1 **Temperature increases soil respiration across ecosystem types and soil development,**

2 **but soil properties determine the magnitude of this effect**

3

4 **Running head:** Temperature effect on soil respiration

5

6 Marina Dacal[1,2*], Manuel Delgado-Baquerizo[3], Jesús Barquero[3], Asmeret Asefaw Berhe[4],

7 Antonio Gallardo[3], Fernando T. Maestre[2,5] & Pablo García-Palacios[6]

8

9 [1]Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey

10 Juan Carlos, C/ Tulipán s/n, 28933 Móstoles, Spain

11 [2]Instituto Multidisciplinar para el Estudio del Medio "Ramon Margalef", Universidad de

12 Alicante, Carretera de San Vicente del Raspeig s/n, 03690 San Vicente del Raspeig, Spain

13 [3]Departamento de Sistemas Físicos, Químicos y Naturales, Universidad Pablo Olavide,

14 41704 Sevilla, Spain.

15 [4]Department of Life and Environmental Sciences; University of California, Merced CA

16 95343, USA

17 [5]Departamento de Ecología, Universidad de Alicante, Carretera de San Vicente del

18 Raspeig s/n, 03690 San Vicente del Raspeig, Spain

19 [6]Instituto de Ciencias Agrarias, Consejo Superior de Investigaciones Científicas, Serrano

20 115 bis, 28006, Madrid, Spain.

21

22

23 [*] Correspondence e-mail: marina.dacal1@gmail.com

24

25

Abstract

Soil carbon losses to the atmosphere, via soil heterotrophic respiration, are expected to increase in response to global warming, resulting in a positive carbon-climate feedback. Despite the well-known suite of abiotic and biotic factors controlling soil respiration, much less is known about how the magnitude of soil respiration responses to temperature changes over soil development and across contrasting soil properties. Here, we investigated the role of soil development stage and soil properties in driving the responses of soil heterotrophic respiration to increasing temperatures. We incubated soils from eight chronosequences ranging in soil age from hundreds to million years, and encompassing a wide range of vegetation types, climatic conditions, and chronosequences origins, at three assay temperatures (5, 15 and 25ºC). We found a consistent positive effect of assay temperature on soil respiration rates across the eight chronosequences evaluated. However, soil properties such as organic carbon concentration, texture, pH, phosphorus content, and microbial biomass determined the magnitude of temperature effects on soil respiration. Finally, we observed a positive effect of soil development stage on soil respiration that did not alter the magnitude of assay temperature effects. Our work reveals that key soil properties alter the magnitude of the positive effect of temperature on soil respiration found across ecosystem types and soil development stages. This information is essential to better understand the magnitude of the carbon-climate feedback, and thus to establish accurate greenhouse gas emission targets.

Keywords: climate warming, land carbon-climate feedback, microbial biomass, nutrient availability, soil chronosequences, soil texture.

Introduction

Temperature is a key driver of heterotrophic soil respiration (hereafter soil respiration), –a major process of carbon (C) loss to the atmosphere (Bond-Lamberty, Bailey, Chen, Gough, & Vargas, 2018; Bond-Lamberty & Thomson, 2010; Zhou et al., 2016). Global warming is expected to accelerate the rate of soil respiration (Davidson & Janssens, 2006; Kirschbaum, 2006), reinforcing climate change with a land C-climate feedback embedded in the Intergovernmental Panel on Climate Change (IPCC) projections (Ciais et al., 2014). Despite the recognized importance of an accurate representation of this feedback in Earth System Models to establish appropriate greenhouse gas emission targets (Bradford et al., 2016), the extent to which climate change will increase soil C losses to the atmosphere via soil respiration is still highly uncertain (Arora et al., 2013; Exbrayat, Pitman, & Abramowitz, 2014). Learning more about how and why soil properties regulate the magnitude of soil respiration responses to elevated temperatures is essential to accurately predict the land C-climate feedback in a warmer world.

To build confidence in the projected magnitude of the land C-climate feedback, the response of soil respiration to climate warming should be addressed across large spatial scales and encompassing a wide range of soil development stages. Beyond temperature, it is also critical to determine the influence of other key abiotic and biotic factors that regulate soil respiration (Guo et al., 2017; Rustad, Huntington, & Boone, 2000; Schindlbacher, Schnecker, Takriti, Borken, & Wanek, 2015). These include key soil abiotic drivers such as organic carbon (SOC), texture (i.e., the percentage of sand, silt, and clay), pH, and phosphorus (P), as well as biotic properties such as microbial biomass (Bradford, Watts, & Davies, 2010; Karhu et al., 2014). For instance, soil texture influences soil respiration by controlling water and nutrient availability (Delgado-

3

75 Baquerizo et al., 2013) and regulating the potential of soil minerals to physically and

76 chemically stabilize organic carbon (Rasmussen et al., 2018). A previous study showed

77 that soils with higher proportion of clay sized particles also had higher microbial activity

78 due to greater water and nutrient availability, leading to higher soil respiration (Karhu et

79 al., 2014). Further, soil respiration increases as microbial biomass rises (Wang, Dalal,

80 Moody, & Smith, 2003). Despite the knowledge accumulated about soil respiration

81 drivers, much less is known about how soil properties modulate soil respiration responses

82 to warming.

83   Soils are known to develop from centuries to millennia, resulting in important

84 changes in key abiotic properties (Crews et al., 1995; Vitousek, 2004; Wardle, Bardgett,

85 et al., 2004). For example, young soils are known to accumulate organic carbon during

86 soil development from centuries to millennia (Schlesinger, 1990), and older soils are

87 expected to support more acid, and P depleted soils compared with younger substrates

88 (Doetterl et al., 2018; Laliberté et al., 2013). Importantly, although soil properties do

89 change as soil develops over geological timescales, the parent material does not vary.

90 Because of this, soil development has been suggested as a good model system to

91 investigate the role of soil abiotic and biotic properties in driving the responses of soil

92 respiration to disturbances such as increasing temperatures (Orwin et al., 2006). A

93 number of studies performed at individual soil chronosequences have investigated

94 whether soil development stage influences soil respiration rates, showing contrasting

95 results. Whereas some studies found an enhancing effect of soil development on soil

96 respiration (J. L. Campbell & Law, 2005; Law, Sun, Campbell, Van Tuyl, & Thornton,

97 2003), others observed that soil respiration rates decreased as soil develops (Tang et al.,

98 2008; Wang, Bond-Lamberty, & Gower, 2002). These differences are likely due to site-

99 specific variations in soil development trajectories between chronosequences with

100   contrasting parent material and climatic conditions (Alfaro, Manzano, Marquet, &

101   Gaxiola, 2017). Therefore, to gain a more comprehensive understanding of how soil

102   development affects soil respiration and its response to temperature, such effects should

103   be evaluated both within single chronosequences but also across multiple

104   chronosequences occurring in different ecosystem types with contrasting environmental

105   conditions (e.g. climate, parent material, soil origin, etc.).

106   Beyond soil properties and soil development, other mechanisms may also

107   modulate soil respiration responses to temperature. For instance, substrate depletion and

108   thermal acclimation have been demonstrated to alter soil respiration responses to

109   temperature (Bradford et al., 2010; Hartley, Hopkins, Garnett, Sommerkorn, & Wookey,

110   2008). Temperature accelerates microbial activity, leading to an increase in soil

111   respiration (Hochachka & Somero, 2002). However, microorganisms develop several

112   mechanisms to acclimate to the ambient temperature regime such as changes in enzyme

113   and membrane structures. Hence, when subjected to the same temperature range, the

114   microbial activity and soil respiration of acclimated microorganisms would be lower

115   compared to the not acclimated ones (Hochachka & Somero, 2002). Therefore, thermal

116   acclimation to the ambient temperature regime may help to reduce the magnitude of soil

117   respiration responses to temperature (Bradford et al., 2019; Dacal, Bradford, Plaza,

118   Maestre, & García-Palacios, 2019). At the same time, such acceleration in microbial

119   activity with temperature may also cause an important reduction in the availability of

120   readily decomposable C sources, leading to substrate depletion (Cavicchioli et al., 2019;

121   Schindlbacher et al., 2015). Consequently, substrate depletion can limit microbial

122   processes such as soil respiration (Walker et al., 2018). Given that such mechanisms may

123   mitigate soil respiration responses to temperature, they should also be evaluated to

124   improve the accuracy in the predictions of the land C-climate feedbacks.

125   Herein, we used soil development as an ecological model system to test the

126   importance of soil properties in driving the responses of soil respiration to changes in

127   temperature. To such an end, we take advantage of soils collected from eight

128   chronosequences (Delgado-Baquerizo et al., 2019, 2020) located in Arizona (AZ; USA),

129   California (CAL; USA), Colorado (CO; USA), Hawaii (HA; USA), New Mexico (JOR;

130   USA), Chile (CH), Spain (CI) and Australia (WA) to perform an independent laboratory

131   assay based on short-term soil incubations at three assay temperatures (5, 15 and 25ºC).

132   These chronosequences range from hundreds to million years and encompass a wide

133   range of vegetation types (i.e., grasslands, shrublands, and forests), climatic conditions

134   (arid, continental, temperate and tropical), and origins (i.e., sand dunes, sedimentary and

135   volcanic; see Table 1 for more details). Further, we addressed whether soil respiration

136   and its response to temperature change over soil development either within or across

137   chronosequences. Finally, we assessed whether thermal acclimation influences soil

138   respiration responses to temperature across contrasting ecosystem types and soil

139   development stages.

140

141   **Materials and methods**

142   *Study design and field soil collection*

143   The environmental conditions of the eight chronosequences used spanned a wide gradient

144   in climatic conditions (MAT from 8.7 to 19.55ºC, and MAP from 276 to 1907 mm) and

145   soil properties (SOC from 0.6 to 25.3 and the percentage of clay plus silt from 3.8 to 44.1,

146   Table 1). The selected chronosequences included four to six stages of soil development.

147   Stage number one corresponds to the youngest soil, whereas four, five, or six correspond

148   to the oldest one within each chronosequence. Each chronosequence was considered a

149   site, so the total number of sites and stages surveyed in our study is 8 and 41, respectively.

150   At each stage, we established a 50 m x 50 m plot for conducting field surveys. Three

151   parallel transects of 50 m length, spaced 25 m apart, formed the basis of the plot. The

152   total plant cover and the number of perennial plant species (plant diversity) were

153   determined in each transect using the line-intercept method (Delgado-Baquerizo et al.,

154   2019). All of the sites were surveyed between 2016 and 2017 using a standardized

155   sampling protocol (Delgado-Baquerizo et al., 2019). At each plot, three composite soil

156   samples (five soil cores per sample: 0 – 10 cm depth) were collected under the canopy of

157   the dominant ecosystem vegetation type (e.g., grasses, shrubs, and trees). Soil samples

158   were collected during the same days within each soil chronosequence. After field

159   collection, soils were sieved at 2 mm, and a fraction was immediately frozen at -20ºC for

160   soil microbial biomass analyses. The rest of the soil was air-dried for a month and used

161   for biochemical analyses and laboratory incubations.

162

163   *Soil abiotic properties*

164   We measured the following abiotic soil properties in all samples: soil organic C (SOC),

165   texture (% of clay + silt), pH, and available soil phosphorus (soil P). To avoid

166   confounding effects associated with having multiple laboratories performing soil

167   analyses, all dried soil samples were shipped to Spain (Universidad Rey Juan Carlos) for

168   laboratory analyses. The concentration of SOC was determined by colorimetry after

169   oxidation with a mixture of potassium dichromate and sulfuric acid at 150º C for 30

170   minutes (Anderson & Ingram, 1993). Soil pH was measured with a pH meter in a 1:2.5

171   suspensions of dry soil mass to deionized water volume. Soil texture (% clay + silt) was

172   determined on a composite sample per chronosequence stage, according to Kettler,

173   Doran, & Gilbert (2001). Olsen P (soil P hereafter) was determined by extraction with

174   sodium bicarbonate, according to Olsen, Cole, Watanabe, & Dean (1954). Mean annual

175   temperature (MAT) and mean annual precipitation (MAP) values for the soils of each site

176   were obtained using Wordclim version 2.0 (Fick & Hijmans, 2017), which provides

177   global average climatic data for the 1970-2000 period.

178

179   *Soil microbial biomass*

180   We estimated soil microbial biomass by measuring phospholipid fatty acids (PLFAs).

181   These were extracted from freeze-dried soil samples using the method described in Bligh

182   & Dyer (1959), as modified by Buyer & Sasser (2012). The extracted PLFAs were

183   analysed on an Agilent Technologies 7890B gas chromatograph with an Agilent DB-5

184   ms column (Agilent Technologies, CA, USA). The biomarkers selected to indicate total

185   bacterial biomass are the PLFAs i15:0, a15:0, 15:0, i16:0, 16:1ω7, 17:0, i17:0, a17:0,

186   cy17:0, 18:1ω7 and cy19:0, and the biomarker to indicate total fungal biomass is the

187   PLFA 18:2ω6. Using the selected PLFA biomarkers, the biomass was calculated for each

188   soil sample (Frostegård & Bååth, 1996; Rinnan & Bååth, 2009). Total microbial biomass

189   includes the sum of all bacterial and fungal biomarkers plus that of other soil microbial

190   biomarkers such as the eukaryotic C18:1w9.

191

192   *Laboratory incubations and soil heterotrophic respiration measurements*

193   We conducted short-term (10 h) incubations of our soil samples, in accordance with

194   previous studies (Atkin & Tjoelker, 2003; Bradford et al., 2010; Hochachka & Somero,

195   2002; Tucker, Bell, Pendall, & Ogle, 2013), at 5, 15, and 25ºC at 60% of WHC. The short

196   timescale used was chosen to prevent acclimation to the assay temperatures used in the

197   laboratory. The incubation temperatures (5, 15 y 25ºC) were selected to cover the range

198   spanned by the MAT values of the eight chronosequences studied (from 8.7 to 19.55ºC).

199   Additionally, such incubation temperatures are similar to the ones used in previous

200   studies (Bradford et al., 2008, 2019; Dacal et al., 2019). Soil samples were incubated in

201   96-deepwell microplates (1.3 mL wells) by adding *c.* 0.5 g soil per well. All soil samples

202   were run in triplicate (laboratory replicates). Incubations were performed in growth

203   chambers under dark conditions and 100% air humidity. Microplates were covered with

204   polyethylene film to prevent soil drying but to allow gas exchange.

205   Soil respiration rates were measured using a modified MicroResp^{TM} technique (C.

206   D. Campbell, Chapman, Cameron, Davidson, & Potts, 2003). Glucose at a dose of 10 mg

207   C g^{-1} dry soil was used as a substrate. It was used to avoid substrate limitation on soil

208   respiration rates (Bradford et al., 2010), as the dose used in our study is supposed to

209   exceed microbial demand (Davidson, Janssens, & Luo, 2006). Soils were incubated at the

210   particular assay temperature (5, 15, and 25ºC) for ten hours. However, the detection plates

211   used to measure soil respiration were only incubated during the last 5 hours to avoid the

212   oversaturation of the detection solution. The absorbance of the detection plate was read

213   immediately before and after its use. Three analytical replicates were run per sample, and

214   the mean of these repeats per assay temperature was used as the observation of potential

215   respiration rate for each sample.

216

217   *Statistical analyses*

218   We evaluated the importance of soil properties in driving the responses of soil

219   respiration to changes in temperature. To do that, we firstly analysed soil respiration

220   responses to assay temperature within and across chronosequences. For within

221   chronosequences analyses, we built eight linear regression models (LM) including soil

222   development stage, assay temperature, the interaction between both variables, SOC,

223   texture, pH, soil P, and microbial biomass as fixed factors. Soil properties were removed

224   until there is a low collinearity between them and soil development stage (i.e. square-root

9

225   VIFs <2, Bradford et al., 2017). However, to evaluate the assay temperature effect on soil

226   respiration across chronosequences, we performed a linear mixed-effects model (LMM)

227   with soil development stage (in years), MAT, assay temperature, SOC, texture, pH, soil

228   P, and microbial biomass as fixed factors, and the chronosequence identity as a random

229   factor. We then compared whether there were differences in the magnitude of the effect

230   of assay temperature on soil respiration among chronosequences, using the standardized

231   coefficients of assay temperature obtained in the within chronosequence LMs. Finally,

232   we tested whether biotic and abiotic factors drive the response of soil respiration to

233   temperature. For doing so, we built LMMs that incorporated soil development stage (in

234   years) and assay temperature as fixed factors, and chronosequence identity as a random

235   factor using different subsets of data. Specifically, we grouped the chronosequences in

236   two levels according to each of the environmental conditions and soil properties

237   considered such as the origin of the chronosequence, MAT, SOC, texture, pH, P, and

238   microbial biomass. Then, we ran the model described above separately for each group of

239   data to evaluate how the magnitude of the effect of temperature on soil respiration

240   changes between the models using groups of data with contrasting environmental

241   conditions and soil properties. In most cases, each of the groups of data included four

242   chronosequences each (i.e., half of the chronosequences studied each). We classified each

243   chronosequence by the mean across the whole chronosequence of each of the selected

244   variables to avoid separating different stages of the same chronosequence in different

245   groups. The threshold to distinguish between both groups of each category was

246   established at the value closest to the mean among all observations that allow having the

247   same or almost the same number of chronosequences in each group.

248   On the other hand, to evaluate the effect of soil development on soil respiration

249   and its response to temperature we used the same approach described above for evaluating

10

250   the effect of assay temperature on soil respiration (LMs within chronosequences and an

251   LMM across chronosequences). Additionally, we used two different approximations for

252   soil development stage depending on the spatial scale. When analysing each

253   chronosequence separately, we used the stage (from 1 to 6) to address the effects of soil

254   development stage (Delgado-Baquerizo et al., 2019; Laliberté et al., 2013; Wardle,

255   Bardgett, Walker, & Bonner, 2009; Wardle, Walker, & Bardgett, 2004), given the high

256   level of uncertainty in assigning precise ages for many of the chronosequences studied

257   (Wardle, Walker, et al., 2004). However, when analysing across chronosequences, we

258   used the estimation of years as a measure of soil development stage (Crews et al., 1995;

259   Tarlera, Jangid, Ivester, Whitman, & Williams, 2008) to compare chronosequences

260   covering contrasting ranges of soil development stages.

261   Finally, to test whether the thermal acclimation of soil respiration to the ambient

262   temperature regime influences the soil respiration responses to assay temperature over

263   soil development, we performed an LMM as that described above. We statistically

264   controlled for differences in soil microbial biomass by including it as a covariate in the

265   model (Bradford et al., 2019, 2010; Dacal et al., 2019). All the statistical analyses were

266   conducted using the R 3.3.2 statistical software (R Core Team, 2015). The linear mixed-

267   effects models (LMMs) were fitted with a Gaussian error distribution using the 'lmer'

268   function of the lme4 package (Bates, Mächler, Bolker, & Walker, 2015). Response data

269   were transformed by taking the natural logarithm of each value when needed to meet the

270   assumptions of normality and homogeneity of variance.

271

272   **Results**

273   *Effects of abiotic and biotic drivers on soil respiration responses to temperature*

274   First, we found a consistent and positive significant effect of assay temperature on soil

275   respiration both within and across chronosequences (P < 0.001 in all cases, Figure 1 and

276   2, Table S1 and S2, respectively). The magnitude of this positive effect varied between

277   chronosequences (Figure 3). For instance, the assay temperature effect in a Mediterranean

278   sedimentary chronosequence from California (CAL) was 84.5% (95% CI= 51.07%-

279   117.96%) and 144.44% (95% CI = 94.63% - 146.63%) greater than in a Mediterranean

280   sandy chronosequence in Western Australia (WA) or a volcanic forest chronosequence

281   from Hawaii (HA), respectively (Figure 3).

282   The effect of assay temperature on soil respiration was consistently positive across

283   all the climatic conditions and soil properties evaluated (Figure 4). However,

284   environmental variables altered the magnitude of the assay temperature effect on soil

285   respiration. For instance, the effect of assay temperature was 12.08% (95% CI = 5.40% -

286   18.77%) lower for the volcanic chronosequences compared with the ones with a

287   sedimentary or a dune origin (Figure 4). However, the greatest differences on the

288   magnitude of such effect were observed in sites with contrasting soil texture (Figure 4).

289   Specifically, soils with > 20% silt and clay showed a 43.65% (95% CI = 35.18% -

290   52.12%) higher effect of assay temperature on soil respiration compared with soils with

291   < 20% silt and clay. On the other hand, the effect of assay temperature on soil respiration

292   was 23% (95% CI = 15% - 30%) greater in sites with higher SOC, microbial biomass,

293   and soil P content compared with soils with lower values of such soil properties (Figure

294   4). The magnitude of the assay temperature effect slight differed (i.e., 9% difference; 95%

295   CI = 5% - 17%) between soils with contrasting pH values (Figure 4). On the other hand,

296   the magnitude of the assay temperature effect on soil respiration did not change across

297   soils with contrasting MAT values (Figure 4).

298

299   *Effect of soil development on soil respiration and its response to temperature*

300   When analysing the effect of soil development on soil respiration at every

301   chronosequence separately, we did not observe any significant effect in five out of eight

302   chronosequences (Figure 1, Table S1). We found higher soil respiration rates in older

303   soils than in younger ones in three volcanic chronosequences located in temperate and

304   tropical forests in Chile (i.e., CH, P = 0.016, Figure 1, Table S1), Spain (i.e., CI, P =

305   0.049, Figure 1, Table S1) and Hawaii (i.e., HA, P = 0.009, Figure 1, Table S1). We also

306   observed a positive effect of soil development on respiration across chronosequences (P

307   = 0.004, Figure 2, Table S2). Regardless these results, soil development did not affect

308   respiration responses to temperature neither within nor across chronosequences, as the

309   interaction between soil development and assay temperature was not significant (P > 0.05

310   in all cases).

311

312   *Thermal acclimation of soil respiration to ambient temperature regimes*

313   The site MAT did not affect soil respiration (P = 0.487, Table S2) nor its response to

314   assay temperature (MAT $\times$ assay temperature, P = 0.807), suggesting the absence of

315   acclimation of soil respiration to the ambient temperature regime. The lack of MAT effect

316   on soil respiration was constant across all soil development stages (MAT $\times$ soil

317   development, P = 0.122).

318

319

13

320 **Table 1. Climate origin, vegetation type, age, and environmental conditions for**

321 **eight soil chronosequences**. Chronosequence origin describes the major causal agent of

322 each chronosequence. Climate and vegetation types show the main climatic conditions

323 and the dominant vegetation for each chronosequence. MAT= Mean annual

324 temperature, MAP= Mean annual precipitation, SOC= Soil organic carbon, Soil P= Soil

325 phosphorus, and Microbial biomass= Sum of all bacterial, fungi, and other soil

326 microbial biomarkers.

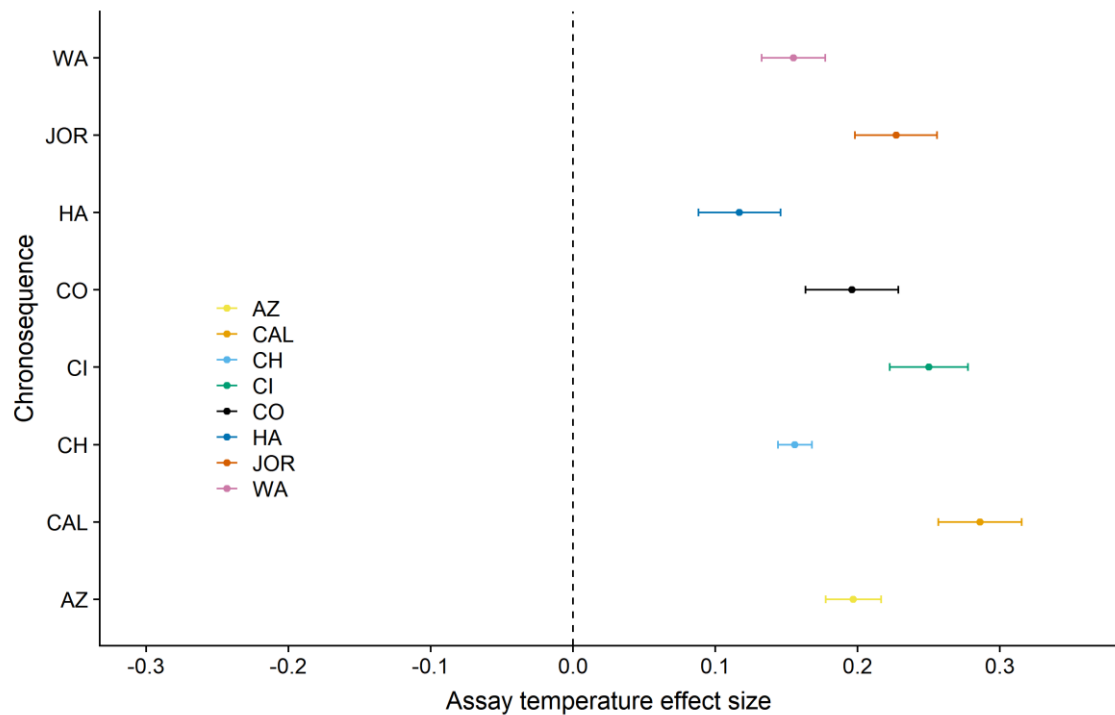| Chronosequences								
Label	AZ	CAL	CH	CI	CO	HA	JOR	WA
Country	USA	USA	Chile	Spain	USA	USA	USA	Australia
Name	SAGA	Merced	Conguillio	La Palma	Coal Creek	Hawaii	Jornada Desert	Jurien Bay
Age	0.9-3000ky	0.1-3000ky	0.06-5000ky	0.5-1700ky	5-2000ky	0.3-4100ky	1.1-25ky	0.1-2000ky
Chronosequence origin	Volcanic	Sedimentary	Volcanic	Volcanic	Sedimentary	Volcanic	Sedimentary	Sand dunes
Climate	Arid	Temperate	Temperate	Temperate	Continental	Tropical	Arid	Temperate
Vegetation type	Forests	Grasslands	Forests	Forests	Grasslands	Forests	Forblands	Shrublands
MAT (ºC)	10.4±1.4	16.3±0.3	8.7±0.8	13.8±1.6	9.3±0.5	15.9±0.5	15.43±0.0	19.6±0.1
MAP (mm)	421±57	378±64	1907±16	451±34	482±7	1895±380	276±4	558±4
SOC (%)	2.6±1.9	4.9±2.9	3.8±3.5	5.1±5.5	3.7±1.0	25.3±12.5	0.6±0.2	1.2±0.6
Texture (% clay+silt)	40.4±28.1	44.1±17	8.3±2.6	23.1±11.7	34.6±3.3	14.3±3.8	18.9±3.5	3.8±1.4
pH	7.2±0.3	6±0.8	5.8±0.4	6.7±0.4	6±0.3	4.2±0.6	8.1±0.4	7.3±1.2
Soil P (%)	0.09±0.02	0.06±0.03	0.02±0.01	0.20±0.05	0.06±0.01	0.07±0.03	0.05±0.01	0.02±0.02
Microbial biomass (nmolPLFA/g soil)	356±371	1733±886	1293±1752	622±738	667±289	5991±1784	126±52	112±63

327

14
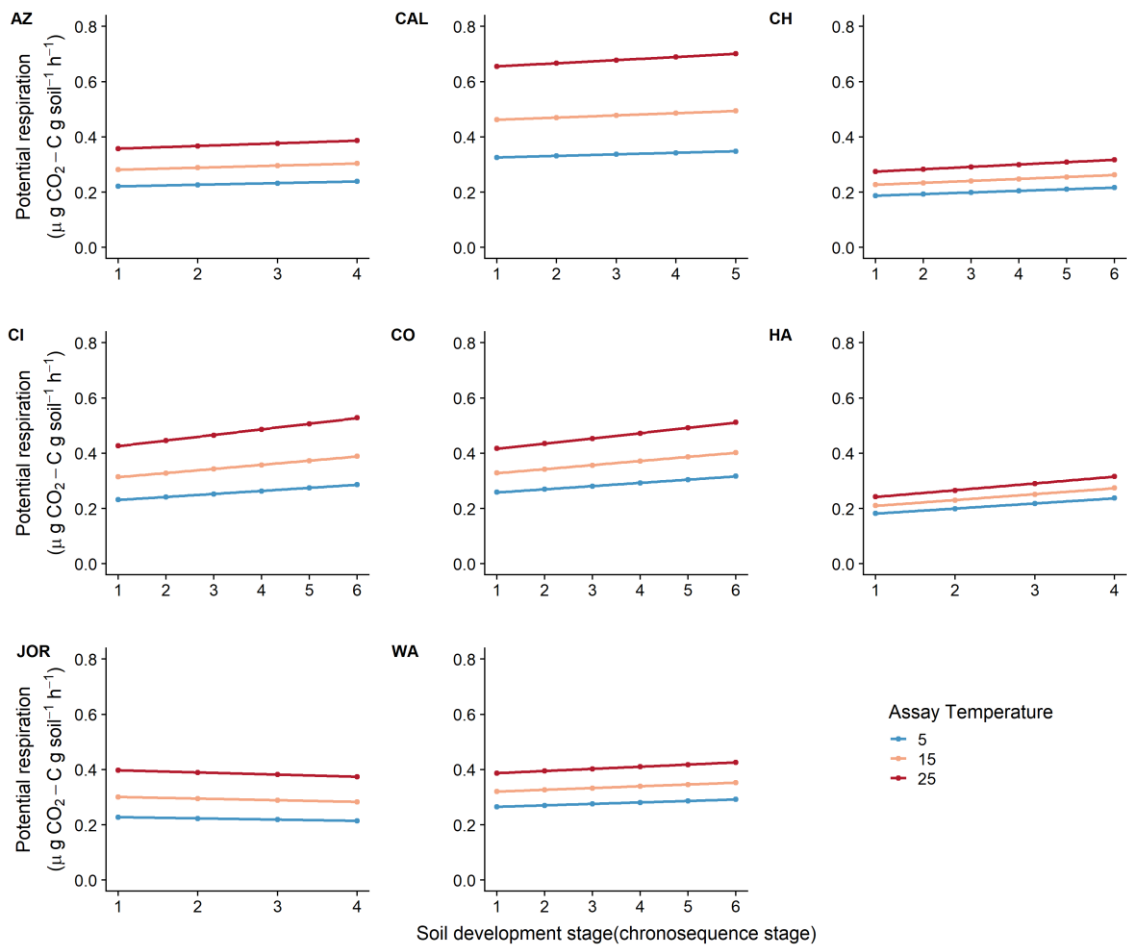
Figure 1. Estimated effects of assay temperature and soil development stage (chronosequence stage) on potential respiration rates at a controlled biomass value and with substrate in excess within chronosequence. The effects were estimated using coefficients from the linear model used for each chronosequence (Table S1). Three outcomes of this model are shown, one for each temperature assayed (i.e. 5, 15, and 25ºC). Specifically, we estimated soil respiration rates using the unstandardized coefficients of the model, along with the mean value of the soil properties included in the model of each chronosequence, one of the assay temperatures and one of the soil development stages observed in each chronosequence.

15

341

342

343
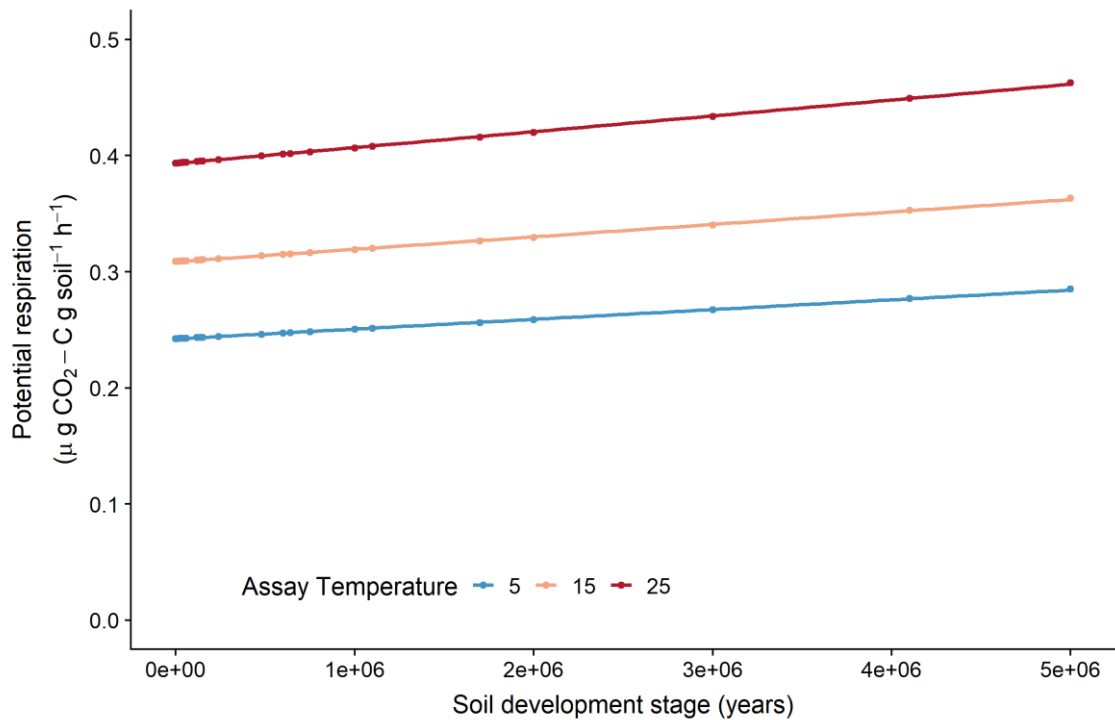
Figure 2. Estimated effects of assay temperature and soil development stage (years) on potential respiration rates at a controlled biomass value and with substrate in excess across chronosequences. The effects were estimated using coefficients from the linear mixed-effects model (Table S2). Three outcomes of this model are shown, one for each temperature assayed (i.e. 5, 15, and 25ºC). Specifically, we estimated soil respiration rates using the unstandardized coefficients of the model, along with the mean value of the soil properties included in the model of each chronosequence, one of the assay temperatures and one of the soil development stages observed across all sites.
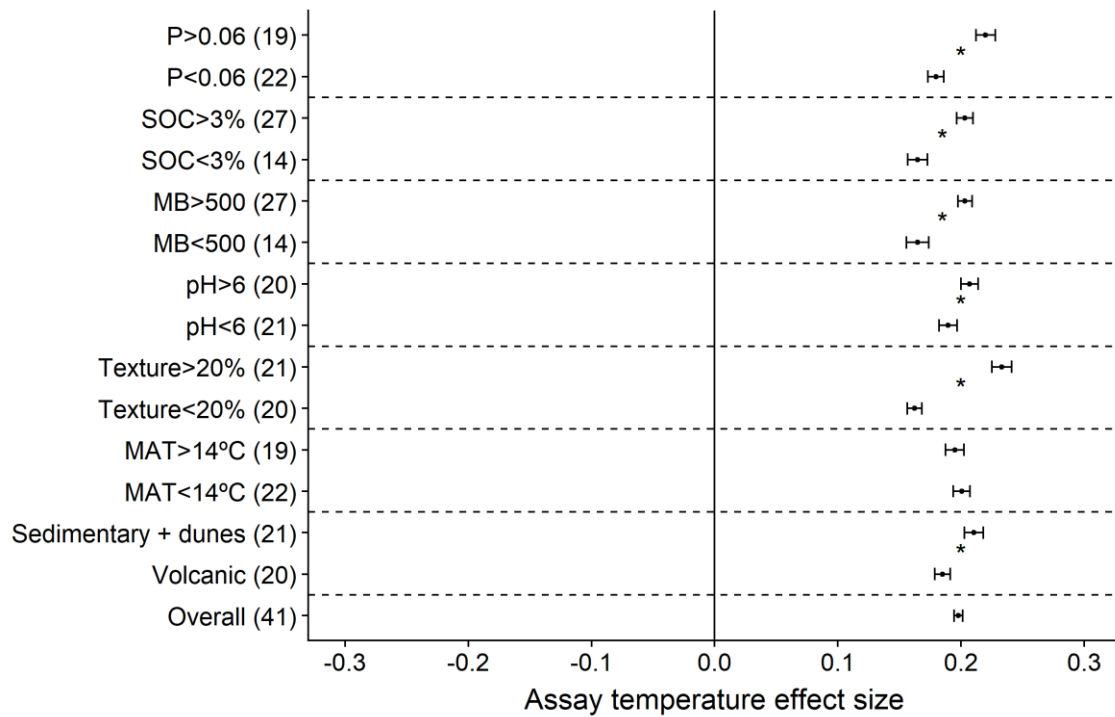
352

353

354

Figure 3. Comparison on the magnitude of the effects of assay temperature on soil respiration among the eight chronosequences studied. The points represent the mean and the error bars correspond to the 95% CI. AZ, JOR, HA presented four stages (n=4), CAL had five stages (n=5) and the rest showed six stages (n= 6).

361

362

Figure 4. Comparison of the effects of assay temperature on soil respiration among

different environmental conditions. The points represent the mean and the error bars

correspond to the 95% CI. Asterisks denote significant differences at $p < 0.05$. The total

n was shown in brackets and it was the result of the number of stages within the

chronosequences x the number of chronosequences included in each level of the

classification. MAT= mean annual temperature, Texture=% of clay + silt, MB= total

microbial biomass, SOC= soil organic carbon, and P= soil phosphorus. Volcanic and

sedimentary + dunes refer to the different origins observed across the eight

chronosequences studied.

372

373

374

375

376

18

Discussion

Our study shows that elevated temperatures consistently increased soil heterotrophic respiration rates across contrasting soil chronosequences. Although older soils tended to support higher soil respiration–especially in volcanic, temperate, and tropical forests–, our findings indicate that soil development did not alter the relationship between heterotrophic respiration and temperature. Conversely, soil properties such as SOC, the amount of clay and silt, pH, microbial biomass, and P content had a significant control on the magnitude of positive temperature effects on soil respiration. Overall, these findings provide new insights into the role of soil properties in driving soil respiration responses to temperature, which are essential to project the magnitude of the land C-climate feedback accurately.

We observed a consistent positive effect of assay temperature on soil respiration within and across chronosequences. Such results agree with previous literature addressing the effects of temperature on soil organic matter decomposition and soil respiration rates (Davidson & Janssens, 2006; Kirschbaum, 2006; Lloyd & Taylor, 1994; Min et al., 2020). The enhancing effect of temperature on soil respiration is largely driven by the acceleration of microbial metabolic rates (Hochachka & Somero, 2002). Importantly, the effect of elevated temperatures on soil respiration was positive in all chronosequences studied, suggesting that this enhancing effect, at least in our study, is independent of the ecosystem type. However, certain chronosequences showed differences in the magnitude of the assay temperature effect between them. That could be explained by our results indicating that environmental conditions and soil biotic and abiotic properties have the ability to determine the magnitude of the consistently positive effect of temperature on soil respiration. For instance, soil respiration responses to assay temperature differed

19

402   depending on the origin of the chronosequence considered. Such results suggest that

403   parent material also influences soil respiration responses to temperature. An explanation

404   for these observed differences could be that soil develops differently according to several

405   factors such as soil parent material (Alfaro et al., 2017; Carlson, Flagstad, Gillet, &

406   Mitchell, 2010; Jenny, 1941). Moreover, we found that the magnitude of the effect of

407   assay temperature was lower in sites with less soil P available. Such results indicate that

408   this nutrient is necessary to sustain microbial activity (Liu, Gundersen, Zhang, & Mo,

409   2012). Further, we also observed differences in the magnitude of the response of soil

410   respiration to elevated temperatures between sites with contrasting amounts of clay and

411   silt. These differences could be caused by the fact that water availability in the soil is

412   expected to increase when the amount of clay and silt in the soil rises (Delgado-Baquerizo

413   et al., 2013), accelerating microbial activity (Karhu et al., 2014; Luo, Wan, Hui, &

414   Wallace, 2001). However, this effect of the amount of clay and silt on soil respiration

415   responses to temperature could disappear at high amounts of clay and silt, as clay and silt

416   may limit microbial access to SOC. Also, the magnitude of the effect of assay

417   temperature on soil respiration increased in sites with greater soil pH, as the microbial

418   activity is negatively affected by acidification (Reth, Reichstein, & Falge, 2005; Rustad

419   et al., 2000). Finally, our results indicated that soil respiration response to assay

420   temperature increases with substrate availability (i.e., SOC) and microbial biomass. This

421   increase in soil respiration rates in response to temperature under high SOC and microbial

422   biomass conditions may cause the acceleration of microbial activity and, subsequently, a

423   substrate depletion and an important reduction of microbial biomass (Cavicchioli et al.,

424   2019). Thus, our findings provide new insights about how soil properties modulate the

425   magnitude of the consistently enhancing effect of temperature on soil respiration.

426

427 In three out of the eight chronosequences evaluated, we found a significant

428 positive effect of soil development on soil respiration rates. Interestingly, all these

429 chronosequences shared a volcanic origin. The different effect of soil development on

430 soil respiration found across chronosequences may be mediated by contrasting parent

431 material between them, leading to variations in the soil development trajectories followed

432 by the eight chronosequences evaluated. The differences in the range of years covered by

433 each of the chronosequences evaluated may also influence the effect of soil development

434 on soil respiration. Such contrasting results observed when analysing each

435 chronosequence separately limits our capacity to draw more general conclusions about

436 how soil C losses to the atmosphere via soil respiration change over soil development,

437 specially under a warming scenario. Such limitations are similar to the ones found in

438 previous studies (J. L. Campbell & Law, 2005; Law et al., 2003; Saiz et al., 2006; Tang

439 et al., 2008; Wang et al., 2002) conducted on a single chronosequence and covering a

440 narrow range of soil development stages (from years to centuries). Therefore, when

441 evaluating soil development effect on soil respiration across chronosequences, we

442 observed a significant enhancing effect of soil development stage on soil respiration. Our

443 findings improve our knowledge about the effect of soil development stage on soil

444 respiration across large spatial scales including different ecosystem types with contrasting

445 environmental conditions and soil properties. Specifically, our results indicated that elder

446 soils have greater soil C losses to the atmosphere than younger ones. Such greater soil

447 respiration rates found in elder soils within some and across chronosequences may be

448 explained by the increase in soil C easily releasable from mineral-SOC associations in

449 soils that had experienced higher weathering (Keiluweit et al., 2015). Conversely, we

450 observed that soil development did not modulate the magnitude of the effect of assay

451 temperature on soil respiration, as the interaction between soil development stage and

21

452   assay temperature was not significant either within or across chronosequences. These

453   results indicate that, no matter how old soils are, soil carbon stocks are highly sensitive

454   to increases in temperature associated with climate change. Thus, although worldwide

455   soils show contrasting ages (Laliberté et al., 2013; Wardle, Bardgett, Walker, Peltzer, &

456   Lagerström, 2008), they present similar soil respiration responses to temperature. Further,

457   the assay temperature effect was at least three times larger in magnitude than the effect

458   of soil development stage on soil respiration. Such results agree with previous studies

459   showing pronounced soil respiration responses to assay temperature (Bradford et al.,

460   2010), especially across large temperature ranges such as those used in our incubations

461   (i.e. from 5 to 25ºC). Consequently, our study supports that soil microbial communities

462   from very different ecosystem types are capable of rapidly responding to increasing

463   temperature, resulting in greater soil respiration.

464

465   A growing body of evidence suggests that thermal acclimation of soil microbial

466   respiration to temperature can be found across large spatial scales (Bradford et al., 2019,

467   2010; Dacal et al., 2019; Ye, Bradford, Maestre, Li, & García-Palacios, 2020). However,

468   we did not find a significant effect of MAT, suggesting that soil respiration is not

469   acclimated to the ambient temperature regime at our sites. This apparent disagreement

470   may be due to the shorter MAT gradient evaluated in our study (i.e., from 8.7ºC to

471   19.55ºC) compared with previous ones (i.e., from -2 to 28ºC; Bradford et al., 2019; Dacal

472   et al., 2019; Ye, Bradford, Maestre, Li, & García-Palacios, 2020). Nevertheless, our

473   results are similar to other cross-biome studies (Carey et al., 2016; Karhu et al., 2014),

474   and may be the result of negligible effects of thermal acclimation on soil respiration when

475   compared with overarching factors such as assay temperature (Hochachka & Somero,

476   2002).

477   In conclusion, we found that assay temperature consistently enhanced soil

478   respiration across contrasting chronosequences. On the other hand, we observed no

479   evidence of thermal acclimation of soil respiration to the ambient temperature regime.

480   Although we observed a positive effect of soil development on soil respiration, it did not

481   change the magnitude of the assay temperature effect. Despite the clear and positive effect

482   of assay temperature on soil respiration observed, soil properties such as SOC, texture,

483   pH, P content, and microbial biomass significantly modified the magnitude of this

484   positive soil respiration response to temperature. Our findings emphasize the role of biotic

485   and biotic soil properties as drivers of soil respiration responses to temperature across

486   biomes and provide new insights to better understand the magnitude of the land C-Climate

487   feedback and to establish accurate greenhouse emission targets.

488

502 also want to thank Lynn Riedel, Julie Larson, Katy Waechter and Drs. David Buckner

503 and Brian Anacker for their help with soil sampling in the chronosequence from

504 Colorado, and to the City of Boulder Open Space and Mountain Parks for allowing us to

505 conduct these collections.

506

507 **Authorship**

508 M.D., M.D.-B. and P.G.P developed the original idea of the analyses presented in the

509 manuscript. M.D.-B. designed the field study and wrote the grant that funded the work.

510 J.B. conducted the laboratory work with inputs from M.D.-B and A.G. M.D. performed

511 the statistical analyses, with inputs from M.D.-B., F.T.M and P.G.P. All authors included

512 A.A.B. contributed to data interpretation. M.D. wrote the first version of the manuscript,

513 which was revised by all co-authors.

514

515 **Competing interests**

516 The authors declare no competing financial interests.

517

518 **References**

519 Alfaro, F. D., Manzano, M., Marquet, P. A., & Gaxiola, A. (2017). Microbial

520   communities in soil chronosequences with distinct parent material: the effect of

521   soil pH and litter quality. *Journal of Ecology*, *105*(6), 1709–1722.

522   https://doi.org/10.1111/1365-2745.12766

523 Anderson, J. M., & Ingram, J. S. I. (1993). *Tropical soil biology and fertility: A*

524   *handbook of methods.* Oxford: CAB International.

525 Arora, V. K., Boer, G. J., Friedlingstein, P., Eby, M., Jones, C. D., Christian, J. R., …

526   Wu, T. (2013). Carbon-concentration and carbon-climate feedbacks in CMIP5

24

527   earth system models. *Journal of Climate*, *26*(15), 5289–5314.

528   https://doi.org/10.1175/JCLI-D-12-00494.1

529   Atkin, O. K., & Tjoelker, M. G. (2003). Thermal acclimation and the dynamic response

530   of plant respiration to temperature. *Trends in Plant Science*, *8*(7), 343–351.

531   https://doi.org/10.1016/S1360-1385(03)00136-5

532   Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-

533   effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48.

534   https://doi.org/10.18637/jss.v067.i01

535   Bligh, E. G., & Dyer, W. J. (1959). A rapid method of total extration and purification.

536   *Canadian Journal of Biochemistry and Physiology*, *37*(8), 911–917.

537   Bond-Lamberty, B., Bailey, V. L., Chen, M., Gough, C. M., & Vargas, R. (2018).

538   Globally rising soil heterotrophic respiration over recent decades. *Nature*,

539   *560*(7716), 80–83. https://doi.org/10.1038/s41586-018-0358-x

540   Bond-Lamberty, B., & Thomson, A. (2010). Temperature-associated increases in the

541   global soil respiration record. *Nature*, *464*(7288), 579–582.

542   https://doi.org/10.1038/nature08930

543   Bradford, M. A., Ciska, G. F., Bonis, A., Bradford, E. M., Classen, A. T., Cornelissen,

544   J. H. C., … Van Der Putten, W. H. (2017). A test of the hierarchical model of litter

545   decomposition. *Nature Ecology and Evolution*, *1*(12), 1836–1845.

546   https://doi.org/10.1038/s41559-017-0367-4

547   Bradford, M. A., Davies, C. A., Frey, S. D., Maddox, T. R., Melillo, J. M., Mohan, J. E.,

548   … Wallenstein, M. D. (2008). Thermal adaptation of soil microbial respiration to

549   elevated temperature. *Ecology Letters*, *11*(12), 1316–1327.

550   https://doi.org/10.1111/j.1461-0248.2008.01251.x

551   Bradford, M. A., McCulley, R. L., Crowther, T. W., Oldfield, E. E., Wood, S. A., &

Fierer, N. (2019). Cross-biome patterns in soil microbial respiration predictable from evolutionary theory on thermal adaptation. *Nature Ecology & Evolution*, *3*(2), 223–231. https://doi.org/10.1038/s41559-018-0771-4

Bradford, M. A., Watts, B. W., & Davies, C. A. (2010). Thermal adaptation of heterotrophic soil respiration in laboratory microcosms. *Global Change Biology*, *16*(5), 1576–1588. https://doi.org/10.1111/j.1365-2486.2009.02040.x

Bradford, M. A., Wieder, W. R., Bonan, G. B., Fierer, N., Raymond, P. A., & Crowther, T. W. (2016). Managing uncertainty in soil carbon feedbacks to climate change. *Nature Climate Change*, *6*(8), 751–758. https://doi.org/10.1038/nclimate3071

Buyer, J. S., & Sasser, M. (2012). High throughput phospholipid fatty acid analysis of soils. *Applied Soil Ecology*, *61*, 127–130.

Campbell, C. D., Chapman, S. J., Cameron, C. M., Davidson, M. S., & Potts, J. M. (2003). A rapid microtiter plate method to measure carbon dioxide evolved from carbon substrate amendments so as to determine the physiological profiles of soil microbial communities by using whole soil. *Applied and Environmental Microbiology*, *69*(6), 3593–3599. https://doi.org/10.1128/AEM.69.6.3593-3599.2003

Campbell, J. L., & Law, B. E. (2005). Forest soil respiration across three climatically distinct chronosequences in Oregon. *Biogeochemistry*, *73*(1), 109–125. https://doi.org/10.1007/s10533-004-5165-9

Carey, J. C., Tang, J., Templer, P. H., Kroeger, K. D., Crowther, T. W., Burton, A. J., … Tietema, A. (2016). Temperature response of soil respiration largely unaltered with experimental warming. *Proceedings of the National Academy of Sciences*, *113*(48), 13797–13802. https://doi.org/10.1073/pnas.1605365113

Carlson, M. L., Flagstad, L. A., Gillet, F., & Mitchell, E. A. D. (2010). Community

577   development along a proglacial chronosequence: Are above-ground and below-

578   ground community structure controlled more by biotic than abiotic factors?

579   *Journal of Ecology*, *98*(5), 1084–1095. https://doi.org/10.1111/j.1365-

580   2745.2010.01699.x

581 Cavicchioli, R., Ripple, W. J., Timmis, K. N., Azam, F., Bakken, L. R., Baylis, M., …

582   Webster, N. S. (2019). Scientists' warning to humanity: microorganisms and

583   climate change. *Nature Reviews Microbiology*, *17*(9), 569–586.

584   https://doi.org/10.1038/s41579-019-0222-5

585 Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, A., … Thornton, P.

586   (2014). Carbon and other biogeochemical cycles. In *Climate Change (2013):The*

587   *physical science basis. Contribution of working group I to the fifth assessment*

588   *report of the Intergovernmental Panel on Climate Change* (pp. 465–570).

589   Cambridge University Press.

590 Crews, T. E., Kitayama, K., Fownes, J. H., Riley, R. H., Herbert, D. A., Mueller-

591   Dombois, D., & Vitousek, P. M. (1995). Changes in soil phosphorus fractions and

592   ecosystem dynamics across a long chronosequence in Hawaii. *Ecology*, *76*(5),

593   1407–1424. https://doi.org/10.2307/1938144

594 Dacal, M., Bradford, M. A., Plaza, C., Maestre, F. T., & García-Palacios, P. (2019). Soil

595   microbial respiration adapts to ambient temperature in global drylands. *Nature*

596   *Ecology & Evolution*, *3*(2), 232–238. https://doi.org/10.1038/s41559-018-0770-5

597 Davidson, E. A., & Janssens, I. A. (2006). Temperature sensitivity of soil carbon

598   decomposition and feedbacks to climate change. *Nature*, *440*.

599   https://doi.org/10.1038/nature04514

600 Davidson, E. A., Janssens, I. A., & Luo, Y. (2006). On the variability of respiration in

601   terrestrial ecosystems : moving beyond Q10. *Global Change Biology*, *12*, 154–164.

602   https://doi.org/10.1111/j.1365-2486.2005.01065.x

603   Delgado-Baquerizo, M., Bardgett, R. D., Vitousek, P. M., Maestre, F. T., Williams, M.

604   A., Eldridge, D. J., … Fierer, N. (2019). Changes in belowground biodiversity

605   during ecosystem development. *Proceedings of the National Academy of Sciences*

606   *of the United States of America*, *116*(14), 6891–6896.

607   https://doi.org/10.1073/pnas.1818400116

608   Delgado-Baquerizo, M., Maestre, F. T., Gallardo, A., Bowker, M. A., Wallenstein, M.

609   D., Quero, J. L., … Zaady, E. (2013). Decoupling of soil nutrient cycles as a

610   function of aridity in global drylands. *Nature*, *502*(7473), 672–676.

611   https://doi.org/10.1038/nature12670

612   Delgado-Baquerizo, M., Reich, P. B., Bardgett, R. D., Eldridge, D. J., Lambers, H.,

613   Wardle, D. A., … Fierer, N. (2020). The influence of soil age on ecosystem

614   structure and function across biomes. *Nature Communications*, *11*(1), 1–14.

615   https://doi.org/10.1038/s41467-020-18451-3

616   Doetterl, S., Berhe, A. A., Arnold, C., Bodé, S., Fiener, P., Finke, P., … Boeckx, P.

617   (2018). Links among warming, carbon and microbial dynamics mediated by soil

618   mineral weathering. *Nature Geoscience*, *11*(8), 589–593.

619   https://doi.org/10.1038/s41561-018-0168-7

620   Exbrayat, J. F., Pitman, A. J., & Abramowitz, G. (2014). Response of microbial

621   decomposition to spin-up explains CMIP5 soil carbon range until 2100.

622   *Geoscientific Model Development*, *7*(6), 2683–2692. https://doi.org/10.5194/gmd-

623   7-2683-2014

624   Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate

625   surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–

626   4315. https://doi.org/10.1002/joc.5086

627 Frostegård, A., & Bååth, E. (1996). The use of phospholipid fatty acid analysis to

628   estimate bacterial and fungal biomass in soil. *Biology and Fertility of Soils*, *22*(1–

629   2), 59–65. https://doi.org/10.1007/s003740050076

630 Guo, H., Ye, C., Zhang, H., Pan, S., Ji, Y., Li, Z., … Hu, S. (2017). Long-term nitrogen

631   & phosphorus additions reduce soil microbial respiration but increase its

632   temperature sensitivity in a Tibetan alpine meadow. *Soil Biology and*

633   *Biochemistry*, *113*, 26–34. https://doi.org/10.1016/j.soilbio.2017.05.024

634 Hartley, I. P., Hopkins, D. W., Garnett, M. H., Sommerkorn, M., & Wookey, P. A.

635   (2008). Soil microbial respiration in arctic soil does not acclimate to temperature.

636   *Ecology Letters*, *11*(10), 1092–1100. https://doi.org/10.1111/j.1461-

637   0248.2008.01223.x

638 Hochachka, P. W., & Somero, G. N. (2002). *Biochemical adaptation: mechanism and*

639   *process in physiological evolution.* New York: Oxford University Press.

640 Jenny, H. (1941). *Factors of soil formation: a system of quantitative pedology*.

641   *Geographical Review*. McGraw-Hill. https://doi.org/10.2307/211491

642 Karhu, K., Auffret, M. D., Dungait, J. A., Hopkins, D. W., Prosser, J. I., Singh, B. K.,

643   … Hartley, I. P. (2014). Temperature sensitivity of soil respiration rates enhanced

644   by microbial community response. *Nature*, *513*(7516), 81–84.

645   https://doi.org/10.1038/nature13604

646 Keiluweit, M., Bougoure, J. J., Nico, P. S., Pett-Ridge, J., Weber, P. K., & Kleber, M.

647   (2015). Mineral protection of soil carbon counteracted by root exudates. *Nature*

648   *Climate Change*, *5*(6), 588–595. https://doi.org/10.1038/nclimate2580

649 Kettler, T. A., Doran, J. W., & Gilbert, T. L. (2001). Simplified method for soil particle-

650   size determination to accompany soil-quality analyses. *Soil Science Society of*

651   *America Journal*, *65*, 849–852.

652 Kirschbaum, M. U. F. (2006). The temperature dependence of organic-matter

653   decomposition — still a topic of debate. *Soil Biology and Biochemistry*, *38*, 2510–

654   2518. https://doi.org/10.1016/j.soilbio.2006.01.030

655 Laliberté, E., Grace, J. B., Huston, M. A., Lambers, H., Teste, F. P., Turner, B. L., &

656   Wardle, D. A. (2013). How does pedogenesis drive plant diversity? *Trends in*

657   *Ecology and Evolution*, *28*(6), 331–340. https://doi.org/10.1016/j.tree.2013.02.008

658 Law, B. E., Sun, O. J., Campbell, J., Van Tuyl, S., & Thornton, P. E. (2003). Changes in

659   carbon storage and fluxes in a chronosequence of ponderosa pine. *Global Change*

660   *Biology*, *9*(4), 510–524. https://doi.org/10.1046/j.1365-2486.2003.00624.x

661 Liu, L., Gundersen, P., Zhang, T., & Mo, J. (2012). Effects of phosphorus addition on

662   soil microbial biomass and community composition in three forest types in tropical

663   China. *Soil Biology and Biochemistry*, *44*(1), 31–38.

664   https://doi.org/10.1016/j.soilbio.2011.08.017

665 Lloyd, J., & Taylor, J. A. (1994). On the temperature dependence of soil respiration.

666   *Functional Ecology*, *8*(3), 315–323.

667 Luo, Y., Wan, S., Hui, D., & Wallace, L. L. (2001). Acclimatization of soil respiration

668   to warming in a tall grass prairie. *Nature*, *413*(October), 622–625.

669   https://doi.org/10.1038/35098065

670 Min, K., Berhe, A. A., Khoi, C. M., van Asperen, H., Gillabel, J., & Six, J. (2020).

671   Differential effects of wetting and drying on soil CO2 concentration and flux in

672   near-surface vs. deep soil layers. *Biogeochemistry*, *148*(3), 255–269.

673   https://doi.org/10.1007/s10533-020-00658-7

674 Olsen, S. R., Cole, C. V., Watanabe, F. S., & Dean, L. A. (1954). Estimation of

675   available phosphorus in soils by extraction with sodium bicarbonate. *USDA*

676   *Circular 939. U.S. Government Printing Office*.

677   Orwin, K. H., Wardle, D. A., Greenfield, L. G., Setälä, H., Orwin, K. H., Wardle, D. A.,

678   & Greenfield, L. G. (2006). Context-dependent changes in the resistance and

679   resilience of soil microbes to an experimental distrubance for three primary plant

680   chronosequences. *Oikos*, *112*(1), 196–208.

681   R Core Team. (2015). R: A language and environment for statistical computing.

682   Vienna, Austria: R Foundation for Statistical Computing. Retrieved from

683   http://www.r-project.org/

684   Rasmussen, C., Heckman, K., Wieder, W. R., Keiluweit, M., Lawrence, C. R., Berhe,

685   A. A., … Wagai, R. (2018). Beyond clay: towards an improved set of variables for

686   predicting soil organic matter content. *Biogeochemistry*, *137*(3), 297–306.

687   https://doi.org/10.1007/s10533-018-0424-3

688   Reth, S., Reichstein, M., & Falge, E. (2005). The effect of soil water content, soil

689   temperature, soil pH-value and the root mass on soil CO2 efflux - A modified

690   model. *Plant and Soil*, *268*(1), 21–33. https://doi.org/10.1007/s11104-005-0175-5

691   Rinnan, R., & Bååth, E. (2009). Differential utilization of carbon substrates by bacteria

692   and fungi in tundra soil. *Applied and Environmental Microbiology*, *75*(11), 3611–

693   3620. https://doi.org/10.1128/AEM.02865-08

694   Rustad, L., Huntington, T., & Boone, R. (2000). Controls on soil respiration:

695   implications for climate change. *Biogeochemistry*, *48*, 1–6.

696   https://doi.org/10.1023/A:1006255431298

697   Saiz, G., Byrne, K. A., Butterbach-Bahl, K., Kiese, R., Blujdea, V., & Farrell, E. P.

698   (2006). Stand age-related effects on soil respiration in a first rotation Sitka spruce

699   chronosequence in central Ireland. *Global Change Biology*, *12*(6), 1007–1020.

700   https://doi.org/10.1111/j.1365-2486.2006.01145.x

701   Schindlbacher, A., Schnecker, J., Takriti, M., Borken, W., & Wanek, W. (2015).

702   Microbial physiology and soil CO2 efflux after 9 years of soil warming in a

703   temperate forest - no indications for thermal adaptations. *Global Change Biology*,

704   *21*(11), 4265–4277. https://doi.org/10.1111/gcb.12996

705   Schlesinger, W. H. (1990). Evidence from chronosequence studies for a low carbon-

706   storage potential of soils. *Nature*. https://doi.org/10.1038/348232a0

707   Tang, J., Bolstad, P. V., Desai, A. R., Martin, J. G., Cook, B. D., Davis, K. J., & Carey,

708   E. V. (2008). Ecosystem respiration and its components in an old-growth northern

709   forest. *Agricultural and Forest Meteorology*, *148*, 171–185.

710   Tarlera, S., Jangid, K., Ivester, A. H., Whitman, W. B., & Williams, M. A. (2008).

711   Microbial community succession and bacterial diversity in soils during 77 000

712   years of ecosystem development. *FEMS Microbiology Ecology*, *64*(1), 129–140.

713   https://doi.org/10.1111/j.1574-6941.2008.00444.x

714   Tucker, C. L., Bell, J., Pendall, E., & Ogle, K. (2013). Does declining carbon-use

715   efficiency explain thermal acclimation of soil respiration with warming? *Global

716   Change Biology*, *19*(1), 252–263. https://doi.org/10.1111/gcb.12036

717   Vitousek, P. (2004). *Nutrient Cycling and Limitation: Hawai'i as a Model System*.

718   Princeton, NJ.: Princeton University Press.

719   Walker, T. W. N., Kaiser, C., Strasser, F., Herbold, C. W., Leblans, N. I. W., Woebken,

720   D., … Richter, A. (2018). Microbial temperature sensitivity and biomass change

721   explain soil carbon loss with warming. *Nature Climate Change*, *8*(10), 885–889.

722   https://doi.org/10.1038/s41558-018-0259-x

723   Wang, Bond-Lamberty, B. P., & Gower, S. T. (2002). Soil surface CO2 flux in a boreal

724   black spruce fire chronosequence. *Journal of Geophysical Research –

725   Atmospheres*, *107*, 1–8. https://doi.org/10.1029/2001jd000861

726   Wang, W. J., Dalal, R. C., Moody, P. W., & Smith, C. J. (2003). Relationships of soil

727 respiration to microbial biomass, substrate availability and clay content. *Soil*

728 *Biology and Biochemistry*, *35*(2), 273–284. https://doi.org/10.1016/S0038-

729 0717(02)00274-2

730 Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., Van Der Putten, W. H., &

731 Wall, D. H. (2004). Ecological linkages between aboveground and belowground

732 biota. *Science*, *304*(5677), 1629–1633. https://doi.org/10.1126/science.1094875

733 Wardle, D. A., Bardgett, R. D., Walker, L. R., & Bonner, K. I. (2009). Among- and

734 within-species variation in plant litter decomposition in contrasting long-term

735 chronosequences. *Functional Ecology*, *23*(2), 442–453.

736 https://doi.org/10.1111/j.1365-2435.2008.01513.x

737 Wardle, D. A., Bardgett, R. D., Walker, L. R., Peltzer, D. A., & Lagerström, A. (2008).

738 The response of plant diversity to ecosystem retrogression: Evidence from

739 contrasting long-term chronosequences. *Oikos*, *117*(1), 93–103.

740 https://doi.org/10.1111/j.2007.0030-1299.16130.x

741 Wardle, D. A., Walker, L. R., & Bardgett, R. D. (2004). Ecosystem properties and

742 forest decline in contrasting long-term chronosequences. *Science*, *305*(5683), 509–

743 513. https://doi.org/10.1126/science.1098778

744 Ye, J., Bradford, M. A., Maestre, F. T., Li, F., & García-Palacios, P. (2020).

745 Compensatory thermal adaptation of soil microbial respiration rates in global

746 croplands. *Global Biogeochemical Cycles*, *34*(6), 0–2.

747 https://doi.org/10.1029/2019gb006507

748 Zhou, L., Zhou, X., Shao, J., Nie, Y., He, Y., Jiang, L., … Hosseini Bai, S. (2016).

749 Interactive effects of global change factors on soil respiration and its components:

750 a meta-analysis. *Global Change Biology*, *22*(9), 3157–3169.

751 https://doi.org/10.1111/gcb.13253

752