

1 Soil respiration variation along an altitudinal gradient in Italian Alps: Disentangling forest
2 structure and temperature effects

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14

15 **Abstract**

16 To understand the main determinants of soil respiration (SR), we investigated the changes of soil
17 respiration and soil physicochemical properties, including soil carbon (C) and nitrogen (N), root
18 C and N, litter C and N, soil bulk densities and soil pH at five forest sites, along an
19 elevation/temperature gradient (404 to 2101 m a.s.l.) in Northern Italy, where confounding
20 factors such as aspect and soil parent material are minimized, but an ample variation in forest
21 structure and composition is present. Our result indicated that SR rates increased with
22 temperature in all sites, and about 55% - 76% of SR was explained by temperature. Annual
23 cumulative SR, ranging between 0.65 and 1.40 kg C m⁻² yr⁻¹, declined along the elevation
24 gradient, while temperature sensitivity (Q₁₀) of SR increased with elevation. However, a high
25 SR rate (1.27 kg C m⁻² yr⁻¹) and low Q₁₀ were recorded in the old conifer forest stand at 1731 m
26 a.s.l., characterized by a complex structure and high productivity, introducing nonlinearity in the
27 relations with elevation and temperature. Reference SR at the temperature of 10°C (SR_{ref}) was

28 not related to elevation. A significant linear negative relationship was found for bulk density
29 with elevation. On the contrary, soil C, soil N, root C, root N, pH and litter mass were better
30 fitted by nonlinear relations with elevation. However, it was not possible to confirm a significant
31 correlation of SR with these parameters once the effect of temperature has been removed (SR_{ref}).
32 These results show how the main factor affecting SR in forest ecosystems along this Alpine
33 elevation gradient is temperature, but its regulating role can be strongly influenced by site
34 biological characteristics, particularly vegetation type and structure. This study also confirms
35 that high elevation sites are rich in C stored in the soil and also more sensitive to climate change,
36 being prone to high carbon losses as CO_2 . Conversely, forest ecosystems with a complex
37 structure, with high SR_{ref} and moderate Q_{10} , can be more resilient.

38 **Keywords:** Soil respiration; temperature; forests; soil; environmental factors; elevation gradient

39 **Introduction**

40 Soil respiration (SR) is the largest biological carbon (C) flux after photosynthesis in terrestrial
41 ecosystems [1]. It largely determines the C balance between the terrestrial biosphere and the
42 atmosphere [2,3,4] and assumes a decisive role in the carbon cycle and terrestrial carbon sink
43 capacity. The soil is the largest C pool in the terrestrial biosphere and has been increasingly
44 recognized to play a crucial role in mitigating global warming resulting from climate change [5,
45 6, 7]. Small changes in soil CO_2 efflux or soil organic C stocks could severely impact the global
46 C cycle [8]. In this regard, SR is one of the fluxes that have received more attention by research
47 for a longer time. The study by Janssens et al. [9] evidenced the relevant role of forest
48 productivity in the determination of SR. Since then, other studies have investigated and
49 quantified the impact of productivity on SR modeling [10, 11]. Apart from productivity, SR is
50 influenced by different abiotic and biotic factors such as soil temperature, moisture, and
51 microbial community, introducing a considerable uncertainty in SR estimates [12,13,14]. Among
52 these factors, the temperature has been the most often studied factor affecting respiratory
53 processes [15,16]. Predicting the SR response to increasing temperature (temperature sensitivity
54 of SR) has been one of the main objectives of research for years; therefore different equations
55 relating soil CO_2 efflux with temperature [17,18,19] or with a combination of temperature and
56 soil humidity have been developed [20]. Nevertheless, the Q_{10} function [21] using the Q_{10}

57 parameter to describe the temperature sensitivity of SR is one of the most widely used models,
58 still mainly employed to quantify the CO₂ efflux from the soil in Earth system models.

59 On the other hand, the elevation is a key driver of climate properties. It plays an essential role in
60 the soil organic matter distribution and may dampen the effects of climate change [14,22,23,24,
61 25]. In general, temperature declines with elevation, thus elevation gradient has been used to
62 assess soil respiration response to temperature in several studies [12,26,27,28]. These studies
63 indicate that CO₂ exchange between soil and atmosphere varies along climatic gradients and that
64 temperature sensitivity (Q₁₀) of SR increases with elevation. They also found a positive
65 relationship between soil organic matter (SOM) and elevation and reported that global soil
66 organic C stock at high elevation is more sensitive to climate change and is predicted to decrease
67 in a warming climate [14,23,29,30,31,32]. However, several researchers have reported opposite
68 trends and found lower SOM and higher SR at a higher elevation [30,33,34]. This variability
69 may be partially due to confounding factors affecting SR other than temperature. Besides
70 elevation, mountain landscapes are, in fact, characterized by substantial changes of other site
71 parameters such as slope and aspect, which can affect microclimatic conditions and, therefore
72 soil C dynamics [35]. Furthermore, due to the heterogeneity of geological substrates, soils of
73 mountain regions are highly diverse over short spatial scales and this can generate marked
74 contrasts in soil biogeochemical functions [36]. Different results have also been found when SR
75 is related to soil organic carbon [26,37].

76 Besides, there is evidence that diverse plant biome types can influence SR rate differently.
77 Therefore, the various plant communities can affect differently, microclimate, soil and litter
78 composition, and root distribution, therefore affecting soil respiration rate [18, 26,38,39,40].
79 However, within the same plant biome, there is a high spatial heterogeneity of SR. Some authors
80 found a possible linkage between the topography, plant community structure (e.g., forest type
81 and speed of regeneration), and SR within the same forest ecosystems [18,38,39,40]. Further,
82 forest management can also play a crucial role in SR [41]. For instance, tree removal can directly
83 influence soil respiration due to the removal itself (i.e., reduction of plant biomass) but even
84 indirectly changing the soil's physicochemical properties and micrometeorological conditions
85 [42].

86 Currently, the temperature dependency of SR and SOC decomposition is a major interest
87 regarding global climate change and the role of terrestrial ecosystems in regulating Earth's
88 climate [43,44]. Therefore, there is a need to better understand the interactions between
89 temperature and soil CO₂ efflux. The general goal of this study is to disentangle the possible
90 multi-effects on SR of soil properties, temperature, SOM, and vegetation structure (tree height in
91 particular) along a plant biome-elevation gradient. In particular, the existing differences in
92 vegetation structure allowed us to investigate the extent to which these biological variables and
93 the induced variation in microclimatology can alter the relation between elevation and SR.

94 Specifically, i), we tested the hypothesis that SR and SOM accumulation change linearly with
95 elevation. We also hypothesized that the Q₁₀ value increases linearly with elevation as well.
96 Furthermore, ii) we analyzed which are the main factors affecting SR other than temperature. To
97 better isolate the effect of temperature on SR, the study was conducted along an
98 altitudinal/temperature gradient in Italian Alps, in conditions where confounding factors like
99 slope, aspect, and soil parent material are minimized. The differences in vegetation structure
100 allowed us to investigate to which extent these biological variables and the induced variation in
101 microclimatology, can alter the relation between elevation and SR.

102 **Material and Methods**

103 **Study areas**

104 Five experimental sites were established between the top of the Rittner Horn mount and the city
105 of Bolzano, Italy, on the southern side of the Alps (Fig 1a). The overall elevation gradient
106 between the highest and the lowest site is 1700 m and the elevation separation between each site
107 is approximately 420 ± 60 m. All sites are characterized by a soil evolved upon a glacial till laid
108 on a porphyric bedrock and an SSE slope orientation. Annual precipitation ranges between 800
109 and 1000 mm.

110

111

112 **Fig 1. (a) Map showing the research site locations selected for this study (b) Scheme of the**
113 **elevation and vegetation gradient present along the studied Alpine slope.**

114 Site A was established in shrubland vegetation of Dwarfing Mountain pine (*Pinus mugo* Turra)
115 near the summit of the Rittner Horn/Corno del Renon mount (see the scheme in Fig 1b). Site B
116 was established in a Norway spruce stand (*Picea abies* (L.) Karst.) at the long-term Fluxnet
117 research station of Renon- Mittelgrünwald/Selva Verde ([https:// doi.org/10.18140/flx/1440173](https://doi.org/10.18140/flx/1440173));
118 The site is characterized by an unvenaged distribution of tree diameters, approaching the
119 structure of old-growth forest stands (45,46]. Site C was located near the location of Riggermoos
120 (Oberbozen/Sopra Bolzano), in a low-density Scots pine (*Pinus sylvestris* L.) stand. Site D was
121 established in a mixed stand of Sessile oak (*Quercus petrea* (Matt.) Liebl.) and Chestnut
122 (*Castanea sativa* L.) and the presence of Scots pine near the village of Signat/Signato. Site E
123 was located in a stand dominated by Downy oak (*Quercus pubescens* Willd.) and Flowering ash
124 (*Fraxinus ornus* L.) on the hill slope just close to the city of Bolzano (Sankt Magdalena/Santa
125 Maddalena). All sites except site A are managed as high forest mainly for wood harvesting. Site
126 A is managed as natural vegetation with occasional harvesting only at forest margins to avoid
127 expanding the pines in the adjacent pasture areas. Tree age was assessed in 2018 by tree ring
128 count: it was found that site B had the oldest trees, slightly above 200 years, while other stands
129 were in the range of 50-100 years. Tree height was assessed in 2020 with the TruePulse sensor
130 (TruPulse 360 B laser range-finder, Laser Tech, Colorado, USA). Details on tree heights and the
131 main characteristics of the research sites are reported in Table 1.

132 **Table 1. General characterization of the study sites.**

Characteristics	Site A	Site B	Site C	Site D	Site E
Elevation (m a.s.l)	2101	1731	1354	865	404
Mean annual Temperature	4	4	12	11	14

(°C)					
Land use	Shrubland	Forest	Forest	Forest	Forest
Mean dominant tree height (m)	1.5	29	18	15	5
Dominant species in the overstory	- Dwarfing Mountain pines (<i>Pinus mugo</i>)	- Norway spruce (<i>Picea abies</i>) - Swiss stone pine (<i>Pinus cembra</i>) - Larch (<i>Larix decidua</i>)	- Scots pine (<i>Pinus sylvestris</i>)	- Sessile oak (<i>Quercus petraea</i>) - Scots Pine (<i>Pinus sylvestris</i>) - Chestnut (<i>Castanea sativa</i>)	- Downy oak (<i>Quercus pubescens</i>) - Flowering ash (<i>Fraxinus ornus</i>)
Main species in the understory	- Intervening grasses (<i>Festuca halleri</i>)	- Rusty leaved alprose (<i>Rhododendron ferrugineum</i>)	- Heather (<i>Erica carnea</i>)	Understory almost absent	- Smoke-bush (<i>Cotinus coggyria</i>) - Succulent plants (<i>Opuntia humifusa</i>)

133

134 **Soil respiration measurements**

135 To quantify SR, ten iron collars (10 cm height, 20 cm diameter) were inserted in the soil, three
136 weeks before the first measurements at each site. Measurements were performed with an opaque

137 survey chamber (Li-8100-104, LI-COR Biosciences, Nebraska, USA) connected to an LI-8100
138 analyzer (LI-COR Biosciences, Nebraska, USA). On each collar, the measurement period was
139 set to 120 s the first 20 s of the measurement were considered dead-band, so the flux
140 computation was limited to 80 s. See Montagnani et al. [8] for further details about the
141 measurement settings. Starting on July 21, 2017, SR measurements were performed periodically,
142 about once per month, until July 20, 2018, for a total of 17 measurement days. The first 4
143 measurement series were performed every three weeks at all the sites. During the winter period,
144 SR measurements were performed only in the locations at a lower altitude because of snow in the
145 high-elevation locations. The measurement calendar for the different sites is provided in S1.
146 During measurements, the air temperature was measured inside the survey chamber (at 0.1 m
147 above ground, RHT Plus, Skye Instruments, UK). A soil temperature profile was installed at
148 control site B according to ICOS protocol [47]. Specifically, we used the -5 cm soil T data
149 provided by a CS605 probe, Campbell Scientific, USA. We recorded soil temperature
150 continuously at 30 min intervals for the whole experimental period (July 2017 - July 2018). In
151 addition, during the period May-July 2018, we placed at all the sites iButton sensors (Maxim
152 integrated, USA) at 5 cm below the soil surface.

153 **Soil sampling and analysis**

154 At the end of the last measurement session (July 2018), leaf litter present in each collar was
155 sampled. The soil in each collar was sampled using a 4.8 split-corer (Eijkelkamp, NL), until 20
156 cm depth. In the laboratory, soil samples were weighed and sieved at 2 mm mesh size to separate
157 roots, stones, and coarse organic matter fragments. Collected leaf litter and fine roots (< 2 mm
158 diameter) were weighted after oven-drying at 105 ± 5 °C. Soil bulk density was determined by
159 dividing the weight of sieved soil by the core volume. Soil pH was measured using a pH-meter
160 (CRISON pH-Meter Basic 20+Electrod: Hach 50 10T CRISON, Barcelona, Spain) in water.
161 Root, litter, and soil samples were analyzed for organic C and N content using a FlashEA™ 1112
162 Elemental Analyzer (Thermo Fisher Scientific, Waltham, MA, USA).

163 **Data elaboration and statistical analysis**

164 The mean amount (\pm SD) of accumulated C and N stock in the soil, root, and litter were
165 computed for each site. Soil and C and N stocks were obtained as follows [48]:

166
$$\text{Soil stock (kg dm}^{-3}\text{)} = C/100 \times BD_{\text{soil}} \text{ (kg m}^{-3}\text{)} \times 0.2 \text{ (m)} \quad \text{Eq.1}$$

167 Where C is the mean soil organic C or total N content, BD_{soil} is the soil bulk density (kg dm⁻³)
168 and 0.2 m is the sampling depth.

169 Root C and N stocks were determined with the same computational approach, using root density
170 (kg dm⁻³) in place of soil BD and root C and N content in place of soil C and N content. Litter C
171 and N amounts were obtained by multiplying the litter mass by C or N content and dividing by
172 the collar area.

173 Soil respiration data collected from each measurement point (collar) were related to chamber air
174 temperature using a logistic model [26]:

175
$$SR = \frac{a}{(1 + b \cdot \exp(-k \cdot T_a))} \quad \text{Eq. 2}$$

176 Where SR is soil respiration, a is the maximum value of SR, b determines the elongation of the
177 SR curve along the x-axis, k is the logistic growth rate or steepness of the SR curve along the x-
178 axis, T_a is air temperature. Furthermore, SR data were also fitted with a Q10 model [49,50]:

179
$$SR = SR_{\text{ref}} \cdot Q_{10}^{\left(\frac{(T_a - T_{\text{ref}})}{10}\right)} \quad \text{Eq.3}$$

180 Where SR is the soil respiration, SR_{ref} is the fitted SR at the reference temperature of 10°C (T_{ref}),
181 Q10 is the temperature sensitivity of SR, defined as the factor by which soil respiration increases
182 with a 10°C temperature increase, and T_a is chamber air temperature.

183 Models were fitted to SR data using the nls package in R software. Model fitness was evaluated
184 based on Akaike's Information Criterion (AIC), R-squared (R^2), Mean Absolute Error (MAE),
185 and Root Mean Squared Error (RMSE). The Q10 model was used to obtain the SR_{ref} and the Q10
186 value for every collar. Linear regression was used to compare the air temperature measured
187 continuously in the reference plot (site B) and air temperature inside the chamber during SR
188 measurements for each collar in each site. The obtained linear regression models were then used
189 to predict chamber air temperature for the whole experimental period, for each collar, with a 30
190 min time resolution. Therefore, the predicted chamber air temperature was used to predict SR

191 values simultaneously for the whole experimental period, based on the logistic models relating
192 SR with chamber temperature. For some collars, it was not possible to obtain a good fitness of
193 the SR data using the logistic model; for these collars, the prediction soil respiration data from
194 temperature was performed using the Q10 model developed for the same collar. Finally, the total
195 cumulative SR for the whole experimental period was determined for each collar at each site.

196 Soil respiration response to biological variables (soil C, root C, litter C, root dry weight, soil N,
197 root N, litter N, litter dry weight) was examined using Spearman's Correlation Test and linear
198 mixed-effects models (LMMs) fitted by restricted maximum likelihood (REML). Before
199 applying LMMs, to avoid statistical errors, Variance Inflation Factor (VIF) was determined for
200 biological variables, and variables with high VIF values were excluded from the model
201 assessment. LMMs were built using the lme4 R package [50,51,52]. The models consisted of
202 both fixed and random effects: biological variables were considered as fixed effects, and
203 sampling plots (collars) nested in each site were used in the random-effects formula. R^2 was used
204 to summarize model goodness-of-fit together with AIC [53,54]. Since computed R^2 by LMMs
205 are a pseudo- R^2 and technically incorrect, the r2glmm R package was used to computing R^2
206 [54]. To exclude the confounding effect of temperature from LMMs and correlations tests,
207 environmental variables were related to SR_{ref} instead of SR [20,26,55]. Furthermore, to assess
208 GPP and SR's correlation, tree height was used as a covariate in LMMs and Spearman test.
209 Statistical comparisons of average soil C and N, root C and N, litter C and N, soil bulk density,
210 soil pH, and soil respiration in the different sites were performed by the Kruskal-Wallis test
211 (Dunn test, $p < 0.05$) for the non-normally distributed data, and a one-way ANOVA for the
212 normally distributed data (Tukey test, $p < 0.05$). The normality of the data and homogeneity of
213 variance was checked by the Shapiro–Wilk test and Levene's test, respectively [56,57]. To check
214 linearity changes of SR, Q10, SOM with elevation, linear and nonlinear polynomial regressions
215 were applied between elevation and environmental variables (soil C and N, root C and N, litter C
216 and N, soil bulk density, soil pH). The linearity changes of these variables with elevation were
217 detected based on the lowest AIC and the highest R^2 . The association of Q10, soil C and soil N
218 with environmental variables were determined using Spearman's Correlation Test. All statistical
219 analyses were performed using R version 3.6.0 ([59], www.r-project.org).

220

221 **Results**

222 **Environmental factors variability along the altitudinal gradient**

223 A significant difference in soil C stock was found only between site E (3891 ± 2756 g C m⁻²), at
224 the lowest altitude, where the C stock was smaller in comparison to sites A, B, and C (Fig 2a).
225 No significant differences were found for soil N stock in the different sites (Fig 2e). Root
226 biomass and root C and N stocks in site A were significantly higher than other sites (Fig 2b, d, f)
227 and litter mass in site B was significantly higher than site E (Fig 2h). However, the accumulated
228 C and N in the litter were not significantly different along the altitudinal gradient (Fig 2c, g).
229 Significant differences were found between pH values in the different sites: the lowest value of
230 soil pH was measured in site B (3.8 ± 0.1) and the highest value in site E (5.9 ± 0.2 , Fig 2i). The
231 highest bulk density value was found in site D (1.01 ± 0.27 g cm⁻³, Fig 2i) and the lowest was
232 found in site B (0.26 ± 0.16 g cm⁻³; Fig 2j).

233

234

235 **Fig 2. Stocks of (a), soil C (b,) root C (c), litter C (d), root dry weight (e,) soil N (f), root N**
236 **(g), litter N (h), litter dry weight (i), soil pH, and soil bulk density (j), estimated in the**
237 **different sites (A-E). Different lowercase letters indicate significant differences between**
238 **sites according to the Kruskal-Wallis or ANOVA tests. Vertical bars represent the**
239 **standard deviation of the mean for each site.**

240 Based on the AIC and R², the linear relationship with elevation appeared in model selection only
241 for soil bulk density i.e., soil bulk density resulted to be linearly related to elevation (Table 2).
242 On the contrary, soil C, soil N, fine root mass, and root C, root N, pH and litter mass data were
243 fitted better with nonlinear relations with elevation (Table 2; more detail about equations can be
244 found in Table S1; supplementary material). Furthermore, a significant negative correlation was
245 found between soil C and soil N with soil pH, mean dominant tree height, and bulk density
246 (Table 3).

247

248 **Table 2. linear and polynomial regressions between the different parameters tested and**
 249 **elevation. Asterisks indicate significance levels: * - $p \leq 0.05$, ** - $p \leq 0.01$, and *** - $p \leq$**
 250 **0.001, n.s. – nonsignificant. BD – soil bulk density; Q10 – temperature sensitivity of soil**
 251 **respiration; SR- cumulated soil respiration; SR_{ref} – respiration at the 10°C reference**
 252 **temperature; lm – linear regression model; Poly-lm – polynomial regression model. The**
 253 **model selection was based on the lowest AIC and the highest R² (in bold).**

Parameters	Elevation					
	Significance		Multiple R ²		AIC	
	lm	Poly-lm	lm	Poly-lm	lm	Poly-lm
Soil C (g C m ⁻²)	***	***	0.28	0.40	764	758
Soil N (g N m ⁻²)	*	*	0.15	0.20	510	509
SR (kg C m ⁻² yr ⁻¹)	***	***	0.33	0.36	34	34
Q10 (kg C m ⁻² yr ⁻¹)	***	**	0.28	0.41	77	67
SR _{ref} (kg C m ⁻² yr ⁻¹)	n.s.	n.s.	<0.01	0.08	139	139
Fine root mass (g m ⁻²)	*	**	0.10	0.24	717	712
Root C (g C m ⁻²)	*	***	0.39	0.80	199	186
Root N (g N m ⁻²)	n.s.	***	0.28	0.80	102	88
Litter mass (g m ⁻²)	n.s.	*	0.07	0.12	774	772
Litter C (g C m ⁻²)	n.s.	n.s.	< 0.01	0.04	222	223
Litter N (g N m ⁻²)	n.s.	n.s.	< 0.01	< 0.01	112	114
pH	**	***	0.63	0.88	22	8
BD (kg dm ⁻³)	***	***	0.32	0.29	9	11

268 **Table 3. Spearman rank coefficients for the correlations between different variables (RDW**
 269 **– root dry weight, LDW – litter dry weight, BD – soil bulk density, Q10 – temperature**
 270 **sensitivity of soil respiration). Asterisks indicate significance levels: * - $p \leq 0.05$, ** - $p \leq$**
 271 **0.01, and *** - $p \leq 0.001$; n.s. – nonsignificant.**

Variable	Soil C	Soil N	RD W	Root C	Root N	LD W	Litter C	Litter N	pH	BD	Tree height
Soil C	1.00 -	0.94 ***	0.14 n.s.	- 0.11 n.s.	- 0.07 n.s.	0.02 n.s.	-0.17 n.s.	- 0.09 n.s.	- 0.62 *	- 0.52 *	0.33 *
Soil N	0.94 ***	1.00 -	0.11 n.s.	0.36 n.s.	0.32 n.s.	0.01 n.s.	-0.36 n.s.	- 0.23 n.s.	- 0.54 *	- 0.39 *	0.21 n.s.
Q10	0.15 n.s.	0.13 n.s.	0.06 n.s.	0.37 n.s.	0.46 n.s.	- 0.08 n.s.	0.01 n.s.	- 0.44 n.s.	- 0.29 n.s.	- 0.23 n.s.	-0.29 *

272

273 Soil respiration

274 Both logistic and Q10 models confirmed that soil respiration rates increased with temperature in
 275 all sites (Fig 3), and the seasonal pattern of SR was similar to that of air chamber temperature
 276 (S1 Fig).

277

278

279

280 **Fig 3. Rates of soil respiration against chamber air temperature in the different sites along**
 281 **the elevation gradient (A-E). The regression lines in the plots were built using the mean**
 282 **values of model parameters (R_{ref} and Q10 value for the Q10 model and a, b, and k value for**
 283 **the logistic model) obtained for different replicate collars of each site (n = 10).**

284 A strong linear relationship was found between observed and predicted SR ($R^2 = 0.73$; S2 Fig;
 285 supplementary material). Temperature explained between 55 % and 76% of the variance in soil
 286 respiration at the experimental sites (Table 4). The Q10 and SR_{ref} values obtained for the
 287 different sites ranged between 1.75 and 2.96, and between 2.17 and 4.49, respectively (Table 4).

288 The Q10 value recorded in site A (highest elevation) was significantly different from the others
 289 (Table 4). A significant linear relationship was identified between Q10 and elevation (Table 2).
 290 However, the trend of Q10 against temperature was better described by a nonlinear relation
 291 (Table 2). Furthermore, a significant negative correlation was found between Q10 and mean
 292 dominant tree height (Table 3). No significant relationship between SR_{ref} and altitude was found
 293 (Table 2). However, significant differences were found between experimental sites, as the
 294 highest SR_{ref} value was recorded in site B and the lowest values in site A, C, and E (Table 4).

295 **Table 4. Mean values of Q10 (temperature sensitivity) and SR_{ref} (soil respiration at the**
 296 **temperature of 10°C) for each site; and the mean value of MAE (Mean Absolute Error),**
 297 **Root Mean Squared Error (RMSE), R^2 (R-square), and AIC (Akaike information**
 298 **criterion) for each model (logistic and Q10). Different letters indicate significant differences**
 299 **between sites. Values are expressed as mean \pm SD.**

	A	B	C	D	E
Q10	2.96 \pm 0.72 ^b	1.83 \pm 0.25 ^a	1.90 \pm 0.24 ^a	1.75 \pm 0.15 ^a	1.75 \pm 0.32 ^a
SR_{ref}	2.17 \pm 0.60 ^a	4.49 \pm 0.71 ^c	2.24 \pm 0.58 ^a	3.17 \pm 1.03 ^b	2.98 \pm 0.41 ^{ab}
AIC logistic model	32.95 \pm 10.45	34.25 \pm 6.45	34.19 \pm 11.65	48.00 \pm 14.55	49.76 \pm 6.70
AIC Q10 model	30.42 \pm 13.69	34.07 \pm 7.31	35.39 \pm 11.53	48.44 \pm 14.13	49.11 \pm 6.60
R^2 logistic model	0.76 \pm 0.21	0.75 \pm 0.20	0.75 \pm 0.16	0.67 \pm 0.11	0.58 \pm 0.10
R^2 Q10 model	0.75 \pm .23	0.71 \pm 0.23	0.68 \pm 0.21	0.61 \pm 0.11	0.55 \pm 0.11
MAE logistic model	1.06 \pm 0.65	1.06 \pm 0.45	0.68 \pm 0.32	1.26 \pm 0.62	1.29 \pm 0.25
MAE Q10 model	1.07 \pm 0.68	1.14 \pm 0.52	0.79 \pm 0.36	1.46 \pm 0.76	1.39 \pm 0.26
RMSE logistic model	1.36 \pm 0.94	1.27 \pm 0.50	0.86 \pm 0.44	1.70 \pm 0.89	1.71 \pm 0.36
RMSE Q10 model	1.38 \pm 1.0	1.36 \pm 0.55	0.99 \pm 0.49	1.87 \pm 1.02	1.77 \pm 0.38

300

301 The cumulative SR in site A was significantly lower than in the other sites (Fig 4). The results of
302 the statistical analysis also confirmed a nonlinear relationship between cumulative SR and
303 elevation (Table 2).

304

305

306 **Fig 4. Total cumulative soil respiration (kg C m⁻² yr⁻¹) calculated for the different sites (A-**
307 **E). Values are indicated on the bars. Error bars indicate standard deviation. Different**
308 **letters on the bars indicate significant differences between sites according to the ANOVA**
309 **test.**

310 Soil C, mean dominant tree height, and litter dry weight resulted in the best variables to explain
311 SR (SR_{ref}; at 10 °C) in LMMs (VIF<10; Table 5). According to the model, about 0.22 of SR was
312 explained by tree height (R² = 0.22, Table 5). Meanwhile, a positive association between SR and
313 mean dominant tree height and a negative association between SR and root C and N were found
314 by Spearman's Correlation Test (Fig 5).

315

316 **Table 5. Results of linear mixed-effects models testing biological variables impact on the**
317 **SR_{ref}; at 10 °C. VIF – Variance Inflation Factor. Parameters in bold show significant**
318 **correlations**

Model variables	Value	VIF	p-value	R ²
Intercept	1.61		0.003	0.34
Soil C	< - 0.01	1.20	0.92	< 0.01
Tree height	0.06	1.28	0.002	0.22
Litter dry weight	< 0.01	1.07	0.14	0.06

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324 **Fig 5. Relations of reference soil respiration at 10°C (SR_{ref}) and different site properties.**

325 **Discussion**

326 **Organic C and N content along the altitudinal gradient**

327 Overall, our data confirms an increase of the soil organic C stock in soil with increasing
328 elevation [7,24, 25,27,59,60,61,62]. The low temperature can limit the decomposition of organic
329 matter at high altitudes, as the temperature is the main driver for the loss of the soil organic C.
330 For this reason, altitude could induce a significant increase in SOM [23,59,62,63,63]. However,
331 SOM increment was not linear along the elevation gradient and therefore, our first hypothesis
332 was not confirmed. The Nonlinear relationship of SOM with elevation and the high value of soil
333 C in site C (with a mean temperature of 12 °C) suggests that other factors other than temperature
334 have influenced SOM accumulation. Different microclimatic or micromorphological conditions
335 caused by differences in slope and aspect can influence C storage in soils [33,35,65]. However,
336 in the present study, all the sites are characterized by similar slopes and by the same south or
337 south-east facing; therefore, we tend to exclude an influence of these factors on soil C
338 accumulation in the examined sites. According to recent studies, SOM is not consistently related
339 to variation in climatic conditions along elevation gradients; it is also strongly affected by
340 productivity or by vegetation type/composition [30,33,66,67]. Our data confirms a significant
341 positive correlation between mean dominant tree height and soil C (Table 3). Therefore, the
342 higher amount of soil C found in the present study at intermediate altitude could be explained by
343 higher site productivity in sites B and C in particular, which is also suggested by the mean
344 dominant tree height.

345 Soil pH and bulk density are considered two of the main variables influencing other soil
346 properties, soil microbial activity and soil respiration [68,69]. Generally, at high elevation, the
347 higher precipitation and lower evapotranspiration rate decrease soil pH by increasing the
348 leaching of basic cations [65,70,71,72,73]. This is confirmed by the strong relationship between

349 elevation and soil pH found in the present study (Table 2, Fig 2). In addition, soil bulk density
350 was significantly diminished by increasing elevation (Fig 2; Table 2). One of the main factors
351 affecting soil bulk density is SOM content [74]. Therefore, the lowest values of soil bulk density
352 at high elevation could be explained by the high amount of soil C, as confirmed by the negative
353 association found between soil C and soil bulk density (Table 3), previously reported in other
354 studies [7, 61,62,75].

355 **Factors affecting soil respiration**

356 The total SR observed in the sites is within the range reported for similar forests [26,60]. The
357 decrease in SR along the elevation gradient observed in the present study could be explained by
358 the reduction of temperature along elevation. In fact, temperature resulted in the main controlling
359 factor on SR, explaining most of the variability of SR. This result is in agreement with other
360 studies performed along altitudinal gradients, reporting that temperature can explain between
361 55% and 76% of the SR variability [6, 9, 14,27,63, 76]. On the other hand, the annual cumulative
362 SR in site B was 2 times larger than in site A, which has the same mean annual temperature. This
363 finding, together with nonlinear SR concentrations with elevation/temperature, suggests that
364 other environmental factors can have a role in regulating SR [34,60]. For instance, Grand et al.
365 [36] reported that soil and vegetation heterogeneity strongly affect soil carbon efflux in complex
366 geomorphic terrain. In the present study, all five sites were established on relative homogeneity
367 of soil substratum; therefore a high SR rate in site B could not be resulted by the confounding
368 role of the soil parent material. Site B is an uneven-aged dense forest stand, and the mean
369 dominant tree height is approximately 29 m (Table 1). Since tree height can be used as a proxy
370 of gross primary production (GPP), the high SR rate in site B could be attributed to high GPP
371 [9,29,66,77,78,79], which can provide substrates for root and microbial respiration through
372 photosynthesis [66,80]. This finding is confirmed by LMMs and correlation test evidencing a
373 significant positive relation between SR_{ref} and mean dominated tree height, therefore indicating
374 that, after removing the effect of temperature, productivity results in one of the main factors
375 affecting SR.

376 At a global scale, SR has been related to soil C, litter production and pH, and negatively
377 correlated with soil bulk density; therefore, a high value of soil C and litter accumulation could
378 lead to an increase in soil respiration [20,66,81,82,83]. In the present study, the highest amount

379 of soil C and dry litter weight were also observed in site B. However, we could not find a
380 significant correlation between SR and soil C and litter dry weight (Fig 5; Table 5).

381 An increase in SR has also been observed as a consequence of increasing soil pH between 4 and
382 7, because of the positive effect of pH on soil microbial activity within this range
383 [1,68,84,85,86]. In contrast, SR and bulk density are generally negatively correlated, as a low SR
384 indicates increasing rates of SOM accumulation and therefore a decrease in bulk density [82].
385 Furthermore, SR declines with increasing bulk density due to the lower soil porosity and oxygen
386 availability for microbial activity in compacted soils [18,59,87]. However, our analysis did not
387 confirm a significant correlation of SR with pH and bulk density (Table 5; Fig 5). Prediction of
388 SR is difficult because of a range of factors such as aspect, slope, and soil types [35,36,60,65]. In
389 the present study, by minimizing the confounding role of these parameters, we conclude that the
390 most important controlling factors on SR along an Alpine elevation gradient were temperature
391 and vegetation type/composition or GPP.

392 **Temperature sensitivity of soil respiration (Q10)**

393 The temperature sensitivity of SR is an important ecological model parameter, and according to
394 previous studies, its value is mainly controlled by temperature [14,17,88,89]. The Q10 and SRref
395 values found at site B substantially confirm the values found by Acosta et al. [90] at the same
396 site (2.0 and 4.09, respectively). Although at a smaller spatial scale, Acosta et al. [90] also found
397 an increasing SRref as a function of stand age (and consequently height). The significant trend of
398 Q10 with elevation in this research confirms the results of previous studies and the higher
399 sensitivity of high elevation ecosystems to global warming [14,91,92,93,94]. However, the only
400 significant difference was found between the Q10 value at site A (higher elevation) and the other
401 sites (Table 4). The Q10 value in site A was also significantly higher than site B, characterized
402 by a similar mean temperature. According to different studies, Q10 is negatively related to pH
403 and positively dependent on soil C [55,95]. However, the amount of soil C and pH could not be
404 the reasons for the lower value of Q10 in site B, which is characterized by a lower pH value and
405 by a similar amount of soil C. Temperature sensitivity of SR can also be affected by forest
406 structure [96]. Dense forest stands with a closed canopy can create a specific understory
407 microclimate by providing a cool shelter during heat waves, which can decrease daily maximum
408 air temperature by up to 5.1 °C [97,98]. Therefore, we can hypothesize that the dense forest stand
409 site B, with the highest mean dominant height, is less sensitive to global warming. This feature
410 was also described by Niu et al. [99] for the same site and confirmed by a significant negative
411 correlation between Q10 and mean dominating tree height (Table 3). Whether a silviculture that
412 maintains high and old forests with a complex structure also achieves a lower sensitivity to
413 climate change by reducing the depletion of C stored in the soil, is a novel research question
414 emerging from this research. If the findings obtained here will be confirmed, it would imply that
415 more conservative forest management can not only maintain current C stocks in the biomass but
416 also leads to a reduced sensitivity to the temperature of the C stored in the soil.

417 **Conclusions**

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420 In this study, a significant nonlinear relationship between SR, SOM, Q10, and elevation was
421 detected along the examined Alpine altitudinal gradient, rejecting our initial linearity hypothesis.
422 Our data confirmed a negative trend between SR and elevation. On the contrary, SOM and Q10
423 showed a positive trend with elevation. These results lead us to conclude that temperature is the
424 major controlling factor on the annual soil respiration, Q10, and SOM, but its regulating role
425 may be strongly affected by site biological characteristics, particularly by GPP or vegetation
426 type/composition. The high value of Q10 detected at high elevation confirmed a higher potential
427 vulnerability of high mountain ecosystems to climate change, where small temperature changes
428 can induce stronger increase CO₂ emissions. However, the site with the highest tree age and
429 height and more complex structure showed high SR_{ref} and moderate Q10, indicating that the
430 length in the life cycle and related changes in forest structure can dampen, to some extent, the
431 effects of climate change on ecosystems and decrease the positive feedback due to soil CO₂
432 emissions to the atmosphere.

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434 **References**

- 435 1. Luo Y, Zhou X. Soil respiration and the environment. Sandiego, CA: Academic Press;
436 2006.
- 437 2. Valentini R, Matteucci G, Dolman AJ, Schulze ED, Rebmann C, Moors EJ, et al.
438 Respiration as the main determinant of carbon balance in European forests. *Nature*. 2000; 404:
439 861-865. DOI: 10.1038/3500908.
- 440 3. Scharlemann JP, Tanner EV, Hiederer R, Kapos V. Global soil carbon: understanding
441 and managing the largest terrestrial carbon pool. *Carbon Manag*. 2014; 5: 81–91.
- 442 4. Makita N, Kosugi Y, Sakabe A, Kanazawa A, Ohkubo S, Tani M. Seasonal and diurnal
443 patterns of soil respiration in an evergreen coniferous forest: Evidence from six years of
444 observation with automatic chambers. *PLoS ONE*, 2018; 13(2): e0192622.
445 <https://doi.org/10.1371/journal.pone.0192622>

- 446 5. Cong WF, Van Ruijven J, Mommer L, De Deyn GB, Berendse F, Hoffland E. Plant
447 species richness promotes soil carbon and nitrogen stocks in grasslands without legumes. *Journal*
448 *of Ecology*. 2014; 102(5): 1163–1170. [DOI 10.1111/1365-2745.12280](https://doi.org/10.1111/1365-2745.12280).
- 449 6. Luo W, Li MH, Sardans J, Lü XT, Wang C, Peñuelas J, Wang Z, Han XG, Jiang Y.
450 Carbon and nitrogen allocation shifts in plants and soils along aridity and fertility gradients in
451 grasslands of China. *Ecol Evol*. 2017; 7(17): 6927–6934, [DOI 10.1002/ece3.3245](https://doi.org/10.1002/ece3.3245).
- 452 7. Devi SB, Sherpa SSSS. Soil carbon and nitrogen stocks along the altitudinal gradient of
453 the Darjeeling Himalayas, India. *Environ Monit Assess*. 2019; 191 (361):
454 <https://doi.org/10.1007/s10661-019-7470-8>
- 455 8. Montagnani L, Badraghi A, Speak AF, Wellstein C, Borruso L, Zerbe S, Zanutelli D.
456 Evidence for a non-linear carbon accumulation pattern along an Alpine glacier retreat
457 chronosequence in Northern Italy. *PeerJ*. 2019; 7:e7703, [DOI 10.7717/peerj.7703](https://doi.org/10.7717/peerj.7703).
- 458 9. Janssens I.A, Lankreijer H, Matteucci G, Kowalski AS, Buchmann N, Epron D.
459 Productivity overshadows temperature in determining soil and ecosystem respiration across
460 European forests. *Glob Chang Biol*. 2001; 7: 269–278.
- 461 10. Hopkins F, Gonzalez-Meler MA, Flower CE, Lynch DJ, Czimczik C, Tang J, Subke JA.
462 Ecosystem-level controls on root-rhizosphere respiration, *New Phytol*. 2013; 199: 339e351,
463 <http://dx.doi.org/10.1111/nph.12271>.
- 464 11. Scandellari F, Zanutelli D, Ceccon C, Bolognesi M, Montagnani L, Cassol P, Melo GW,
465 Tagliavini M. Enhancing prediction accuracy of soil respiration in an apple orchard by
466 integrating photosynthetic activity into a temperature-related model, *Eur J Soil Biol*. 2015; 70:
467 77-87. [Doi: 10.1016/j.ejsobi.2015.07.006](https://doi.org/10.1016/j.ejsobi.2015.07.006).
- 468 12. Zhang ZS, Dong XJ, Xu BX, Chen YL, Zhao Y, Gao YH, Hu YG, Huang L. Soil
469 respiration sensitivities to water and temperature in a revegetated desert. *J. Geophys. Res.*
470 *Biogeosci*. 2015; 120: 773–787. [doi:10.1002/2014JG002805](https://doi.org/10.1002/2014JG002805)
- 471 13. Chen D, Yu M, González G, Zou X, Gao Q. Climate Impacts on Soil Carbon Processes
472 along an Elevation Gradient in the Tropical Luquillo Experimental Forest. *Forests*. 2017. 8; 90:
473 [doi:10.3390/f8030090](https://doi.org/10.3390/f8030090)

- 474 14. Ma M, Zang Z, Xie Z, Chen Q, Xu W, Zhao C, Shen G. Soil respiration of four forests
475 along elevation gradient in northern subtropical China. *Ecol Evol.* 2019; 9: 12846–12857.
- 476 15. Reichstein M, Beer C. Soil respiration across scales: the importance of a model-data
477 integration framework for data interpretation. *J Plant Nutr Soil Sci.* 2008; 171: 344e354.
- 478 16. Subke JA, Bahn M. On the ‘temperature sensitivity’ of soil respiration: Can we use the
479 immeasurable to predict the unknown? *Soil Biol Biochem.* 2008; 42 (9): 1653-1656.
- 480 17. Lloyd J, Taylor JA. On the temperature dependence of soil respiration, *Funct Ecol.* 1994;
481 8(3): 315–323. doi:10.2307/2389824.
- 482 18. Xu M, Qi Y. Soil surface CO₂ efflux and its spatial and temporal variation in a young
483 ponderosa pine plantation in California. *Global Change Biol.* 2001; 7: 667 – 677.
484 <https://doi.org/10.1046/j.1354-1013.2001.00435.x>
- 485 19. Janssens IA, Dore S, Epron D, Lankreijer H, Buchmann N, Longdoz B, Brossaud J,
486 Montagnani L. Climatic influences on seasonal and spatial differences in soil CO₂ efflux. In:
487 Valentini R (ed) *Fluxes of carbon, water and energy of European forests.* Berlin: Springer; 2003.
- 488 20. Reichstein M, Rey A, Freibauer A, Tenhunen J, Valentini R, Banza R. Modeling
489 temporal and large-scale spatial variability of soil respiration from soil water availability,
490 temperature and vegetation productivity indices. *Global Biogeochem Cycles.* 2003; 17: [doi:](https://doi.org/10.1029/2003GB002035)
491 [10.1029/2003GB002035](https://doi.org/10.1029/2003GB002035).
- 492 21. Van’t Hoff JH. Lectures on theoretical and physical chemistry. In *Chemical Dynamics*
493 Part I (pp. 224–229). London: Edward Arnold. Vereecken, H., Pachepsky, Y., Simmer, C.,
494 Rihani, J., Kunoth, A., Korres, W., et al., 2016. On the role of patterns in understanding the
495 functioning of soil-vegetation atmosphere systems. *J Hydrol.* 1898; 542: 63–86.
496 <https://doi.org/10.1016/j.jhydrol.2016.08.053>
- 497 22. Lomolino MV. Elevation gradients of species-density: historical and prospective views.
498 *Glob Ecol Biogeogr.* 2001; 10: 3–13.
- 499 23. Prietzel J, Zimmermann L, Schubert A, Christophel D. Organic matter losses in German
500 Alps forest soils since the 1970s most likely caused by warming. *Nat Geosci.* 2016; 1-8, [DOI:](https://doi.org/10.1038/NGEO2732)
501 [10.1038/NGEO2732](https://doi.org/10.1038/NGEO2732)

- 502 24. Shedayi AA, Xu M, Naseer L, Khan B. Altitudinal gradients of soil and vegetation
503 carbon and nitrogen in a high altitude nature reserve of Karakoram ranges. SpringerPlus. 2016;
504 5: 320. DOI 10.1186/s40064-016-1935-9
- 505 25. Jiang L, He Z, Liu J, Xing C, Gu X, Wei C, Zhu J, Wang X. Elevation Gradient Altered
506 Soil C, N, and P Stoichiometry of *Pinus taiwanensis* Forest on Daiyun Mountain. Forests. 2019;
507 10: 1089. doi:10.3390/f10121089
- 508 26. Rodeghiero M, Cescatti A. Main determinants of forest soil respiration along an
509 elevation/temperature gradient in the Italian Alps. Glob Chang Biol. 2005; 11: 1024–1041. doi:
510 [10.1111/j.1365-2486.2005.00963.x](https://doi.org/10.1111/j.1365-2486.2005.00963.x)
- 511 27. Shi Z, Wang JS, He R, Fang YH, Xu ZK, Quan W, Zhang ZX, Ruan HH. Soil
512 respiration and its regulating factor along an elevation gradient in Wuyi Mountain of Southeast
513 China. Chinese J Ecol. 2008; 27 (4): 563-568.
- 514 28. Luo S, Liu G, Li Z, Hu C, Gong L, Wang M, Hu H. Soil respiration along an altitudinal
515 gradient in a subalpine secondary forest in China. iForest. 2014; 8: 526-532.
- 516 29. Kane ES, Valentine DW, Schuur EAG, Dutta K. Soil carbon stabilization along climate
517 and stand productivity gradients in black spruce forests of interior Alaska. Can. J. For. Res.
518 2005; 35: 2118–2129.
- 519 30. Djukic L, Zehetner F, Tatzber M, Gerzabek MH. Soil organic-matter stocks and
520 characteristics along an Alpine elevation gradient. J Plant Nutr Soil Sci. 2010; 173: 30–38. DOI:
521 10.1002/jpln.200900027
- 522 31. Kunkel ML, Flores AN, Smith TJ, McNamara JP, Benner SG. A simplified approach for
523 estimating soil carbon and nitrogen stocks in semi-arid complex terrain. Geoderma. 2011; 165
524 (1): 1–11.
- 525 32. Tian Q, He H, Cheng W, Bai Z, Wang Y, Zhan X. Factors controlling soil organic
526 carbon stability along a temperate forest altitudinal gradient. Sci Rep. 2016; 6: 18783. DOI:
527 10.1038/srep18783
- 528 33. Garcia-Pausas J, Casals P, Camarero L, Huguet C, Sebastia MT, Thompson R, Romanya
529 J. Soil organic carbon storage in mountain grasslands of the Pyrenees, effects of climate and

- 530 topography. *Biogeochemistry*. 2007; 82: 279–289. [https://](https://doi.org/10.1007/s10533-007-9071-9)
531 [doi.org/https://doi.org/10.1007/s10533-007-9071-9](https://doi.org/10.1007/s10533-007-9071-9).
- 532 34. Zimmermann M, Meir P, Bird MI, Malhi Y, Ccahuana AJQ. Temporal variation and
533 climate dependence of soil respiration and its components along a 3000 m altitudinal tropical
534 forest gradient. *Global Biogeochem Cy*. 2010; 24: GB4012. [doi: 10.1029/2010GB003787](https://doi.org/10.1029/2010GB003787)
- 535 35. Kobler J, Zehetgruber B, Jandl R, Dirnböck T, Schindlbacher A. Effects of slope aspect
536 and site elevation on seasonal soil carbon dynamics in a forest catchment in the Austrian
537 Limestone Alps. 19th EGU General Assembly, EGU2017, proceedings from the conference
538 held. 2017; 23-28 April, in Vienna, Austria, p.16691
- 539 36. Grand S, Rubin A, Verrecchia EP, Vittoz P. Variation in Soil Respiration across Soil and
540 Vegetation Types in an Alpine Valley. *PLoS ONE*. 2016; 11 (9): e0163968.
541 <https://doi.org/10.1371/journal.pone.0163968>
- 542 37. Migliavacca M, Reichstein M, Richardson AD, Colombo R, Sutton MA, Lasslop G.
543 Semiempirical modeling of abiotic and biotic factors controlling ecosystem respiration across
544 eddy covariance sites. *Global Change Biology*. 2011; 17(1): 390-409. DOI: 10.1111/j.1365-
545 2486.2010.02243.x.
- 546 38. Bréchet L, Ponton S, Alméras T, Bonal D, Epron D. Does spatial distribution of tree size
547 account for spatial variation in soil respiration in a tropical forest?. *Plant Soil*. 2011; 347 (293):
548 <https://doi.org/10.1007/s11104-011-0848-1>
- 549 39. Xu X, Shi Z, Li D, Zhou X, Sherry RA, Luo Y. Plant community structure regulates
550 responses of prairie soil respiration to decadal experimental warming. *Glob Change Biol*. 2015;
551 21: 3846-3853. <https://doi.org/10.1111/gcb.12940>
- 552 40. Tian Q, Wang D, Tang Y, Li Y, Wang M, Liao C, Liu F. Topographic controls on the
553 variability of soil respiration in a humid subtropical forest. *Biogeochemistry*. 2019; 145: 177–
554 192. <https://doi.org/10.1007/s10533-019-00598-x>
- 555 41. Tonon G, Dezi S, Ventura M, Scandellari F. The Effect of Forest Management on Soil
556 Organic Carbon. In: Sauer TJ, Eiler JM, Sivakumar MVK (eds) *Sustaining Soil Productivity in*

- 557 Response to Global Climate Change: Science, Policy, and Ethics. John Wiley & Sons, Inc. 2011;
558 pp 225–238
- 559 42. Greiser C, Meineri E, Luoto M, Ehrlén J, Hylander K. Monthly microclimate models in a
560 managed boreal forest landscape. *Agri For Meteorol.* 2018; 250–251: 147–158.
561 <https://doi.org/10.1016/j.agrformet.2017.12.252>.
- 562 43. Carey JC, Tang J, Templer PH, Kroeger KD, Crowther T, et al. Temperature response of
563 soil respiration largely unaltered with experimental warming. *PNAS.* 2016; 113 (48): 13797–
564 13802.
- 565 44. Tang J, Cheng H, Fang C. The temperature sensitivity of soil organic carbon
566 decomposition is not related to labile and recalcitrant carbon. *PLoS ONE.* 2017; 12 (11):
567 e0186675. <https://doi.org/10.1371/journal.pone.0186675>
- 568 45. Montagnani L, Manca G, Canepa E, Georgieva E, Acosta M, Feigenwinter C, Janous D.
569 A new mass conservation approach to the study of CO₂ advection in an alpine forest. *J. Geophys.*
570 *Res. Atmos.* 2009; 114: D07306, DOI:10.1029/2008JD010650.
- 571 46. Xu X, Yi C, Montagnani L, Kutter E. Numerical Study of the Interplay between
572 Thermo-topographic Slope Flow and Synoptic Flow on Canopy Transport Processes, *Agric For*
573 *Meteorol.* 2018; 255: 3-16. <https://doi.org/10.1016/j.agrformet.2017.03.004>.
- 574 47. Gielen B, Acosta M, Altimir N, Buchmann N, Cescatti A, Ceschia E, Fleck S. Soil-
575 meteorological measurements at ICOS monitoring stations in terrestrial ecosystems. *Int*
576 *Agrophys.* 2019; 32: 645-664. DOI: 10.1515/intag-2017-0048
- 577 48. Ventura M, Panzacchi P, Muzzi E, Magnani F, Tonon G. Carbon balance and soil carbon
578 input in a poplar short rotation coppice plantation as affected by nitrogen and wood ash
579 application. *New Forests.* 2019. <https://doi.org/10.1007/s11056-019-09709-w>
- 580 49. Richards FJ. A flexible growth function for empirical use. *J Exp Bot.* 1959; 10: 290 –
581 300.
- 582 50. Janssens IA, Pilegaard K. Large seasonal changes in Q₁₀ of soil respiration in a beech
583 forest. *Glob Chang Biol.* 2003; 9: 911- 918.

- 584 50. Crawley M.J. *The R Book*. Chichester: John Wiley & Sons, Ltd.; 2007.
- 585 51. Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. *Mixed Effects Models and*
586 *Extensions in Ecology with R*. New York: Springer; 2009.
- 587 52. Bates D, Maechler M, Bolker B, Walker S. *lme4: linear mixed-effects models using*
588 *Eigen and S4*. R package version 1.1-7; 2014.
- 589 53. Nakagawa S, Holger S. A general and simple method for obtaining R^2 from generalized
590 linear mixed effects models. *Methods Ecol Evol*. 2013; 4: 133-142.
- 591 54. Jaeger BC, Edwards LJ, Das K, Sen PK. An R^2 Squared Statistic for Fixed Effects in the
592 Generalized Linear Mixed Model. *J Appl Stat*. 2016; 44 (6): 1086–1105
- 593 55. Meyer N, Welp G, Amelung W. The temperature sensitivity (Q₁₀) of soil respiration:
594 Controlling factors and spatial prediction at regional scale based on environmental soil classes.
595 *Global Biogeochem Cy*. 2018; 32: 306–323. <https://doi.org/10.1002/2017GB005644>
- 596 56. Shapiro SS, Wilk MB. Analysis of variance test for normality. *Biometrika*. 1965; 52:
597 591–611.
- 598 57. Levene H. In *Contributions to Probability and Statistics: Essays in Honor of Harold*
599 *Hotelling*, I. Olkin et al. eds., Stanford University Press, 1960; 278-292.
- 600 58. R Core Team. *R: A language and environment for statistical computing*. R Foundation
601 for Statistical Computing, Vienna, Austria. 2019. Available online at <https://www.R-project.org/>.
- 602 59. Wang G, Zhou Y, Xu X, Ruan H, Wang J. Temperature Sensitivity of Soil Organic
603 Carbon Mineralization along an Elevation Gradient in the Wuyi Mountains, China. *PLoS ONE*.
604 2013; 8(1): e53914. [doi:10.1371/journal.pone.0053914](https://doi.org/10.1371/journal.pone.0053914)
- 605 60. Chatterjee A, Jenerette GD. Variation in soil organic matter accumulation and metabolic
606 activity along an elevation gradient in the Santa Rosa Mountains of Southern California, USA. *J*
607 *Arid Land*. 2015; 7(6): 814–819. [doi: 10.1007/s40333-015-0085-1](https://doi.org/10.1007/s40333-015-0085-1)
- 608 61. Tsozuéa D, Nghonda JP, Tematio P, Basga SD. Changes in soil properties and soil
609 organic carbon stocks along an elevation gradient at Mount Bambouto, Central Africa. *Catena*.
610 2019; 175: 251–262. <https://doi.org/10.1016/j.catena.2018.12.028>

- 611 62. de la Cruz-Amo L, Bañares-de-Dios G, Cala V, Granzow-de la Cerda I, Espinosa CI,
612 Ledo A, Salinas N, Macía M.J, Cayuela L. Trade-offs among aboveground, belowground, and
613 soil organic carbon stocks along altitudinal gradients in Andean Tropical Montane Forests. *Front.*
614 *Plant Sci.* 2020; 11:106. [doi: 10.3389/fpls.2020.00106](https://doi.org/10.3389/fpls.2020.00106)
- 615 63. Kirschbaum MUF. The temperature dependence of organic-matter decomposition-still a
616 topic of debate. *Soil Biol Biochem.* 2006; 38: 2510-2518
- 617 64. He X, Hou E, Liu Y, Wen D. Altitudinal patterns and controls of plant and soil nutrient
618 concentrations and stoichiometry in subtropical China. *Sci Rep.* 2016; 6: 24261. DOI:
619 10.1038/srep24261
- 620 65. Griffiths PR, Madritch MD, Swanson AK. The effects of topography on forest soil
621 characteristics in the Oregon Cascade Mountains (USA): Implications for the effects of climate
622 change on soil properties. *For Ecol Manag.* 2009; 257(1): 1-7.
- 623 66. Bahn M, Rodeghiero M, Anderson-Dunn M, Dore S, Gimeno C, et al. Soil respiration in
624 European grasslands in relation to climate and assimilate supply. *Ecosystems.* 2008; 11: 1352–
625 1367. [DOI: 10.1007/s10021-008-9198-0](https://doi.org/10.1007/s10021-008-9198-0)
- 626 67. Shi Y, Baumann F, Ma Y, Song C, Uhn PK, Scholten T, He JS. Organic and inorganic
627 carbon in the topsoil of the Mongolian and Tibetan grasslands: pattern, control and implications.
628 *Biogeosciences.* 2012; 9: 2287–2299. [doi:10.5194/bg-9-2287-2012](https://doi.org/10.5194/bg-9-2287-2012)
- 629 68. Vanhala P. Seasonal variation in the soil respiration rate in coniferous forest soils. *Soil*
630 *Biol Biochem.* 2002; 34: 1375–1379.
- 631 69. Zhang YY, Wu W, Liu H. Factors affecting variations of soil pH in different horizons in
632 hilly regions. *PLoS One.* 2019; 14(6): e0218563. [doi: 10.1371/journal.pone.0218563](https://doi.org/10.1371/journal.pone.0218563)
- 633 70. Martí C, Badía D. Characterization and classification of soils along two altitudinal
634 transects in the Eastern Pyrenees, Spain. *Arid Soil Res Rehabil.* 1995; 9: 367-383. [DOI:](https://doi.org/10.1080/15324989509385905)
635 [10.1080/15324989509385905](https://doi.org/10.1080/15324989509385905)
- 636 71. Smith JL, Halvorson JJ, Jr HB. Soil properties and microbial activity across a 500 m
637 elevation gradient in a semi-arid environment. *Soil Biol Biochem.* 2002; 34: 1749–1757.

- 638 72. Seibert J, Stendahl J, Sørensen R. Topographical influences on soil properties in boreal
639 forests. *Geoderma*. 2007; 141(1–2): 139–148.
- 640 73. Badía D, Ruiz A, Girona A, et al. The influence of elevation on soil properties and forest
641 litter in the Siliceous Moncayo Massif, SW Europe. *J Mt Sci*. 2016; 13: 2155–2169.
642 <https://doi.org/10.1007/s11629-015-3773-6>
- 643 74. Klopfenstein ST, Hirmas DR, Johnson W. Relationships between soil organic carbon
644 and precipitation along a climosequence in loess-derived soils of the Central Great Plains, USA.
645 *Catena*. 2015; 133: 25–34. <http://dx.doi.org/10.1016/j.catena.2015.04.015>
- 646 75. Schrumpf M, Schulze ED, Kaiser K, Schumacher, J. How accurately can soil organic
647 carbon stocks and stock changes be quantified by soil inventories?. *Biogeosciences*. 2011; 8:
648 1193–1212. <https://doi.org/10.5194/bg-8-1193-2011>.
- 649 76. Keenan TF, Migliavacca M, Papale D, Baldocchi D, Reichstein M, Torn M, Wutzler T.
650 Widespread inhibition of daytime ecosystem respiration. *Nat Ecol Evol*. 2019; 3(3): 407–415.
651 doi: 10.1038/s41559-019-0809-2
- 652 77. Reichstein M, Ciais P, Papale D, Valentini R, Running S, Viovy N. Reduction of
653 ecosystem productivity and respiration during the European summer 2003 climate anomaly: a
654 joint flux tower, remote sensing and modelling analysis. *Glob Change Biol*. 2007; 13(3): 634–
655 651. DOI 10.1111/j.1365-2486.2006.01224.x
- 656 78. Yu GR, Zhu XJ, Fu YL, He HL, Wang QF, Wen XF. Spatial patterns and climate drivers
657 of carbon fluxes in terrestrial ecosystems of China *Global Change Bio*. 2013; 119: 798–810.
658 <https://doi.org/10.1111/gcb.12079>
- 659 79. Chen S, Zou J, Hu Z, Lu Y. Climate and vegetation drivers of terrestrial carbon fluxes: a
660 global data synthesis. *Adv Atmos Sci*. 2019; 36: 679–696.
- 661 80. Ma J, Liu R, Li C, Fan L, Xu G, Li Y. Herbaceous layer determines the relationship
662 between soil respiration and photosynthesis in a shrub-dominated desert plant community. *Plant*
663 *Soil*. 2020, 449: 193–207. <https://doi.org/10.1007/s11104-020-04484-6>

- 664 81. Raich JW, Tufekciogul A. Vegetation and soil respiration: Correlations and controls.
665 Biogeochemistry. 2000; 48: 71–90. <https://doi.org/10.1023/A:1006112000616>
- 666 82. Chen Q, Wang Q, Han X, Wan S, Li L. Temporal and spatial variability and controls of
667 soil respiration in a temperate steppe in northern China. Global Biogeochem Cycles. 2010; 24:
668 GB2010. [doi:10.1029/2009GB003538](https://doi.org/10.1029/2009GB003538).
- 669 83. Oertel C, Matschullat J, Zurba K, Zimmermann F, Erasmi S. Greenhouse Gas Emissions
670 From Soil - A review, Chemie der Erde. 2016; 76: 327–352, [doi:10.1016/j.chemer.2016.04.002](https://doi.org/10.1016/j.chemer.2016.04.002).
- 671 84. Andersson S, Nilsson SI. Influence of pH and temperature on microbial activity,
672 substrate availability of soil-solution bacteria and leaching of dissolved organic carbon in a mor
673 humus. Soil Biol Biochem. 2001; 33 (9): 1181–1191. [https://doi.org/10.1016/S0038-](https://doi.org/10.1016/S0038-0717(01)00022-0)
674 [0717\(01\)00022-0](https://doi.org/10.1016/S0038-0717(01)00022-0)
- 675 85. Reth S, Reichstein M, Falge E. The effect of soil water content, soil Temperature, soil
676 pH value and the root mass on soil CO₂ efflux- a modified model. Plant Soil, 2005; 268: 21-33.
- 677 86. Chappell C, Johnson A. Influence of pH and bulk density on carbon dioxide efflux in
678 tree urban wetland types. Professional Agricultural Workers Journal. 2015; 3 (1, 5).
679 <http://tuspubs.tuskegee.edu/pawj/vol3/iss1/5>
- 680 87. Mordhorst A, Peth S, Horn R. Influence of mechanical loading on static and dynamic
681 CO₂ efflux on differently textured and managed Luvisols. Geoderma. 2014; 219–220: 1–13.
- 682 88. Chen B, Liu S, Ge J, Chu J. Annual and seasonal variations of Q10 soil respiration in the
683 sub-alpine forests of the Eastern Qinghai-Tibet Plateau, China. Soil Biol Biochem. 2010; 42:
684 1735-1742
- 685 89. Feng J, Wang J, Song Y, Zhu B. Patterns of soil respiration and its temperature
686 sensitivity in grassland ecosystems across China, Biogeosciences. 2018; 15: 5329–5341,
687 <https://doi.org/10.5194/bg-15-5329-2018>

- 688 90. Acosta M, Pavelka M, Montagnani L, Kutsch W, Lindroth A, Juszczak R, Janouš D. Soil
689 surface CO₂ efflux measurements in Norway spruce forests. Comparison between four different
690 sites across Europe — from boreal to alpine forest. *Geoderma*. 2013; 192: 295-303. DOI:
691 [10.1016/j.geoderma.2012.08.027](https://doi.org/10.1016/j.geoderma.2012.08.027).
- 692 91. Zhou T, Shi P, Hui D, Luo Y. Global pattern of temperature sensitivity of soil
693 heterotrophic respiration (Q₁₀) and its implications for carbon-climate feedback, *J Geophys Res-*
694 *Biogeo*. 2009; 114: 271–274, <https://doi.org/10.1029/2008JG000850>, 2009.
- 695 92. Song X, Peng C, Zhao Z, Zhang Z, Guo B, Wang W, Jiang H, Zhu Q. Quantification of
696 soil respiration in forest ecosystems across China. *Atmos Environ*. 2014; 94: 546–551,
697 <https://doi.org/10.1016/j.atmosenv.2014.05.071>
- 698 93. Zhou W, Hui D, Shen W. Effects of Soil Moisture on the Temperature Sensitivity of Soil
699 Heterotrophic Respiration: A Laboratory Incubation Study. *PLoS ONE*. 2014; 9(3): e92531.
700 [doi:10.1371/journal.pone.0092531](https://doi.org/10.1371/journal.pone.0092531)
- 701 94. Zhao J, Li R, Li X, Tian L. Environmental controls on soil respiration in alpine meadow
702 along a large altitudinal gradient on the central Tibetan Plateau. *Catena*. 2017; 159: 84–92.
703 <https://doi.org/10.1016/j.catena.2017.08.007>
- 704 95. Zhou Z, Guo C, Meng H. Temperature sensitivity and basal rate of soil respiration and
705 their determinants in temperate forests of North China. *PLoS One*. 2013; 8(12): e81793.
706 <https://doi.org/10.1371/journal.pone.0081793>
- 707 96. Quan Q, Wang C, He N, Zhang Z, Wen X, Su H, Wang Q, Xue J. Forest type affects the
708 coupled relationships of soil C and N mineralization in the temperate forests of northern China.
709 *Sci Rep*. 2014; 4: 6584, [DOI: 10.1038/srep06584](https://doi.org/10.1038/srep06584),
- 710 97. Rambo TR, North MP. Canopy microclimate response to pattern and density of thinning
711 in a Sierra Nevada forest. *For Ecol Manag*. 2009; 257 (2): 435-442,
712 <https://doi.org/10.1016/j.foreco.2008.09.029>
- 713 98. Arx GV, Dobbertin M, Rebetez M. Spatio-temporal effects of forest canopy on
714 understory microclimate in along-term experiment in Switzerland. *Agr Forest Meteorol*. 2012;
715 166–167: 144–155, <https://doi.org/10.1016/j.agrformet.2012.07.018>

716 99. Niu S, Luo Y, Fei S, Yuan W, Schimel D, Law BE, et al. Thermal Optimality of Net
717 Ecosystem Exchange of Carbon Dioxide and Underlying Mechanisms. *New Phytol.* 2012; 194
718 (3): 775-783, DOI: 10.1111/j.1469-8137.2012.04095.x.

719 **Supporting Information**

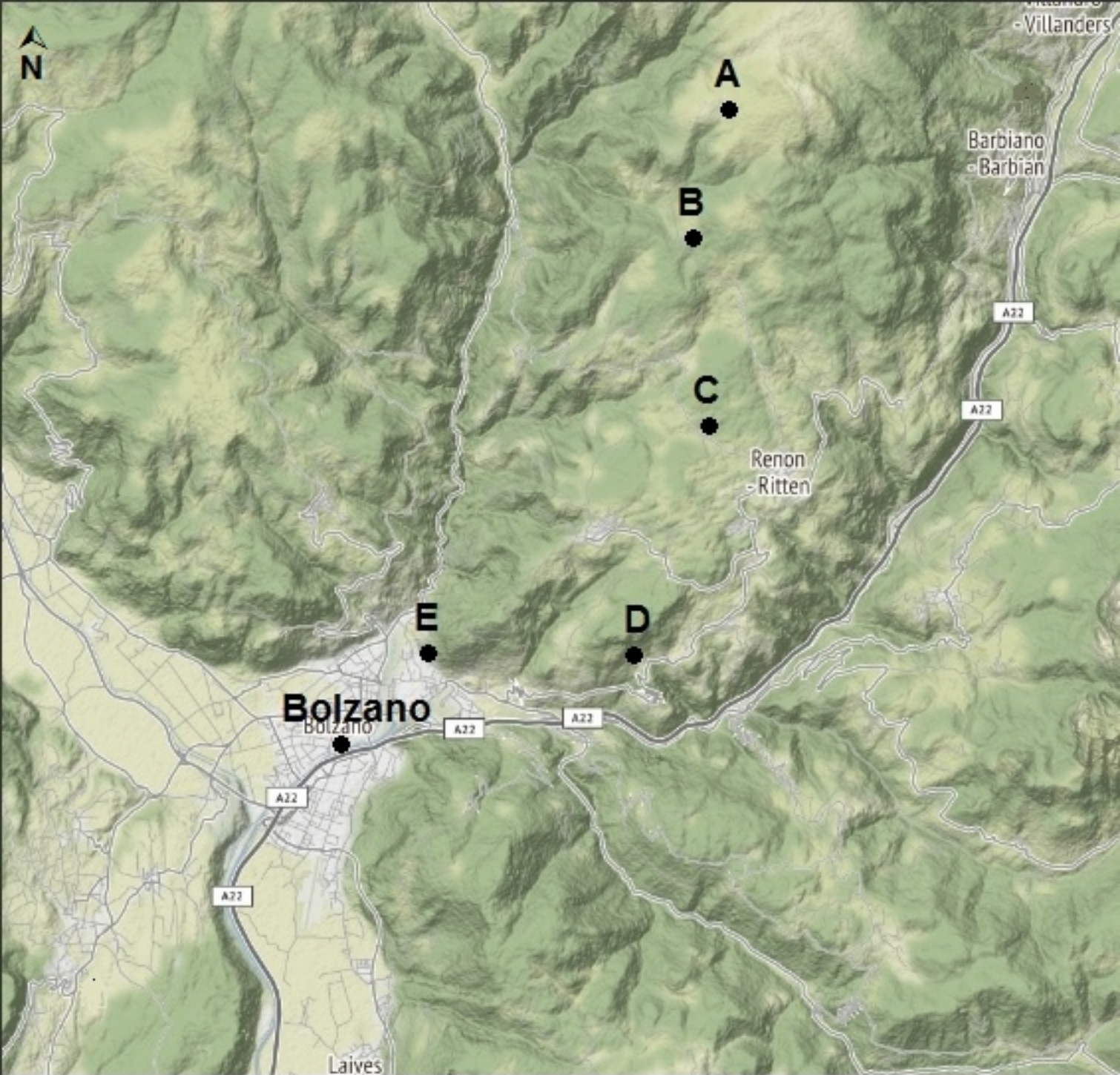
720 **S1. Collected soil respiration data by soil chambers.** Used for soil respiration modeling

721 **S2. Measured soil physicochemical properties.** Used for the analysis.

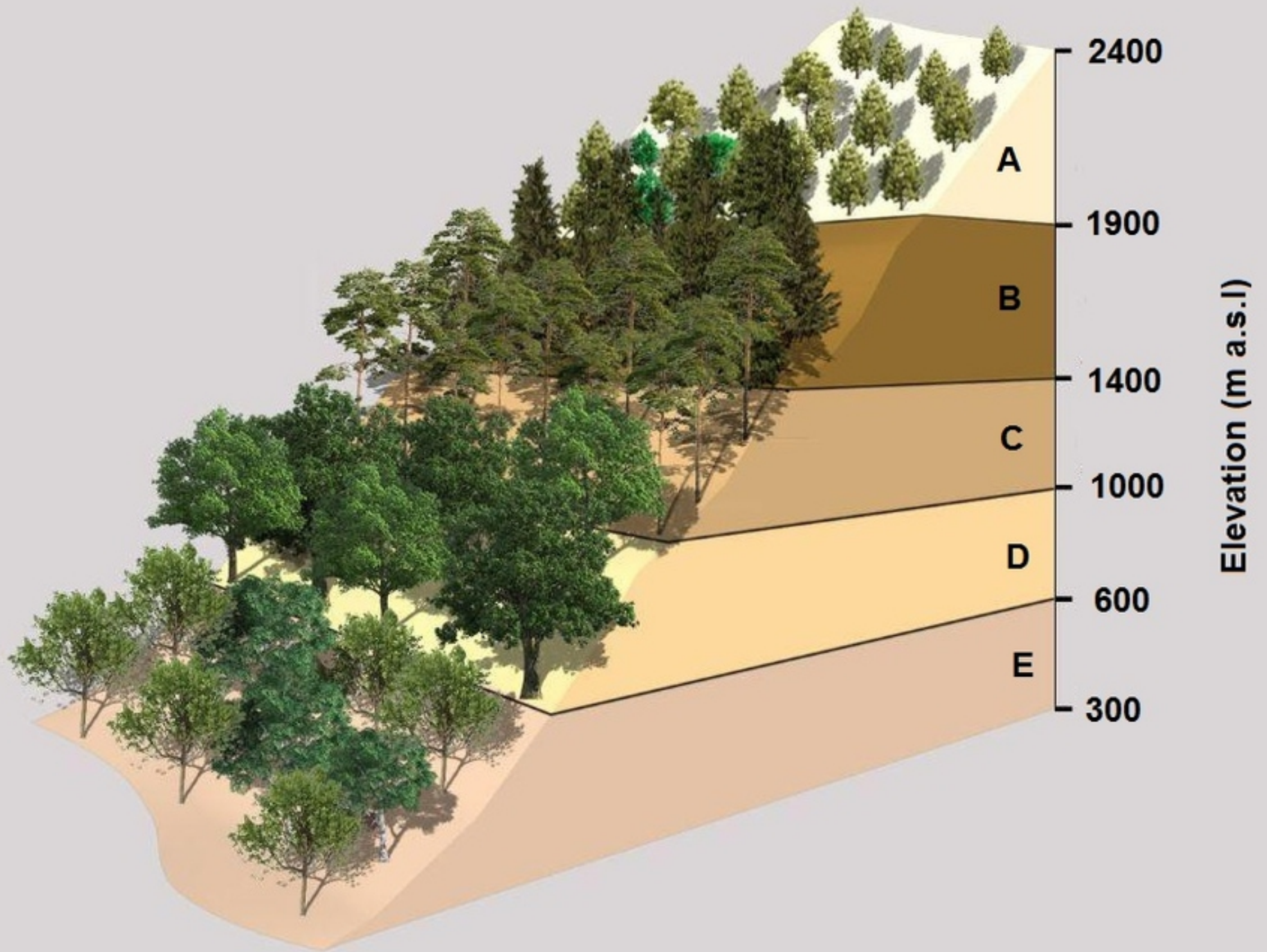
722 **S1 Fig. Predicted daily mean air temperature (°C, closed circles) and soil CO₂ fluxes (μmol**
723 **CO₂ C m⁻² s⁻¹, open circles) during the experimental period (July 2017- July 2018).** Mean
724 annual air temperature (T_{air}, °C) and total cumulative soil respiration in the entire experimental
725 period (SR, kg C m⁻²) are indicated for each site on the top of the relative plots.

726 **S2 Fig. Observed soil respiration vs. predicted soil respiration by model.**

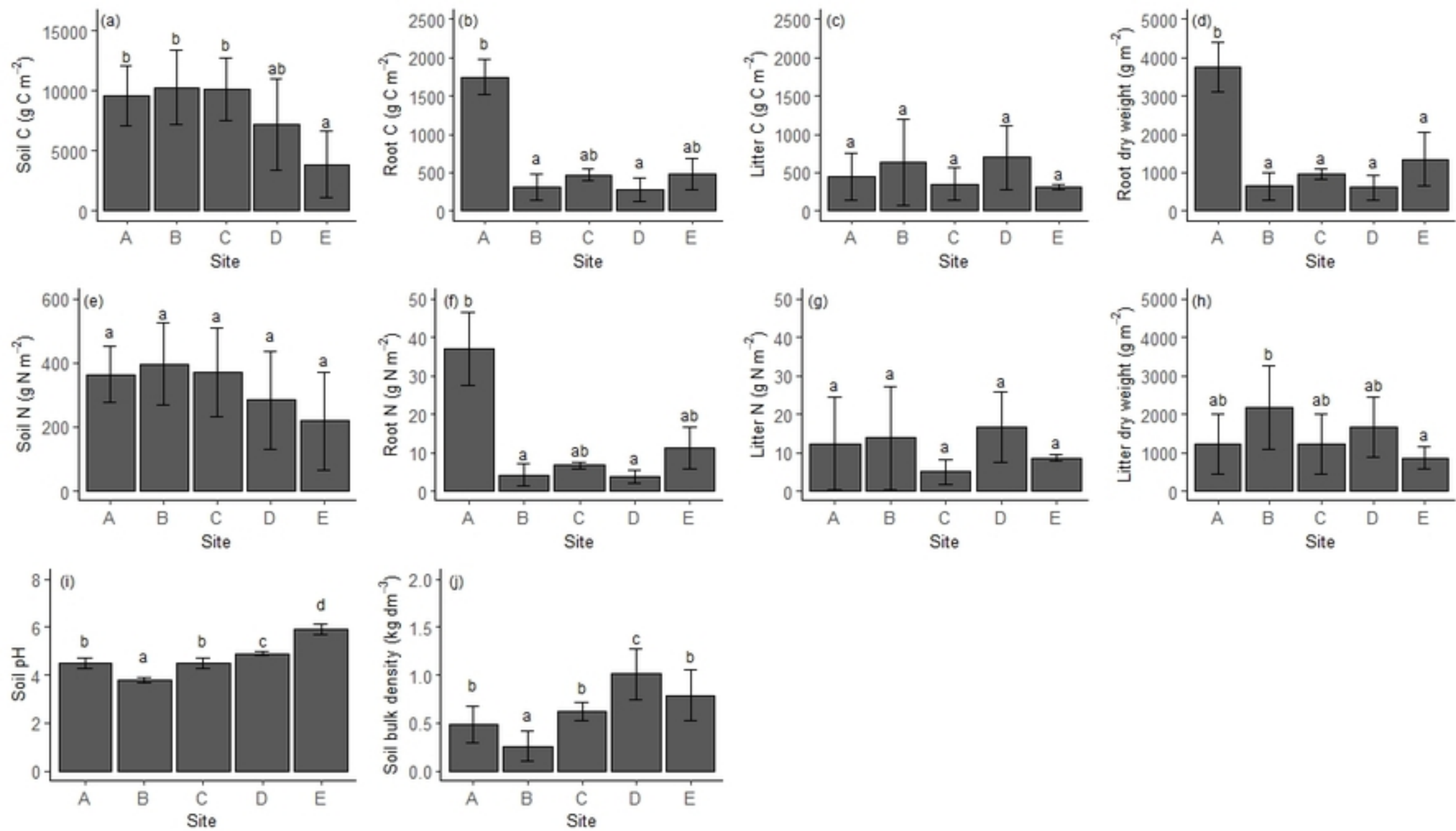
727 **S1 Table. The developed equations by linear and polynomial regressions between the**
728 **different parameters tested and elevation.** BD – soil bulk density; Q₁₀ – temperature
729 sensitivity of soil respiration; SR- cumulated soil respiration; SR_{ref} – respiration at the 10°C
730 reference temperature; Elev – elevation.



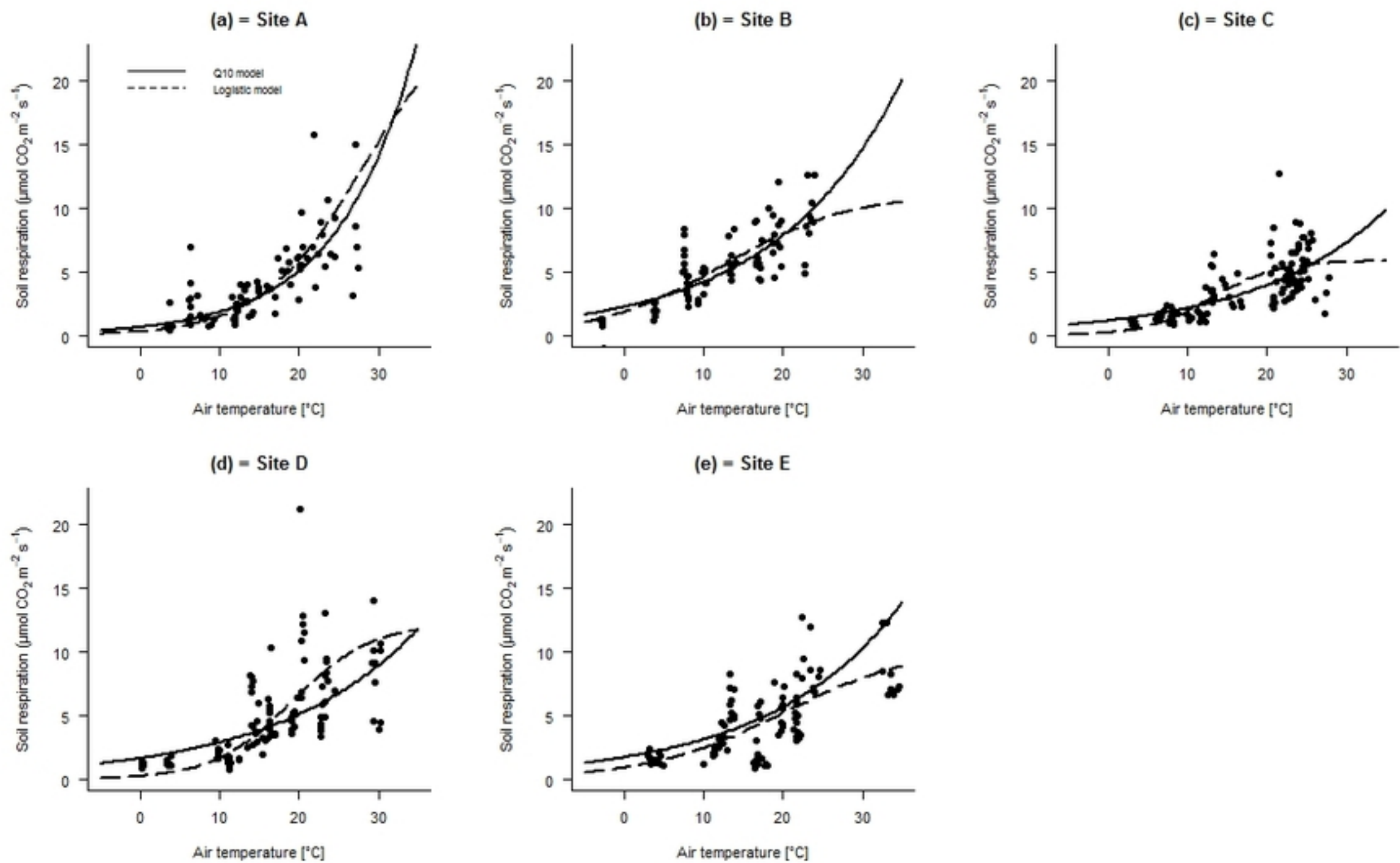
Figure



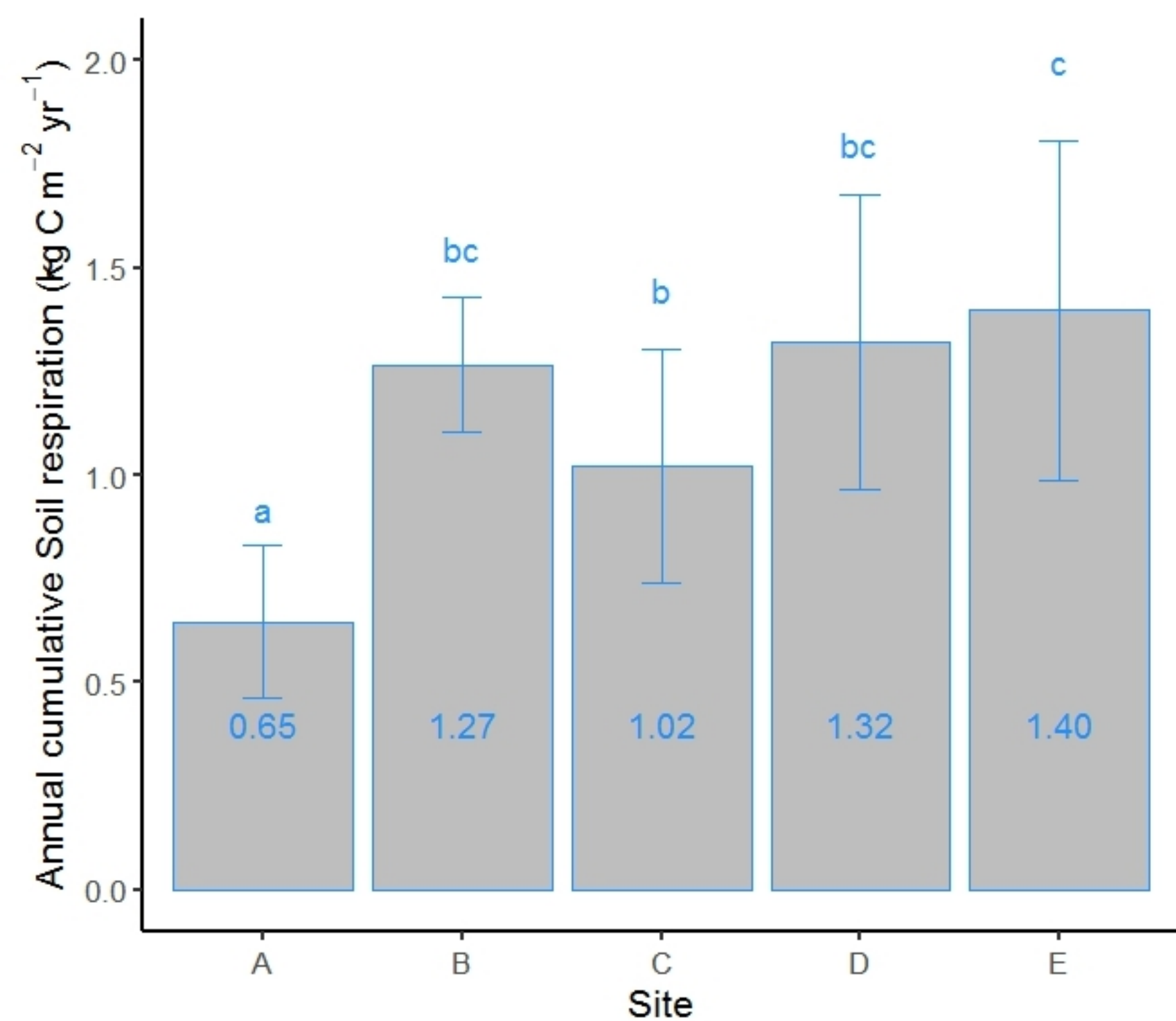
Figure



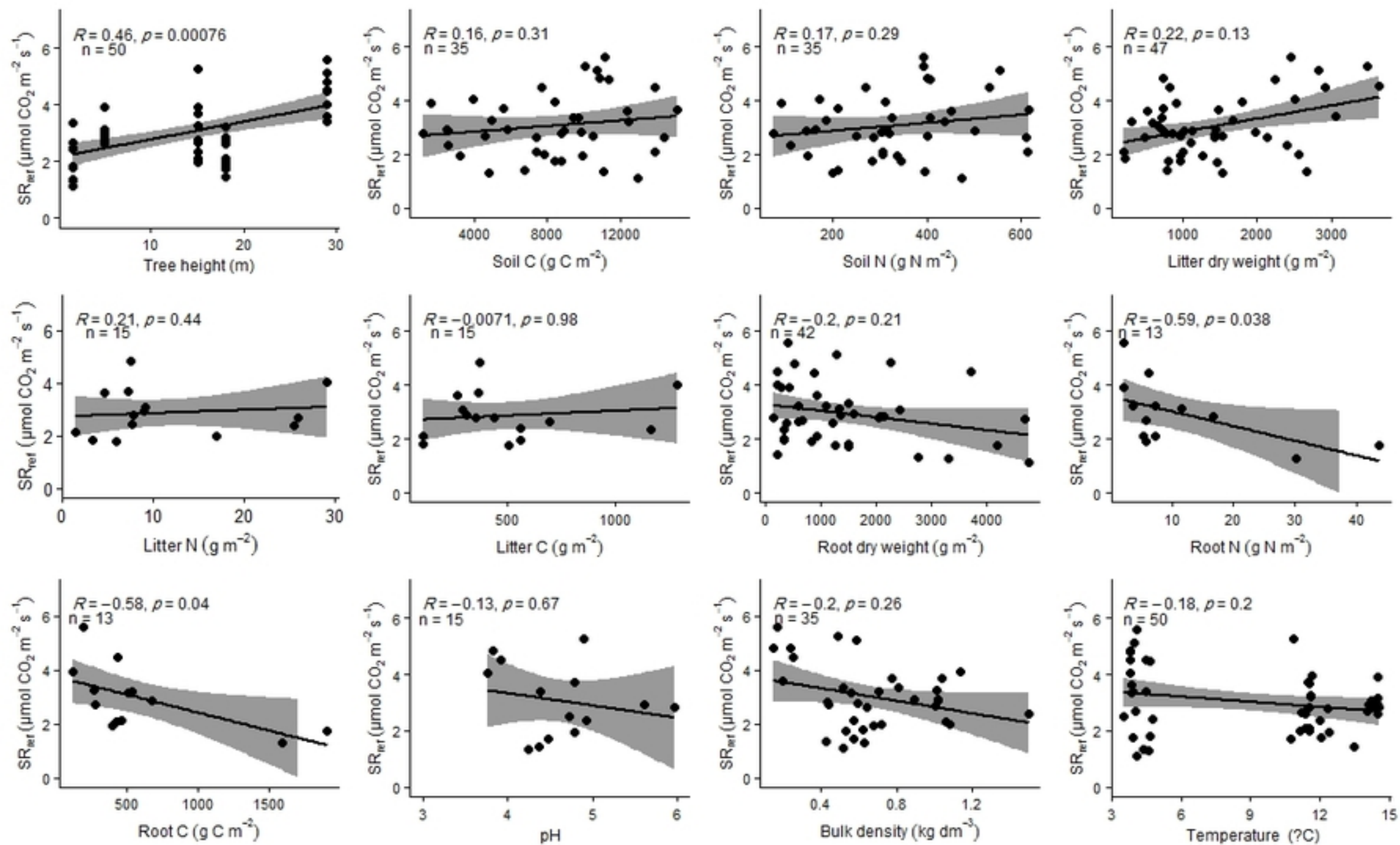
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