  ( $p = 0.015$ ), a unit increase in  
181 shallow FRC does not significantly increase shallow SOC ( $p = 0.19$ ) (based on the slopes in Figure S7).



182  
183  
184 Figure 2. Standardized fine root carbon (FRC) and soil organic carbon (SOC). FRC and SOC are shown  
185 by soil depth along with a 1:1 line. Data points above the 1:1 line suggest inferred net accrual of SOC  
186 while data points below the 1:1 line suggest inferred priming. (a) Forests have no significant relationship  
187 between standardized FRC and SOC while (b) in grasslands the slope of the relationship between deep  
188 roots and deep SOC (>30 cm) is steeper (linear regression slope= 1.2,  $p=0.015$ ) than the slope between

189 shallow roots and shallow SOC (<30 cm depth; slope=0.9, p=0.19). Detailed statistics across depths and  
190 ecosystem type are provided in Figure S7 and S8.

### 191 *Lowest inferred priming in deep grassland soils*

192 Using the standardized shallow and deep FRC-SOC relationships above, we quantified residuals from the  
193 1:1 line, i.e., the difference between observed SOC value at a given site and the expected SOC value at a  
194 theoretical 1:1 line. We used these residuals as indicators of net SOC accrual or net priming relative to  
195 FRC inputs. Inferred SOC accrual corresponds to relatively more SOC being stored than incoming FRC  
196 (i.e., data points above the 1:1 line), and inferred priming corresponds to lower SOC being stored than  
197 incoming FRC (i.e., below the 1:1 line) (Figure 2). We found that forests exhibited great variation in  
198 inferred SOC accrual or priming relative to grasslands, which were primarily SOC accruing (Figure 3). In  
199 addition to ecosystem type, the degree of accrual or priming was predicted by factors related to moisture  
200 availability (aridity and MAP), soil texture and micronutrients (Table S6). In grasslands, priming  
201 increased with decreasing moisture availability, clay content and micronutrients; particularly in shallow  
202 soil layers (Figure S9). In forests, the variability in inferred priming was harder to explain, with the best-  
203 fit model explaining up to 44% of the variability in priming versus 73% in grasslands (Table S6). Deep  
204 forest soil dynamics remain particularly elusive as we could only explain up to 26% of the variability in  
205 inferred priming (Table S6). For example, we observed some indication of higher priming in warmer  
206 forests (Figure S10) compared to cooler forests, but this explained only 20% of the variability in priming.  
207

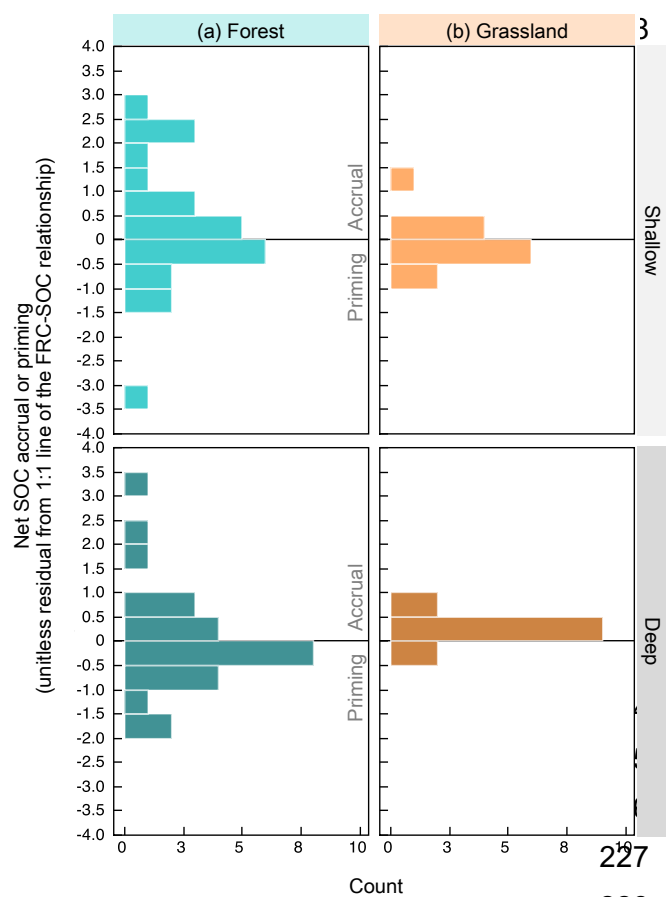


Figure 3. Distributions of inferred SOC accrual or priming. SOC accrual or priming is inferred from residuals of the 1:1 line between standardized FRC and SOC; see Figure 2. Data distributions are shown for shallow (<30 cm depth) and deep (30-200 cm) layers from both (a) forest and (b) grassland sites. Bins above the zero line are reflective of sites net SOC accrual and bins below the zero line reflect net priming. See Figure S12 for raw data points of the distributions.

## 230 Discussion

### 231 *Unexplained variability in forest root-soil carbon relationships*

232 There are several possible explanations for why forest FRC-SOC relationships and priming may be highly  
233 variable compared to grasslands. In this section, we use existing literature to discuss possible mechanisms  
234 behind our results.

235  
236 First, grasslands typically have higher root:shoot ratios than forests and thus grassland root inputs may  
237 represent a dominant source of fresh carbon input into the soil<sup>17,27,28</sup>. Conversely, in forests, root:shoot can  
238 vary considerably across climate gradients and aboveground inputs may also be an important source of  
239 fresh carbon inputs into the soil, especially in deciduous forests<sup>27</sup>. This could mean that FRC inputs and  
240 FRC-induced priming are less influential on soil C processes compared to aboveground litter inputs in  
241 forests versus grasslands, although we did not see any evidence for aboveground litterfall rates predicting  
242 forest SOC either (Figure S2). It is possible that increased aboveground litterfall also led to priming in  
243 forests, as previously observed in temperate and tropical forests<sup>29-32</sup>.

244

245 Second, in forests and in woody plants, maximum rooting depths vary widely and differ from the more  
246 conserved rooting depths of grasslands<sup>16,33</sup>. This rooting depth variation would also influence the  
247 relationship between FRC and SOC, given the hypothesis that deeper roots have a greater propensity for  
248 mineral interactions and thus contribute to persistent SOC pools<sup>26</sup>. In our data we also observed generally  
249 deeper and more variable depth distributions of FRC and SOC in forests compared to grasslands (Figure  
250 S4). The variability in forest FRC-SOC relationships suggests that factors other than FRC contribute to  
251 forest SOC accrual to a greater extent than in grassland soils.

252  
253 Third, the chemical composition of litter and root inputs may vary more across forest types compared to  
254 grasslands, making the relationship between FRC inputs and SOC accumulation across forests harder to  
255 predict. Graminoid species can be chemically relatively simple compared to other plants<sup>34</sup>. In contrast,  
256 tree species are known to differentially affect decomposition and soil C and N cycling<sup>35,36</sup>, including the  
257 magnitude of the rhizosphere priming effect<sup>37</sup>. Leaf and root litter from some tree species can be a source  
258 of tannins and other phenolics that affect soil processes<sup>38-40</sup>, and the presence or absence of tannin-rich  
259 species on our forest sites may represent an important source of variability in forest SOC dynamics. For  
260 example, tannin-rich litter could promote SOC stabilization while cellulose-rich litter could stimulate  
261 priming<sup>41</sup>. Thus, plant litter quality influences priming or stabilization of SOC, and greater variability in  
262 litter quality in forests compared to grasslands could potentially contribute to our observed high variation  
263 in forest SOC dynamics<sup>42</sup>.

264  
265 Fourth, grassland plant roots typically have higher absorptive:transport root ratios and a greater  
266 proportion of absorptive roots with short lifespans, which could imply greater exudation and greater root  
267 litter contribution to SOC, respectively<sup>43,44</sup>. Given the generally greater physiological activities of fine  
268 compared to coarse roots<sup>43</sup>, a greater relative abundance of high-turnover, absorptive roots in grasslands  
269 compared to forests<sup>45</sup> might also result in greater activity rates of soil microbes. This greater microbial  
270 activity could also be higher in grasslands than in forests because grassland roots decompose faster than  
271 forest roots<sup>46</sup>. Thus, we might expect greater rates of microbial necromass production where fine root  
272 abundance is relatively greater, given fine root exudate activities and associated rhizosphere microbial  
273 growth and death<sup>47</sup>. Evidence is accumulating that microbial necromass is a meaningful component of  
274 persistent SOC stocks<sup>47-49</sup>. We might expect, then, that where absorptive root litter production is greater,  
275 necromass and thus SOC accrual might also be greater.

276  
277 Fifth, higher and more variable precipitation in forests compared to grasslands could drive variability in  
278 the activity of decomposition enzymes and reactive metals<sup>19</sup>. Thus, mineralogical limits to C storage,  
279 driven by variations in the amount and reactivity of clay minerals and reactive metals, may be more  
280 important controls on forest SOC than litter inputs<sup>19,50</sup>. Since our predictive models do not include  
281 detailed proxies defining mineralogical limits to C storage, we may be missing some explanatory power  
282 and thus seeing high variability in forests. Furthermore, our grassland sites, on average, have half the  
283 mean annual precipitation of our forest sites. Thus, plant growth, litter inputs and decomposition could all  
284 be more moisture limited in grasslands than in forests, such that C inputs and not mineralogical limits are  
285 a more important factor for stabilizing SOC in grasslands.

286  
287 Lastly, forests have the added complexity of a variety of mycorrhizal symbionts that could be influencing  
288 plant-soil processes and belowground carbon allocation in ways different than in grasslands, which are

289 often limited to arbuscular mycorrhizal types that have a lower carbon demand (Figure S11)<sup>51-53</sup>.  
290 Dominant mycorrhizal association type was not a significant predictor in any of our models, but it is  
291 likely that fungal biomass would have been a better predictor (data unavailable). FRC and fungal biomass  
292 together would better capture the forest variability in total belowground carbon allocation. Furthermore,  
293 high variation in mycorrhizal types and other microbial community types in forests would also lead to  
294 diverse decomposition dynamics<sup>e.g., 54</sup>. Overall, it makes sense that while we were able to explain inferred  
295 priming in grasslands using simple climate, soil texture, and nutrient information, inferred priming in  
296 forests would require additional predictors including information about root systems, litter quality,  
297 mineralogical limits to C storage, and microbial community structure and function.

## 298 ***Limitations***

299 Our inferred priming proxy allows us to explore potential relationships between FRC and SOC and offers  
300 hypotheses to probe the drivers of SOC formation and persistence. However, our approach has  
301 limitations. First, our proxy does not account for all the belowground C inputs into SOC. We only  
302 consider standing fine root biomass in our calculations. Ideally, inputs to SOC should include  
303 rhizodeposits, and should incorporate information about root and fungal turnover rates<sup>55</sup>, but these data  
304 were unavailable. Second, we did not have a way to account for variation in the decomposition of  
305 incoming root litter. In other words, at sites where we saw high inferred priming, there may have simply  
306 been efficient decomposition of fresh root litter. Root litter decomposition rates in the first year can vary  
307 widely in forests, with estimates suggesting 20-40% mass loss<sup>56</sup>. Thus, we expect that this variability  
308 further contributed to the lack of a clear FRC-SOC relationship in forests. Third, as is the case with many  
309 observational studies, it is difficult to ascribe causation to correlative relationships. A variety of climate  
310 and edaphic factors could be driving both FRC and SOC, thus resulting in the observed relationships.

## 311 ***Conclusions***

312 In the last few decades, paradigm shifts in SOC research suggest that root carbon inputs are central to  
313 organic matter formation and stabilization<sup>5</sup>. We found that at broad spatial scales, FRC and SOC are  
314 related but these trends were driven by grasslands and not forests across the NEON gradient. We also  
315 investigated whether deeper roots are associated with higher deep SOC, which is presumed to be more  
316 stable, and found support for this in grasslands but again not in forests. Our hypothesis that stabilization  
317 of FRC into SOC would be highest under conditions of high moisture and mineral surface availability  
318 (using clay content as a proxy) was supported in grasslands. Future data collection efforts at the  
319 continental scale and beyond should quantify other belowground carbon inputs (e.g., root turnover and  
320 exudation, and microbial biomass turnover) into soils to enable a more mechanistic understanding of FRC  
321 and SOC linkages across biomes. Nevertheless, in the context of management strategies of increasing  
322 FRC to increase SOC, root biomass will likely be the main trait that can be measured and managed, and  
323 not root turnover<sup>2</sup>. Thus, our analysis provides a useful benchmark of how FRC and SOC are related  
324 across broad scales and ecosystems.

325  
326 Unlike grasslands, forests displayed high variability in FRC-SOC relationships, both across space and  
327 depth, likely due to the potentially higher complexity in root-soil interactions in forests. Thus, forests may  
328 not be ideal settings to increase SOC through fresh root carbon inputs as this may result in priming-  
329 induced SOC losses and increased CO<sub>2</sub> emissions via increased root litter and SOM decomposition.

330 Predictors of this forest priming effect, especially in deeper layers, remain elusive and can serve as an  
331 important future research trajectory. Grassland soils with relatively high moisture and clay content, may  
332 serve as settings in which increased root-derived SOC sequestration may be promoted at depth, although  
333 replication across climate gradients and detailed measurements of root dynamics are needed to  
334 confidently project SOC accrual.  
335

## 336 **Materials and methods**

### 337 *Sites and data*

338 The root and soil carbon data used for this study were collected by NEON, a continental-scale ecological  
339 monitoring program spanning 47 terrestrial sites and all major US ecoclimatic regions. We used data from  
340 the NEON ‘megapits’, which include measurements of soil chemical properties, physical properties, and  
341 root biomass (Table S1). We downloaded these data from the Soils Data Harmonization (SoDaH)  
342 database<sup>22</sup> (data accessed Jul 2020) which includes NEON data<sup>57</sup> among other network data sources. Data  
343 from other networks were not considered in this study because sites infrequently measured root biomass  
344 and soil chemistry profiles to depth in the same location. Four NEON sites (STER, KONA, PUUM, and  
345 TOOL) were excluded from our study because root data were not collected in the NEON ‘megapits’.  
346 Thus, 43 of the 47 NEON sites were included in our analyses. All 43 sites had mineral soil horizons, and  
347 17 of the 43 sites had organic soil horizons (15 forests and 2 high latitude grasslands/tundra). Site  
348 metadata such as mean annual temperature, mean annual precipitation, and site-wide dominant plants  
349 were taken from SanClements et al<sup>58</sup>. We also calculated an aridity index as MAP (mm) standardized by  
350 MAT (degree Celsius) using the formula  $MAP/(MAT+13)$ . The 13 was added to adjust for negative MAT  
351 values<sup>59</sup> and lower values represent more arid conditions. Land cover was ascertained by NEON  
352 scientists and was based on the NLCD land cover classifications<sup>60</sup> from NEON field site information  
353 tables ([link](#)).

### 354 *Sample collection and processing*

355 The NEON megapit sampling effort was a one-time measurement conducted by NEON staff and the  
356 USDA Natural Resource Conservation Service (NRCS) over the course of 2014-2018. At each site,  
357 NEON scientists and contractors excavated a 2 m deep (or to bedrock) soil pit in the vicinity of the  
358 NEON eddy covariance tower. The timing of sampling varied across the growing season and was not  
359 always at peak biomass. NRCS soil scientists then assigned soil taxonomy *in situ*, and by taxonomic  
360 horizon to the bottom of the pit. These samples were then sent to the Kellogg Soil Survey Laboratory in  
361 Lincoln, Nebraska where, after passing through a 2 mm sieve, they were analyzed for a host of physical  
362 and chemical properties including bulk density, particle size, total C, nitrogen (N), phosphorous (P),  
363 metals, and other edaphic properties using standard NRCS methods<sup>61</sup>.

364 At each NEON megapit, root samples were collected across depth profiles. Samples were  
365 collected in 10-cm depth increments to 1 m depth, then in 20-cm depth increments to 2 m depth by cutting  
366 10-cm deep x 10 cm wide soil monoliths, in three vertical profiles on the left, middle, and right side of the  
367 pit. Roots were hand-sorted from these monoliths, visually classified as live or dead, and diameter was  
368 measured. Most NEON sites (30 sites out of 43) classified “fine roots” as less than 2 mm diameter.  
369 However, 13 sites had a different methodological protocol and used a 4 mm diameter cutoff. Of these,

370 nine were forests, three were rangelands/grasslands (hereafter, grassland), and one was a shrubland. Note  
371 that we statistically tested the hypothesis that having different fine root diameter cut offs may be related  
372 to our observed variability in forest FRC-SOC relationships. This hypothesis was not supported in a  
373 Wilcoxon rank test of the residuals from the FRC-SOC relationship when comparing the two diameter  
374 classes ( $Z = 0.59$ ,  $p = 0.55$ ). Other studies<sup>62</sup> have also found that root biomass from these two diameter  
375 classes are highly correlated across sites in fine root databases, and that in the NEON sites, the diameter  
376 sampling differences do not influence properties such as rooting depth distribution<sup>62</sup>.

377 Root biomass was measured after oven-drying the samples at 65°C for at least 48 hours. Dried  
378 root samples were sent to the University of Wyoming for analysis of C concentrations using elemental  
379 analysis. The three vertical pit profiles per megapit were averaged prior to ingestion into SoDaH and used  
380 in our statistical analysis. Despite the 4 mm diameter exceptions, we consider the root stock to represent  
381 ‘fine-root biomass’ throughout the manuscript.

382 Lastly, we used annual litterfall fluxes (forest sites only) as a covariate in an exploratory analysis  
383 (see Table S1 for data sources). Briefly, annual litterfall was measured by collecting all material dropped  
384 from the forest canopy with a diameter <2 cm and a length <50 cm using elevated 0.5 m<sup>2</sup> PVC traps.  
385 Traps were deployed (20 plots per site) near the megapits. We used the total mass (leaves, needles, twigs,  
386 etc. all added) collected by the traps over the course of a growing season to estimate annual productivity.  
387 Where multiple years of data were available, the average flux was used.

### 388 *Data alignment*

389 Alignment of FRC and SOC data was necessary due to different sampling strategies for roots and  
390 soils. Roots were sampled at fixed (10 or 20 cm) increments through the profile, while soils were sampled  
391 once in each taxonomic horizon regardless of horizon depth. Therefore, we aligned the root data with the  
392 corresponding soil horizon. Fine root biomass C stocks (FRC) were calculated as the product of root  
393 biomass (g m<sup>-2</sup>) in a given depth interval and FRC concentration (%). SOC stocks were calculated as the  
394 product of soil organic C concentration (%), bulk density (kg/cm<sup>3</sup>), and sampling depth (cm), then  
395 converted to kg m<sup>-2</sup> by multiplying by  $1 \times 10^3$ .

### 396 *Calculation of beta coefficients*

397 In order to investigate the relationship between depth profiles of FRC and SOC, we calculated  
398 beta values using an exponential decay curve (Eq. 1), which describes how stocks change with depth<sup>18,63</sup>.  
399 Of the 43 NEON sites, 36 were used to calculate beta coefficients. Seven sites (BARR, CLBJ, GRSM,  
400 GUAN, JORN, LAJA, TEAK) were excluded because beta coefficients could not be calculated due to too  
401 few SOC measurements in the profile. Soil organic carbon and FRC may accumulate primarily in surface  
402 soils and to varying degrees deeper in the profile, or there may be a gradual and consistent increase at  
403 each depth interval. These different accumulation patterns can be captured in an exponential function (Eq.  
404 1), where a higher beta coefficient indicates a deeper distribution of root or SOC, relative to a lower beta.  
405 We converted each depth profile (FRC or SOC) at each site into one beta coefficient to facilitate these  
406 analyses.

407 Beta coefficients ( $\beta$ ) were calculated using the following function<sup>18,63</sup>:

$$408 \quad Y = 1 - (\beta)^d \quad \text{Eq. 1}$$

410

411 In Eq. 1,  $Y$  is the cumulative fraction of either SOC or root biomass in a given layer with respect to the  
412 whole profile, and  $d$  is the depth (cm) measured at the bottom of that layer. For every depth layer at every  
413 site, we solved for  $\beta$  in Eq. 1 for both SOC ( $\beta_{SOC}$ ) and root biomass ( $\beta_{roots}$ ). These  $\beta$  values were used as  
414 starting parameters at discrete points through the depth profile, and we used the iterative Bound  
415 Approximation by Quadratic Approximation (BOBYQA) method (package `minqa` in R) <sup>64</sup> to interpolate  
416 between points and resolve the function across the continuous depth profile at each site <sup>65</sup>. The  
417 BOBYQA-resolved  $\beta_{SOC}$  and  $\beta_{FRC}$  values were used as response and fixed effect variables, respectively, in  
418 mixed effects models.

#### 419 *Statistical analyses*

420 We analyzed relationships between SOC, FRC, and other climatic and edaphic covariates using linear  
421 mixed-effects models. We analyzed FRC-SOC relationships in three ways wherein FRC and SOC stocks  
422 were: 1) summed across the whole profile, 2) separated by organic and mineral soil horizons, and 3)  
423 described as beta coefficients as a function of depth. For each analysis, we constructed a null (random  
424 effects only) model, a full model, and then reduced models that lacked covariates. We selected best-fit  
425 models based on the lowest Akaike Information Criterion (AIC) score aside from the full model, to avoid  
426 overparameterization, or the sample-size corrected AIC (AICc) score when the data set contained fewer  
427 than 40 observations <sup>66</sup>. In whole-profile and by-horizon analyses, the full model included SOC as the  
428 response and FRC, mean annual temperature (MAT), mean annual precipitation (MAP), clay percent, and  
429 land cover (ecosystem type) as fixed effects and maximum profile depth as a random effect. We also  
430 verified that sampling depth does not influence our analyses by conducting a multiple regression analysis  
431 including all covariates and maximum profile depth and found that profile depth was not a significant  
432 parameter ( $p = 0.57$ , partial  $r^2 = 0.01$ ). Lastly, we explored the role of mycorrhizal associations by adding  
433 dominant mycorrhizal type (arbuscular, ectomycorrhizal or mixed) <sup>51</sup> as a fixed effect but saw no  
434 significant relationships or model improvements. Across the mixed-effects models, we report the  
435 significance level (p-value) calculated using Satterthwaite's method (`lmerTest` R package) <sup>67</sup>, a test  
436 statistic ( $\chi^2$ ), and marginal pseudo- $R^2$  (`sjstats` R package) <sup>68</sup>. The fixed effects of the best fit model were  
437 tested using analysis of variance (Anova function in the R package `car`) <sup>69</sup>. Forest and grassland land cover  
438 types were tested and shrublands and cultivated lands were excluded from this analysis due to limited  
439 sample size. Assumptions of homoscedasticity, low variance inflation factors and normal data  
440 distributions were verified for each statistical model.

#### 441 *Inferred SOC accrual and priming*

442 We calculated inferred net accrual or priming using residuals, which measure the difference between  
443 observed and predicted values, from the shallow (<30 cm) and deep (>30 cm depth) FRC-SOC  
444 relationships. Specifically, we determined the residual difference between the observed SOC and  
445 expected SOC along a standardized 1:1 line, which represents a theoretical scenario where each unit of  
446 FRC input results in an equivalent unit increase in SOC (Figure S7 and S8). This 1:1 line serves as the  
447 baseline for assessing if SOC levels are higher or lower than expected based on FRC inputs. The  
448 calculated residuals, therefore, act as a proxy for SOC accrual (when observed values exceed the  
449 expected) or priming (when observed values are less than expected) in relation to FRC inputs.  
450 Furthermore, we employed multiple regression models to explore the potential factors influencing this  
451 inferred priming or accrual, as detailed in Table S6. These models allow us to identify and evaluate  
452 variables that may affect the relationship between FRC and SOC across different sites and conditions.  
453

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469 **Author contributions**

470 AM, JAM, SW-L, KG, EK-S, ASG, DP, KL, WRW, RBJ, SJT-D and ML conceptualized the study. AM,  
471 JAM, SW-L and KG performed the analyses. AAB, SAB, MG, JMF, ASG, CM, DP, KL, WRW, and  
472 SW-L provided data. AM wrote the manuscript with input from all coauthors. RBJ, KL and WRW  
473 acquired funding.

474 **Competing interests**

475 The authors declare no competing interests.

476 **Data availability**

477 All data used in this manuscript are publicly available from the National Ecological Observatory Network  
478 (NEON) and the corresponding data product names are reported in Supplementary Table S1.

479 **Code availability**

480 Code used in the study is available as a supplementary materials file.  
481  
482

483 **References**

- 484
- 485 1. Bossio, D. A. *et al.* The role of soil carbon in natural climate solutions. *Nature Sustainability* **3**, 391–
- 486 398 (2020).
- 487 2. Kell, D. B. Breeding crop plants with deep roots: their role in sustainable carbon, nutrient and water
- 488 sequestration. *Ann. Bot.* **108**, 407–418 (2011).
- 489 3. Jackson, R. B. *et al.* The Ecology of Soil Carbon: Pools, Vulnerabilities, and Biotic and Abiotic
- 490 Controls. *Annu. Rev. Ecol. Evol. Syst.* **48**, 419–445 (2017).
- 491 4. Rasse, D. P., Rumpel, C. & Dignac, M.-F. Is soil carbon mostly root carbon? Mechanisms for a
- 492 specific stabilisation. *Plant Soil* **269**, 341–356 (2005).
- 493 5. Rocci, K. S. *et al.* Bridging 20 years of soil organic matter frameworks: Empirical support, model
- 494 representation, and next steps. *J. Geophys. Res. Biogeosci.* **129**, e2023JG007964 (2024).
- 495 6. Lajtha, K., Bowden, R. D. & Nadelhoffer, K. Litter and root manipulations provide insights into soil
- 496 organic matter dynamics and stability. *Soil Sci. Soc. Am. J.* **78**, S261–S269 (2014).
- 497 7. Bowden, R. D. *et al.* Litter Input Controls on Soil Carbon in a Temperate Deciduous Forest. *Soil*
- 498 *Science Society of America Journal* **78**, S66–S75 (2014).
- 499 8. Pierson, D. *et al.* Mineral stabilization of soil carbon is suppressed by live roots, outweighing
- 500 influences from litter quality or quantity. *Biogeochemistry* **154**, 433–449 (2021).
- 501 9. Dijkstra, F. A., Zhu, B. & Cheng, W. Root effects on soil organic carbon: a double-edged sword.
- 502 *New Phytol.* **230**, 60–65 (2021).
- 503 10. Sokol, N. W. *et al.* The path from root input to mineral-associated soil carbon is dictated by habitat-
- 504 specific microbial traits and soil moisture. *Soil Biol. Biochem.* **193**, 109367 (2024).
- 505 11. Miltner, A., Bombach, P., Schmidt-Brücken, B. & Kästner, M. SOM genesis: microbial biomass as a
- 506 significant source. *Biogeochemistry* **111**, 41–55 (2012).
- 507 12. Keiluweit, M. *et al.* Mineral protection of soil carbon counteracted by root exudates. *Nat. Clim.*
- 508 *Chang.* **5**, 588–595 (2015).
- 509 13. Bastida, F. *et al.* Global ecological predictors of the soil priming effect. *Nat. Commun.* **10**, 3481
- 510 (2019).
- 511 14. Bailey, V. L., Pries, C. H. & Lajtha, K. What do we know about soil carbon destabilization?
- 512 *Environ. Res. Lett.* **14**, 083004 (2019).
- 513 15. Kuzyakov, Y., Friedel, J. K. & Stahr, K. Review of mechanisms and quantification of priming
- 514 effects. *Soil Biol. Biochem.* **32**, 1485–1498 (2000).
- 515 16. Tumber-Dávila, S. J., Schenk, H. J., Du, E. & Jackson, R. B. Plant sizes and shapes above and
- 516 belowground and their interactions with climate. *New Phytol.* **235**, 1032–1056 (2022).
- 517 17. Qi, Y., Wei, W., Chen, C. & Chen, L. Plant root-shoot biomass allocation over diverse biomes: A
- 518 global synthesis. *Global Ecology and Conservation* **18**, e00606 (2019).
- 519 18. Jackson, R. B. *et al.* A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**,
- 520 389–411 (1996).
- 521 19. Heckman, K. A. *et al.* Moisture-driven divergence in mineral-associated soil carbon persistence.
- 522 *Proc. Natl. Acad. Sci. U. S. A.* **120**, e2210044120 (2023).
- 523 20. Cusack, D. F. & Turner, B. L. Fine Root and Soil Organic Carbon Depth Distributions are Inversely
- 524 Related Across Fertility and Rainfall Gradients in Lowland Tropical Forests. *Ecosystems* **24**, 1075–
- 525 1092 (2021).
- 526 21. Malhotra, A. *et al.* The landscape of soil carbon data: Emerging questions, synergies and databases.
- 527 *Progress in Physical Geography: Earth and Environment* **43**, 707–719 (2019).
- 528 22. Wieder, W. R. *et al.* SoDaH: the SOils DAta Harmonization database, an open-source synthesis of
- 529 soil data from research networks, version 1.0. *Earth System Science Data* **13**, 1843–1854 (2021).
- 530 23. Weintraub, S. R. *et al.* Leveraging Environmental Research and Observation Networks to Advance
- 531 Soil Carbon Science. *Journal of Geophysical Research: Biogeosciences* **124**, 1047–1055 (2019).

- 532 24. Garten, C. T. A disconnect between O horizon and mineral soil carbon – Implications for soil C  
533 sequestration. *Acta Oecologica* **35**, 218–226 (2009).
- 534 25. Fraterrigo, J. M., Ream, K. & Knoepp, J. D. Tree Mortality From Insect Infestation Enhances  
535 Carbon Stabilization in Southern Appalachian Forest Soils. *Journal of Geophysical Research:*  
536 *Biogeosciences* **123**, 2121–2134 (2018).
- 537 26. Rumpel, C. & Kögel-Knabner, I. Deep soil organic matter—a key but poorly understood component  
538 of terrestrial C cycle. *Plant Soil* **338**, 143–158 (2011).
- 539 27. Ma, H. *et al.* The global distribution and environmental drivers of aboveground versus belowground  
540 plant biomass. *Nat Ecol Evol* **5**, 1110–1122 (2021).
- 541 28. Steinaker, D. F. & Wilson, S. D. Belowground litter contributions to nitrogen cycling at a northern  
542 grassland–forest boundary. *Ecology* **86**, 2825–2833 (2005).
- 543 29. Sayer, E. J., Heard, M. S., Grant, H. K., Marthews, T. R. & Tanner, E. V. J. Soil carbon release  
544 enhanced by increased tropical forest litterfall. *Nat. Clim. Chang.* **1**, 304–307 (2011).
- 545 30. Crow, S. E. *et al.* Increased coniferous needle inputs accelerate decomposition of soil carbon in an  
546 old-growth forest. *For. Ecol. Manage.* **258**, 2224–2232 (2009).
- 547 31. Fontaine, S. *et al.* Stability of organic carbon in deep soil layers controlled by fresh carbon supply.  
548 *Nature* **450**, 277–280 (2007).
- 549 32. Sayer, E. J. *et al.* Tropical forest soil carbon stocks do not increase despite 15 years of doubled litter  
550 inputs. *Sci. Rep.* **9**, 18030 (2019).
- 551 33. Canadell, J. *et al.* Maximum rooting depth of vegetation types at the global scale. *Oecologia* **108**,  
552 583–595 (1996).
- 553 34. Meier, C. L. & Bowman, W. D. Links between plant litter chemistry, species diversity, and below-  
554 ground ecosystem function. *Proc. Natl. Acad. Sci. U. S. A.* **105**, 19780–19785 (2008).
- 555 35. Raich, J. W. & Tufekciogul, A. Vegetation and soil respiration: Correlations and controls.  
556 *Biogeochemistry* **48**, 71–90 (2000).
- 557 36. Hobbie, S. E. *et al.* Tree species effects on decomposition and forest floor dynamics in a common  
558 garden. *Ecology* **87**, 2288–2297 (2006).
- 559 37. Yin, L., Dijkstra, F. A., Wang, P., Zhu, B. & Cheng, W. Rhizosphere priming effects on soil carbon  
560 and nitrogen dynamics among tree species with and without intraspecific competition. *New Phytol.*  
561 **218**, 1036–1048 (2018).
- 562 38. Fierer, N., Schimel, J. P., Cates, R. G. & Zou, J. Influence of balsam poplar tannin fractions on  
563 carbon and nitrogen dynamics in Alaskan taiga floodplain soils. *Soil Biol. Biochem.* **33**, 1827–1839  
564 (2001).
- 565 39. Talbot, J. M. & Finzi, A. C. Differential effects of sugar maple, red oak, and hemlock tannins on  
566 carbon and nitrogen cycling in temperate forest soils. *Oecologia* **155**, 583–592 (2008).
- 567 40. Adamczyk, B. *et al.* Plant roots increase both decomposition and stable organic matter formation in  
568 boreal forest soil. *Nat. Commun.* **10**, 3982 (2019).
- 569 41. Huys, R. *et al.* Plant litter chemistry controls coarse-textured soil carbon dynamics. *J. Ecol.* **110**,  
570 2911–2928 (2022).
- 571 42. Craig, M. E. *et al.* Fast-decaying plant litter enhances soil carbon in temperate forests but not  
572 through microbial physiological traits. *Nat. Commun.* **13**, 1229 (2022).
- 573 43. McCormack, M. L. *et al.* Redefining fine roots improves understanding of below-ground  
574 contributions to terrestrial biosphere processes. *New Phytol.* **207**, 505–518 (2015).
- 575 44. Chari, N. R. *et al.* Estimating the global root exudate carbon flux. *Biogeochemistry* **167**, 895–908  
576 (2024).
- 577 45. Jackson, R. B., Mooney, H. A. & Schulze, E. D. A global budget for fine root biomass, surface area,  
578 and nutrient contents. *Proc Natl Acad Sci U S A* **94**, 7362–7366 (1997).
- 579 46. Solly, E. F. *et al.* Factors controlling decomposition rates of fine root litter in temperate forests and  
580 grasslands. *Plant Soil* **382**, 203–218 (2014).
- 581 47. Sokol, N. W. *et al.* Life and death in the soil microbiome: how ecological processes influence  
582 biogeochemistry. *Nat. Rev. Microbiol.* **20**, 415–430 (2022).

- 583 48. Simpson, A. J., Simpson, M. J., Smith, E. & Kelleher, B. P. Microbially derived inputs to soil  
584 organic matter: are current estimates too low? *Environ Sci Technol* **41**, 8070–8076 (2007).
- 585 49. Liang, C., Amelung, W., Lehmann, J. & Kästner, M. Quantitative assessment of microbial  
586 necromass contribution to soil organic matter. *Glob Chang Biol* **25**, 3578–3590 (2019).
- 587 50. Rasmussen, C. *et al.* Beyond clay: towards an improved set of variables for predicting soil organic  
588 matter content. *Biogeochemistry* **137**, 297–306 (2018).
- 589 51. Chaudhary, V. B. *et al.* MycoDB, a global database of plant response to mycorrhizal fungi. *Sci Data*  
590 **3**, 160028 (2016).
- 591 52. Brzostek, E. R., Fisher, J. B. & Phillips, R. P. Modeling the carbon cost of plant nitrogen acquisition:  
592 Mycorrhizal trade-offs and multipath resistance uptake improve predictions of retranslocation. *J.*  
593 *Geophys. Res. Biogeosci.* **119**, 1684–1697 (2014).
- 594 53. Yang, K. *et al.* Mycorrhizal type regulates trade-offs between plant and soil carbon in forests. *Nat.*  
595 *Clim. Chang.* **14**, 91–97 (2023).
- 596 54. Xu, Z. *et al.* The variations in soil microbial communities, enzyme activities and their relationships  
597 with soil organic matter decomposition along the northern slope of Changbai Mountain. *Appl. Soil*  
598 *Ecol.* **86**, 19–29 (2015).
- 599 55. Poirier, V., Roumet, C. & Munson, A. D. The root of the matter: Linking root traits and soil organic  
600 matter stabilization processes. *Soil Biol. Biochem.* **120**, 246–259 (2018).
- 601 56. Berg, B., Johansson, M., Meentemeyer, V. & Kratz, W. Decomposition of tree root litter in a  
602 climatic transect of coniferous forests in northern Europe: A synthesis. *Scand. J. For. Res.* **13**, 402–  
603 412 (1998).
- 604 57. NEON (National Ecological Observatory Network). Soil physical and chemical properties, Megapit  
605 (DP1.00096.001, accessed January 1, 2020); Root biomass and chemistry, Megapit (DP1.10096.001,  
606 accessed January 1, 2020); and Litterfall and fine woody debris production and chemistry  
607 (DP1.10033.001, accessed January 1 2021); PROVISIONAL. Data accessed from  
608 <https://data.neonscience.org/>.
- 609 58. SanClements, M. *et al.* Collaborating with NEON. *BioScience* **70**, 107–107 (2020).
- 610 59. Croitoru, A.-E., Piticar, A., Imbroane, A. M. & Burada, D. C. Spatiotemporal distribution of aridity  
611 indices based on temperature and precipitation in the extra-Carpathian regions of Romania. *Theor.*  
612 *Appl. Climatol.* **112**, 597–607 (2013).
- 613 60. Homer, C. H., Fry, J. A. & Barnes, C. A. The national land cover database. *US Geological Survey*  
614 *Fact Sheet* **3020**, 1–4 (2012).
- 615 61. Burt, R. Soil Survey Staff. Kellogg Soil Survey Laboratory methods manual. *US Department of*  
616 *Agriculture, Natural Resources Conservation Service, National Soil Survey Center, Kellogg Soil*  
617 *Survey Laboratory, Lincoln, NE* (2014).
- 618 62. Lu, M. *et al.* A continental scale analysis reveals widespread root bimodality. *bioRxiv* (2022)  
619 doi:10.1101/2022.09.14.507823.
- 620 63. Gale, M. R. & Grigal, D. F. Vertical root distributions of northern tree species in relation to  
621 successional status. *Canadian Journal of Forest Research* **17**, 829–834 (1987).
- 622 64. Mullen, K. M. *Minqa: Derivative-Free Optimization Algorithms by Quadratic Approximation.*  
623 (2024).
- 624 65. Powell, M. The BOBYQA algorithm for bound constrained optimization without derivatives. (2009).
- 625 66. Wagenmakers, E.-J. & Farrell, S. AIC model selection using Akaike weights. *Psychon. Bull. Rev.*  
626 **11**, 192–196 (2004).
- 627 67. Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. lmerTest Package: Tests in Linear Mixed  
628 Effects Models. *J. Stat. Softw.* **82**, 1–26 (2017).
- 629 68. Lüdtke, D. *Sjstats: Statistical Functions for Regression Models.* doi:10.5281/zenodo.1489175.
- 630 69. Fox, J. *An R Companion to Applied Regression.* (2019).