Inter-annual variability of soil respiration in wet shrublands

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Ecosystems

Peer reviewed version

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1 **Inter-annual variability of soil respiration in wet shrublands: do plants modulate its**

2 **sensitivity to climate?**

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14 **Author contributions**

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Abstract

Understanding the response of soil respiration to climate variability is critical to formulate realistic predictions of future carbon (C) fluxes under different climate change scenarios. There is growing evidence that the influence of long-term climate variability in C fluxes from terrestrial ecosystems is modulated by adjustments in the aboveground-belowground links. Here, we studied the inter-annual variability in soil respiration from a wet shrubland going through successional change in North Wales (UK) during 13 years. We hypothesised that the decline in plant productivity observed over a decade would result in a decrease in the apparent sensitivity of total soil respiration to soil temperature, and that rainfall variability would explain a significant fraction of the inter-annual variability in plant productivity, and consequently, in total soil respiration, due to excess-water constraining nutrient availability for plants. As hypothesised, there were parallel decreases between plant productivity and annual and summer CO_2 emissions over the 13-year period. Soil temperatures did not follow a similar trend, which resulted in a decline in the apparent sensitivity of soil respiration to soil temperature (apparent Q_{10} values decreased from 9.4 to 2.8). Contrary to our second hypothesis, summer maximum air temperature rather than rainfall was the climate variable with the greatest influence on aboveground biomass and annual cumulative respiration. Since summer air temperature and rainfall were positively associated, the greatest annual respiration values were recorded during years of high rainfall. The results suggest that adjustments in plant productivity might have a critical role in determining the long-term-sensitivity of soil respiration to changing climate conditions.

Keywords: plant productivity; Q_{10}; soil C; climate change; drought; heathland; *Calluna vulgaris*

Introduction

Soil respiration represents a major flux of C to the atmosphere, estimated at 98 Pg C yr^{-1} and increasing by 0.1 Pg C yr^{-1} in response to a warming climate (Bond-Lamberty and Thomson 2010). Understanding the long-term responses of soil respiration to current fluctuations in climate and plant productivity is therefore critical to formulate predictions of future C fluxes under the different climate change scenarios. For this purpose, long-term data sets containing climate, vegetation and CO_2 flux information are critically needed but generally unavailable due to the limited duration of most of studies.

Inter-annual variability in soil respiration is affected by an array of usually inter-related factors, including air temperature and rainfall, plant phenology and productivity, and soil nutrient availability (reviewed in Luo and Zhou 2006). At a global scale, annual soil respiration correlates with mean annual air temperature (Raich et al 2002). However, analysis at the biome level suggests that variations in rainfall rather than in temperature drive the annual variability in soil respiration in many ecosystems, including evergreen broadleaf forests, wooded grasslands and open shrublands, where annual soil respiration positively correlates with rainfall (Raich et al 2002). This has been observed at the plot-scale in some warm (tropical and subtropical) and arid ecosystems (Epron et al 2004; Thomas et al 2009; Wang et al 2011), as well as in subalpine forests (Scott-Denton et al 2003) which are seasonally exposed to conditions of low water availability. Often absent in these data sets are those ecosystems exposed to seasonal excess-water conditions, where soil organic matter (SOM) decomposition is constrained due to the low oxygen diffusion into enzymatic reaction sites (Freeman et al 2001). In these excess-water limited ecosystems the occurrence of drought periods can lead to the release of large amounts of soil C due to the activation of a *biogeochemical cascade* under the increased oxygen availability, which accelerates SOM decomposition (Fenner and Freeman 2011). Here,

we present an analysis of the decadal variability of soil respiration in a wet Atlantic shrubland, a typical ecosystem where soil C dynamics and plant productivity are limited by seasonal excess-water conditions.

Despite many studies showing a direct relationship between annual climate and soil respiration, there is growing evidence that the influence of long-term climate variability of C fluxes from terrestrial ecosystems is mediated by adjustments in aboveground-belowground couplings (Stoy et al 2009; Aanderud et al 2011; Shao et al 2014), which suggests that predicting long-term CO_2 fluxes from climate variables alone could lead to large inaccuracies (Richardson et al 2007; Stoy et al 2009; Migliavacca et al 2010). The tight coupling between plant photosynthetic activity and soil respiration has been demonstrated by a range of tree-girdling (Högberg et al 2001; Jing et al 2015), canopy clipping and shading experiments (Wan and Luo 2003; Jia et al 2014), which demonstrated that total soil respiration can be highly variable in response to changes in the supply of recently-fixed C by plants. Further, several studies have shown that annual plant productivity is the most important factor driving the inter-annual variability of soil respiration over the years across a range of spatial scales, and that the direct effect of plant productivity can overrule the influence of climate (Janssens et al 2001; Reichstein et al 2003; Irvine et al 2008; Stoy et al 2009).

At seasonal and annual time scales, the links between plant productivity and soil respiration can be particularly tight in those temperate ecosystems with a marked seasonality, where the supply of photosynthates to soil microorganisms by the plant community follows strong seasonal patterns. Indeed, in these ecosystems the seasonal temperature sensitivity of soil respiration (often indicated as Q_{10} values) reflects the phenological stage of the plant community, which responds to air temperature and drives the patterns of C-fixation and belowground C allocation (Curiel Yuste et al 2004;

Sampson et al 2007; Davidson and Holbrook, 2009; Wang et al 2010). While the intrinsic or "pure" temperature sensitivity of ecosystem respiration seems to converge across climatic zones and ecosystem types (Mahecha et al 2010), the apparent temperature sensitivity of ecosystem or soil respiration spans over a much broader range across ecosystems (Davidson et al 2006; Zhou et al 2009; Mahecha et al 2010). This broader range in apparent temperature sensitivity originates from the integration of e.g. plant productivity and soil C pool size on soil respiration, and illustrates the variety and complexity of responses of the respiratory fluxes to temperature depending on site properties. Recently, several works showed that the temperature sensitivity of microbial soil respiration is modulated by the supply of fresh C inputs by plants, with decreases in Q_{10} correlated to a reduction of labile soil C availability (Curiel-Yuste et al 2010; Thiessen et al 2013). Thus, changes in plant productivity over time might play a critical role in the long-term-sensitivity of soil respiration to a changing climate.

Wet temperate shrublands are an example of an ecosystem with a marked seasonality, where soil respiration strongly depends on photosynthesis (Larsen et al 2007), and where the intrinsic temperature sensitivity of respiration might be confounded by the effects of plant phenology on soil respiration, and by the occurrence of excess-water conditions that limit SOM decomposition. These wet shrublands are often characterised by the presence of organo-mineral soils, which are seasonally exposed to excess-water conditions. In the UK, wet shrublands dominated by *Calluna vulgaris* with organo-mineral soils occupy 1.96 million ha (Hall et al 2014) and have one of the highest soil C densities across habitats (Reynolds et al 2013), with a potential C sequestration capacity that is more than the double of that of peatlands (Quin et al 2015). However, they might be more sensitive to inter-annual variations in rainfall due to the limited capacity of the soil to buffer drying events, in comparison to peatlands. In order to forecast future CO_2 emissions from these

121 ecosystems under the different climate change scenarios, it is critical to analyse the

122 contribution of plant and climate controls to soil respiration.

123 To address this question, we studied the inter-annual variability in total soil respiration

124 from a wet shrubland in North Wales (UK) during 13 years. Previously we have shown,

125 using a whole-ecosystem climate change experiment, that warming and summer droughts

126 could lead to the destabilisation of large amounts of soil organic C in this shrubland

127 through the stimulation of total soil respiration (Sowerby et al 2010; Domínguez et al

128 2015). Here, we analysed the response of soil respiration to ambient fluctuations of

129 temperature, rainfall and plant productivity at a decadal time scale. We analysed the

130 evolution of apparent temperature sensitivity of soil respiration and studied the response

131 of this variable to changes in plant productivity. Specifically, our hypotheses were that:

132 1) changes in plant productivity would significantly affect the apparent sensitivity of

133   respiration to soil temperature

134 2) rainfall variability would explain a significant fraction of the inter-annual variability

135   in plant productivity, and consequently, of the inter-annual variability in total soil

136   respiration due to excess-water constraints on SOM mineralization and nutrient

137   availability for plants (Emmett et al 2004).

138

139 **Material and Methods**

140

141 *Site description*

142

143 The study was carried out near Clocaenog Forest at NE Wales, UK (53º03'19"N,

144 3º27'55"W) , situated at 490 m a.s.l. Mean annual air temperature is 8.2 ºC and rainfall is

145 1411 mm (automated weather station located at the site, 2000-2012 period). Inter-annual

146 variations of air temperature and rainfall are strongly influenced by the North Atlantic

147 Oscillation (NAO), with high winter and spring temperatures and high rainfall during

148 years of high (positive) NAO index and vice versa (Ottersen et al 2001). The ecosystem

149 is an upland Atlantic heathland dominated by *Calluna vulgaris* (L.) Hull (> 60 % of plant

150 biomass), with *Vaccinium myrtilus* L., *Empetrum nigrum* L. and *Deschampsia flexuosa*

151 (L.) Trin. The ecosystem has remained unmanaged and undisturbed over at least the last

152 25 years, and has moved from a "mature" to "degenerate" phase of heathland succession

153 (Gimingham 1972).

154 The soil at the site can be classified as Ferric stagnopodzol in the Hafren Series in the Soil

155 Survey of England and Wales (Cranfield University, 2014). Organic matter content in the

156 topsoil (0- 10 cm) is 89%, with a C:N ratio of 37.4 and a bulk density of 0.09 g cm^{-3}.

157 Soils at 18-20 cm (total depth of the soil) have organic matter content of 37%, and bulk

158 density of 0.41 g cm^{-3}. See Robinson et al (2016) for further details on soil properties at

159 the site.

160

161 *Soil respiration measurements*

162

163 Soil respiration rates (CO_2 efflux from soil surface to atmosphere) were measured in three

164 experimental plots of 4 m × 5 m, which had a 0.5-m buffer strip around the perimeter

165 (Beier et al 2004). These were the control plots in a field-scale experimental manipulation

166 that aimed to study the vulnerability of the ecosystem to warming and summer drought

167 (Sowerby et al 2010; Domínguez et al 2015). In these control plots no treatment was

168 applied, and thus the plots were under ambient temperature and rainfall conditions. The

169 plots were established in 1999, and soil respiration has been monitored from summer

170 1999 to date.

171

Soil respiration results presented here were measured fortnightly between January 2000

and December 2012 within permanent PVC collars of 10 cm diameter, inserted 5 cm into

the soil. Three collars per plot were used (a total of 9 collars); these collars did not exclude

roots, and therefore measurements of CO_2 efflux included both heterotrophic respiration

from soil microorganisms, as well as autotrophic respiration from roots within the collars.

Measurements were taken in the afternoon, between 12:00 and 15:00, using portable

infrared gas analysers (EGM-2, PP Systems until 2008 and LI-8100 automated soil CO_2

flux system onwards) coupled to soil respiration chambers. Due to technical limitations,

during 2005 measurements were restricted to the spring and summer seasons.

181

Abiotic variables

Meteorological conditions (air temperature and humidity, rainfall and wind speed) have

been monitored by an automated weather station located at the site, with hourly

recordings, starting in 1999 to date. Data collection was incomplete during 2006 and 2007

due to technical problems, and climate data for missing dates were gathered from the

Alwen Dam MET station, located 6 km away from our experimental site (Met Office,

2012). Monthly North Atlantic Oscillation (NAO) index values, representing the

difference between the normalised sea level pressure over Gibraltar and the normalised

sea level pressure over Southwest Iceland (Jones et al 1997) were gathered from a public

data repository (http://www.cru.uea.ac.uk/cru/data/nao/).

At the plot level, soil temperature was continuously measured at 5 cm soil depth by

Reference Thermistor sensors (Probe 107, Campbell Scientific, Logan, UT, USA). Due

to technical problems the soil temperature data set for 2007 and 2008 was incomplete.

195   Soil moisture (0–10 cm depth) was measured at every routine visit to the site using a theta

196   probe (ML-2, Delta-T, Cambridge, UK) and a soil moisture meter (HH2, Delta-T) until

197   2009. In 2009, TDR probes (CS616, Campbell Scientific, Logan, UT, USA) were inserted

198   into the soil at 5 cm for a continuous monitoring of soil moisture (hourly recordings).

199

200   *Vegetation Data*

201   Plant community composition and biomass were monitored most years, excepting 2004-

202   2006, at the end of the growing season using the pin-point method. In each plot three

203   permanent 0.5×0.5 m^2 subplots were established and a grid of 100 pins was lowered

204   through the vegetation. Every touch of vegetation was recorded to the nearest 1 cm

205   indicating the species, the plant part (leaf, flower, or stem) and its status (green, dry,

206   dead). Calibration between pin-point measurements and plant biomass was conducted

207   using a destructive sampling outside the experimental plots in 2000, and relationships

208   between pin-point measurements and plant biomass were established for each plant

209   species.

210   All data sets are available from CEH´s Environmental Information Platform

211   (https://eip.ceh.ac.uk/). See Supplementary Material for links to archived data.

212

213   *Data analysis*

214   For each date we calculated the number of growing degree days (GDD) from air

215   temperature data, according to Roltsch et al. (1999): $GDD_i = (Tmax_i + Tmin_i)/ 2 - T_{low}$

216   where T_{max} and T_{min} are the maximum and minimum air temperatures for each single day

217   i, respectively, and T_{low} is the lower threshold temperature for plant growth, which was

218   set to 5 ºC (Beier et al 2004). Upper threshold temperature for growth (T_{high}) was set to

219   25 ºC. GDD_i was set to zero if $GDD_i < 1$ or if $GDD_i > (T_{high} - T_{low})$.

220

221   Annual and seasonal cumulative CO_2 emissions were calculated assuming that the routine

222   measurements taken in the afternoon represented the daily maximum rate of CO_2 efflux,

223   as described in Domínguez et al. (2015). Based on a diurnal study conducted in 2002, we

224   calculated the daily average respiration rates as 87% of that maximum. Then, average

225   seasonal rates were calculated, and finally seasonal cumulative CO_2 emissions were

226   obtained by multiplying the seasonal rates by the number of days in each season. Annual

227   emissions were calculated as the sum of all the seasonal emissions. Spring, summer,

228   autumn and winter seasons correspond to March-May, June-August, September-

229   November and December-February, respectively.

230

231   The apparent temperature sensitivity of soil respiration was assessed for each year using

232   two models (excluding 2005 due to limited respiration data available, and 2007 and 2008

233   due to incomplete soil temperature data sets). In the first model, respiration data was fitted

234   against soil temperature (at 5 cm depth) using an exponential function: $SR = ae^{bT}$, where

235   SR is soil respiration, T is soil temperature, and a and b are fitted constants. Q_{10} values

236   were calculated as: $Q_{10} = e^{10b}$ (Suseela et al 2012).

237

238   In the second model, the square root of the respiration data was fitted against soil

239   temperature using a lineal relationship: $SR^{1/2} = a(T - T_{min})$, where SR is soil respiration, a

240   is a fitted constant, T is soil temperature, and T_{min} is the apparent minimum temperature

241   for microbial activity (Ratwosky et al 1982). This "square-root model" is frequently used

242   to describe microbial activity below the optimum temperature for growth, and it better

243   describes the sensitivity of heterotrophic respiration when the temperature range is below

244   25 ºC, in comparison to the Arrhenius equation (Pietikäinen et al 2005). T_{min} can be

245   calculated from the slope and intercept of the models; this parameter is frequently used

246   to compare the capacity to grow at low temperatures across different microbial

247   communities (Pietikäinen et al 2005; Rinnan et al 2009; Rinnan et al 2011).

248

249   We applied additive mixed models to analyse whether climate and soil moisture,

250   temperature and respiration rates followed any significant time trend over the 13-year

251   period, using the mgcv package in R 3.2.3. Each time series was modelled as a function

252   of two smoothing factors as fixed terms. The first term, accounting for annual cycles, was

253   a function of the Julian day of each measurement, and used cyclic penalized cubic

254   regression spline smooth. The second term, accounting for possible decadal time trends,

255   was a function of the cumulative number of days since the date of the first measurement

256   in each series (January 2000), using thin-plate regression spline or cubic regression spline

257   smooths. We followed the recommendations by Zuur et al (2009) to account for the proper

258   temporal autocorrelation structure. First, we fitted a model without autocorrelation

259   structure, using restricted maximum likelihood. This model was compared against

260   different alternative models which considered different autocorrelation structures

261   (compound symmetry, continuous autocorrelation structure of order 1, moving average

262   correlations of different orders, spherical and exponential correlation). The optimal model

263   was selected based on Akaike Information Criteria (AIC). Validation of the selected

264   model included graphical examination of normalised residuals to check for homogeneity

265   and independency. For soil moisture, the 2000-2008 and the 2009-2012 periods were

266   analysed separately, due to the different periodicity of measurements in each data set.

267 Details of the selected models for each time series are given in Supplementary Material,

268 Table S1.

269

270 The relationships among climate and vegetation variables were first explored using

271 bivariate scatterplots and principal component analyses (PCA). As many climate

272 variables were mutually correlated, we selected some key variables to be used as

273 predictors for soil CO_2 emissions, based on the three first factors extracted by a PCA

274 analysis of climate data. Selected variables include: 1) average of summer daily maximum

275 air temperatures (highly correlated with annual and spring maximum temperatures, and

276 winter minimum air temperatures), 2) spring minimum air temperature, 3) summer

277 rainfall (used as an index of rainfall variability, significantly related to annual and spring

278 rainfall). Likewise, vegetation information was reduced to the total aboveground biomass

279 and the abundance of C-fixing (photosynthetically active) biomass of the dominant plant

280 species (*Calluna vulgaris*), as a surrogate for productivity of the plant community. This

281 variable was highly correlated with bryophyte biomass.

282 A PCA was then applied to the selected climate and vegetation variables together with

283 annual soil respiration, summer average soil temperature and summer average soil

284 moisture to explore the patterns of covariation among climate, vegetation and respiration.

285 To assess the influence of the selected climate predictors (summer maximum air

286 temperatures, spring minimum temperatures and summer rainfall) on summer and annual

287 CO_2 emissions, we applied linear mixed models, using the nlme package in R 3.2.3. First,

288 we fitted a model that included the three climate predictors as fixed terms without any

289 temporal autocorrelation structure, using restricted maximum likelihood. This model was

290 compared against different alternative models which considered different autocorrelation

291 structures, in which the year of measurement was included as a repeated measures factor.

292 The model with the best autocorrelation structure was selected based on AIC. Then, we

293 evaluated the optimal structure of the fixed terms, by applying a sequential backwards

294 deletion of the fixed terms included in this model, using the maximum likelihood as fit

295 method. The optimal model was selected based on AIC and refitted using restricted

296 maximum likelihood. Model validation included graphical examination of normalised

297 residuals to check for homogeneity and normality. We verified the independency of

298 predictors included in the final model (variance inflation factor < 2).

299

300 Similarly, linear mixed models that considered the temporal autocorrelation of vegetation

301 and respiration measurements over the years were applied to check for significant

302 relationships between the number of GDDs in each summer season and the plant

303 productivity variables (total aboveground biomass and *C. vulgaris* C-fixing biomass), as

304 well as to study the relationships between CO_2 emissions, apparent sensitivity of soil

305 respiration to soil temperature and plant productivity.

306

307 **Results**

308 *Climate and vegetation variability*

309 Over the 13 years some climate variables followed a significant time trend. The additive

310 mixed model for average daily temperatures explained a 70% of the variance,

311 decomposing air temperature time series into seasonal cycle and long-term trend (Fig 1

312 a,b; Table S1). The smooth function for the long-term trend revealed an upward pattern

313 in air temperatures between 2004 and 2006 (1000-2200 days after the start of the study),

314 followed by a downward trend between 2006 and 2012 (Fig 1b). This decline was more

315 evident for maximum summer air temperatures, which decreased between 2006 and 2012

316 following the downward trend of the NAO over that period (lower summer NAO index

317   values, in comparison to the 2000-2005 period, Fig 2a). The additive mixed model for

318   daily rainfall explained a very limited proportion of its variance (4 %, Table S1), but

319   suggested some downward trend between 2000 and 2006 (Fig 1d). This trend was more

320   evident when cumulative winter rainfall for each year was calculated (Fig 2b).

321   The fitted additive mixed model for soil temperature (0-50 cm) explained an 86 % of its

322   variance and revealed a strong seasonal pattern, with maximum temperatures reached by

323   mid-August (Fig 3a, b, Table S1). Summer and winter inter-annual averages were 11.1

324   and 3.4 ℃, respectively (Fig. 3a). Temperatures were particularly low during the winters

325   of 2001, 2010 and 2011, when they remained below 2 ℃. In agreement with the records

326   of air temperatures, an upward trend in soil temperature was observed between 2004 and

327   2006 (1000-2200 days after the start of the study, Fig. 3 c). However, the downward trend

328   detected for air temperature between 2006 and 2012 was not observed for soil

329   temperature. Soil moisture seasonal variation was much more irregular than that of soil

330   temperature (Fig 3d). Soils were particularly wet in winter 2000 and 2010. The lowest

331   moisture records ($< 0.2 \text{ m}^3 \text{ m}^{-3}$) were observed in summer 2006. Since 2010 seasonal

332   differences decreased, soils being wetter during the summer. The fitted additive models

333   did not performed well at describing seasonal or long-term trends in soil moisture, in

334   particular for the 2008-2012 period (Table S1).

335   Aboveground biomass showed a 14% inter-annual variability (average ± standard

336   deviation of 3.4 ± 0.48 kg m^{-2}), which was closely linked to the variability in summer

337   minimum and maximum temperatures, indicated by the number of growing-degree days

338   (Fig 4a, Table S2). Consequently there was a trend for a reduction in total aboveground

339   biomass at the site between 2006 and 2012. Likewise, the productivity of the plant

340   community, measured by the abundance of C-fixing biomass of dominant *C. vulgaris*,

341   was significantly related to summer air temperatures (Fig 4b, Table S2). When this index

342 was expressed in terms of deviation from the inter-annual average, a clear pattern of

343 decreased plant productivity at the site was observed over the studied decade, in particular

344 between 2006 and 2011 when productivity decreased by a 30 % (Fig 4c).

345

346 *Soil respiration variability*

347 Soil respiration in this shrubland followed a strong seasonal pattern, with winter rates

348 usually lower than 50 mg C m^{-2} h^{-1} and peaks of >200 mg C m^{-2} h^{-1} during the summer

349 months (June, July and August) coinciding with the maximum plant phenological

350 development (Fig 5a, b). The fitted additive model revealed a clear downward trend in

351 soil respiration rates over the 13-year period (Fig 5c, Table S1). Consequently, the was a

352 decline in annual emissions, ranging from 904 g C m^{-2} in 2000 to 275 g C m^{-2} in 2011,

353 with an average of 490 g C m^{-2} for the 2000-2012 period and a 42 % inter-annual

354 variability (Fig 5c). Summer and autumn respiration accounted for 42 % and 29 % of

355 annual CO_2 emissions, respectively, while spring and winter respiration only represented

356 18 % and 13 % of annual respiration, respectively. The downward trend in annual

357 cumulative respiration was caused by strong declines in spring, summer and autumn

358 respiration rates (Fig 6). The decline in summer respiration was remarkable, being

359 reduced by more than 50 % between 2000 and 2012. This change occurred without a

360 concurrent decrease in average soil temperatures during the summer season (Fig 6), which

361 resulted in a decline in *apparent* temperature sensitivity, indicated by the Q_{10} values (Fig

362 7a). The two models used to describe apparent temperature sensitivity (the Q_{10} and the

363 "square-root model") gave similar results, explaining similar percentages of the annual

364 variance of the soil respiration rates and showing similar decreases in apparent

365 temperature sensitivity over time. We therefore used the Q_{10} model for all further

366 analysis.

367 For those years for which the comparison between plant biomass and temperature

368 sensitivity of soil respiration was possible (8 out of 13 years), we found that *apparent*

369 temperature sensitivity was positively related to aboveground plant biomass (Fig 7b,

370 Table S3). Maximum *apparent* temperature sensitivity ($Q_{10} > 9$) was recorded during the

371 first studied years, when aboveground biomass was greater than 4 kg m^{-2}.

372

373 *Influence of climate on soil respiration*

374 In the multivariate analysis, summer maximum air temperatures and the abundance of *C.*

375 *vulgaris* C-fixing biomass were closely associated to annual cumulative soil respiration

376 (Fig 8). Interestingly, annual respiration was decoupled from average soil temperature in

377 the summer season. Instead, there was a trend for a positive association between summer

378 soil moisture and annual respiration (Fig 8).

379 Table 1 shows the results of the mixed models applied to summer and annual cumulative

380 CO_2 emissions, with a selection of climate variables (summer maximum temperatures

381 and rainfall, and spring minimum temperatures) as predictors. For both summer and

382 annual emissions, the model with the highest empirical support (lowest AIC) included

383 summer maximum temperatures as the only fixed factor, and a spherical temporal

384 autocorrelation structure. The graphical examination of the response of annual respiration

385 to summer temperatures suggested a non-linear pattern, with a peak in annual cumulative

386 respiration when the average of daily maximum temperatures during the summer season

387 was around 18 ºC, and slight decreases during warmer years (Fig 9b). Therefore, we fitted

388 a non-linear additive mixed model, using a smooth function of summer temperatures as

389 predictor for annual cumulative respiration. This model was significant, but had slightly

390 lower empirical support (lower AIC) than the linear mixed model (data not shown).

391 In contrast to one of our initial hypotheses, no pattern of covariation between seasonal or

392 annual respiration and rainfall was detected, neither between plant productivity and

393 rainfall (data not shown). No significant relationship was observed between average soil

394 temperature during the summer season and summer or annual cumulative respiration

395 (data not shown).

396 As plant productivity was significantly related to summer air temperatures, summer soil

397 respiration was also associated with aboveground plant biomass, although this

398 relationship was marginally significant ($p = 0.059$, Table 2). The relationship between

399 plant biomass and annual respiration was non-significant (Table 2).

400

401 **Discussion**

402 Wet shrublands dominated by *Calluna vulgaris* are ecosystems with a high potential

403 capacity for C sequestration (Quin et al 2015). In our studied wet shrubland, experimental

404 climate manipulations have shown that soil respiration in this type of ecosystem has a

405 particular sensitivity to warming and recurrent summer droughts, that does not attenuate,

406 but instead, increases at decadal time-scales (Domínguez et al, 2015), suggesting that the

407 current predictions of climate change might result in the release of a significant amount

408 of the organic C stored in the soil in these ecosystems. Long-term data sets covering

409 periods of inter-annual variability in climate and plant productivity are needed to

410 understand the drivers of soil respiration in these ecosystems, and to improve the

411 predictions of potential soil C losses under the projected climate change scenarios. Our

412 work provides unique information about the response of soil respiration to climate

413 fluctuations in these ecosystems.

17

414   Annual fluxes of CO_2 from the soil to the atmosphere ranged from 904 g C m^{-2} to 275 g

415   C m^{-2}, with an average of 490 g C m^{-2} for the 2000-2012 period, and 45 % inter-annual

416   variability. This inter-annual average is equivalent to 13.5 % of the organic C stored in

417   the top 5 cm of the soil at our site (estimated at 3.6 kg C m^{-2}). This value is in agreement

418   with other studies of CO_2 fluxes in shrubland ecosystems across Europe, estimating that

419   annual soil respiration represents 3-12 % of the soil organic C pool (Beier et al 2009).

420   The relatively high losses of C to the atmosphere through soil respiration are related to

421   the size of the soil organic C pool; organo-mineral soils in these wet shrublands contain

422   large organic C stocks, much of which becomes accessible to soil microbes under

423   appropriate temperature and moisture conditions, which leads to high rates of

424   heterotrophic respiration (Beier et al 2009). In addition, in wet (hydric) shrublands the

425   relative belowground C allocation is by far greater than in mesic and dry (xeric)

426   shrublands (Beier et al 2009), which results in high root respiration rates. In spite of the

427   size of the respiration fluxes, wet *C. vulgaris* shrublands are net C sinks, sequestering

428   between 1.26 and 3.50 t C ha^{-1} year^{-1} (Beier et al 2009; Quin et al 2015), although the

429   recurrence of extreme climate events such as summer droughts may turn these ecosystems

430   into C sources (Sowerby et al 2010).

431

432   *Influence of climate on soil respiration*

433

434   Over the studied period air temperature was determined by a large-scale climatic pattern,

435   the NAO. Inter-annual variability of soil respiration (both annual and summer emissions)

436   was significantly related to summer air temperatures, and therefore summer and annual

437   emissions declined markedly between 2006 and 2012 coinciding with a downward trend

438   of the NAO. However, the parallel decreases in annual respiration and plant productivity

439 (Figs 4c and 5c), the positive association between plant biomass and the apparent

440 sensitivity of soil respiration to soil temperature (Fig. 7 b), and the decoupling between

441 summer or annual cumulative respiration and average summer soil temperature over the

442 studied period (Figs 6 and 8) suggest that the climate effect on soil respiration could be

443 mediated by the background relationship between climate and plant productivity.

444 In temperate *C. vulgaris* shrublands, soil and ecosystem respiration depend strongly on

445 photosynthesis (Larsen et al 2007). Root respiration is coupled with photosynthetic

446 activity (Kuzyakov and Gavrishkova 2010), and because heterotrophic microbes may

447 preferably use short-lived C pools (Trumbore 2000), heterotrophic respiration also

448 depends primarily on plant inputs (Högberg et al. 2001; Irvine et al. 2005; Knohl et al.

449 2005) and therefore, indirectly on site productivity. Thus, plant productivity might have

450 a critical role in determining the impact of a changing climate on soil respiration from

451 these wet shrublands. Our results agree with recent findings that suggest that ecosystem

452 respiration and net ecosystem exchange strongly respond to environmental variability at

453 short (daily, weekly) time scales, while at longer (annual, decadal) time scales the

454 biological responses to climate variability or ecosystem development (such as changes in

455 plant productivity or functional diversity, and variations in the soil C pools), rather than

456 the climate variability *per se,* determine the C fluxes (Richardson et al. 2007; Stoy et al

457 2009; Mahecha et al 2010; Marcolla et al 2011; Delpierre et al. 2012; Shao et al 2014;

458 Knapp et al 2015). In any case, our study is merely observational, and therefore the

459 observed relationships between plant productivity and respiration might not be causal.

460 Further experimental work (for instance, simultaneous manipulations of air temperatures

461 and plant productivity in a factorial design) would be needed to confirm the role of plant

462 productivity in the response of soil respiration to climate variability at our site.

19

463 Annual emissions reached their maximum when average maximum summer temperature

464 was around 18 ℃, with slight decreases at warmer temperatures. Those years with

465 summer maximum temperatures above 18 ℃ (2003, 2005 and 2006) were anomalous hot

466 years, particularly 2003 when the heat and drought caused a Europe-wide reduction in

467 primary productivity (Ciais et al 2005). Instead the studied wet shrubland responded to

468 the heat and drought of 2003 with an increase in biomass and a decrease in litterfall

469 (Peñuelas et al 2007). Given the common positive relationship between litter

470 accumulation and soil respiration (Maier and Kress 2000; Sulzman et al 2005; Liu et al

471 2008), the slight decrease in soil respiration might be caused by a reduction in litter

472 accumulation during the warmest years. Soil moisture limitation during these warm years

473 is not likely to be the reason for the this pattern, as experimental manipulation of rainfall

474 in this ecosystem has shown that the reduction of soil moisture enhances respiration, and

475 that the stimulation of respiration can be sustained with soil moisture reductions as high

476 as 30 % (Domínguez et al 2015).

477 In contrast to one of our initial hypotheses, we found no pattern of covariation between

478 annual or seasonal rainfall and respiration, despite our experimental manipulation of

479 rainfall showed that summer drought clearly stimulates respiration, with the heterotrophic

480 component likely being more responsive to drought (Sowerby et al 2008; Domínguez et

481 al 2015). As climate at our site is determined by the NAO, high winter/spring

482 temperatures and high rainfall values are associated during years of high (positive) NAO

483 index and vice versa. Therefore maximum values of annual soil respiration were recorded

484 during years of high precipitation (Fig 8), leading to an apparent disagreement with the

485 results from the experimental climate manipulations at our site, which considered air

486 temperature and rainfall as separate factors. Interestingly, there was a decoupling between

487 average summer soil temperatures and summer soil CO_2 emissions. It is likely that during

488 the warm and wet summers the high soil water content had a thermal buffering effect,

489 soils being less exposed to fluctuations in air temperature. Indeed, soil drying in wet

490 organic soils increases the sensitivity of SOM decomposition to air temperature, and

491 intensifies the losses of soil organic C during drying events (Ise et al, 2008). The frequent

492 positive association between summer temperatures and rainfall at our site might prevent

493 greater losses of soil C through respiration during the summer seasons.

494

495 *Plant productivity and apparent temperature sensitivity*

496 Annual apparent Q_{10} values were high, considerably above the range of mean apparent

497 Q_{10} for different biomes (1.43 to 2.03, Zhou et al 2009). These high Q_{10} values are typical

498 for high latitude (Zhou et al 2009) and other ecosystems with a marked seasonality, where

499 the Q_{10} reflects the response of soil respiration to the phenological stage of the plant

500 community, which drives the supply of recently assimilated C compounds to roots and

501 soil microbes (Curiel-Yuste, 2004; Davidson and Holbrook, 2009; Wang et al 2010). Our

502 soil respiration measurements included autotrophic root respiration, and therefore

503 seasonal soil respiration rates were strongly influenced by seasonality and plant activity,

504 which confound the "pure" or intrinsic temperature response of microbial respiration.

505 High apparent Q_{10} values may also be indicative of the large contribution of the

506 autotrophic component to soil respiration (Wei et al 2010), which might be due to the

507 relatively high partitioning of biomass into the root system in hydric *C. vulgaris*

508 shrublands, in comparison to other mesic and xeric shrublands (Beier et al 2009).

509 Over the duration of the study there was a decline in the apparent sensitivity of soil

510 respiration to temperature, which was significantly related to the decrease in the standing

511 aboveground biomass (Fig 7). The observed decrease in plant productivity might result

512 in a decline in soil respiration due to a reduction, not only in the autotrophic fraction, but

513 also in the heterotrophic component, as discussed above. Our results suggest that the

514 supply of labile C substrates by plant roots might play a key role in regulating the

515 sensitivity of the soil C efflux to soil temperature. This idea is supported by recent

516 experimental works showing that the temperature sensitivity of microbial respiration is

517 modulated by the supply of labile C substrates, with decreases in Q_{10} values under a

518 shortage of fresh C inputs by plants (Curiel-Yuste et al 2010; Thiessen et al 2013), and

519 increases in the Q_{10} of SOM decomposition by rhizophere priming effects (Zhu and

520 Cheng, 2011). Some theoretical models and soil incubation studies have shown that the

521 mineralization of chemically recalcitrant or structurally complex substrates have a higher

522 Q_{10} than the mineralization of more labile substrates (Knorr et al 2005; Fierer et al 2009),

523 and therefore we could have expected an increase in temperature sensitivity as the relative

524 abundance of labile, plant-derived C inputs to soil decreases. However, under field

525 conditions the complexity of the processes involved in SOM decomposition often results

526 in deviations from these theoretical models (Davidson and Janssens, 2006). Fresh plant

527 C inputs have been shown to stimulate the mineralization of more complex, recalcitrant

528 organic C pools through microbial priming (Bader et al 2007; Dijkstra and Cheng, 2007;

529 Fontaine et al 2007; Zhu and Cheng 2011; Thiessen et al 2013). Thus, it is necessary to

530 consider not only the relative sizes of C pools of varying recalcitrance, but also how they

531 interact to fully understand the response of SOM decomposition to temperature

532 (Kirschbaum 2004; Knorr et al 2005).

572 In addition to the observed decline in maximum summer temperatures between 2006 and

573 2012, which was linked to a decline in plant productivity, the process of ageing of the

574 plant community could also partly explain the decrease in site productivity over the 13

575 years, and consequently, the decline in apparent temperature sensitivity and annual soil

576 respiration. Our studied shrubland has remained unmanaged and undisturbed over at least

577 the last 25 years, and has moved from a "mature" to "degenerate" phase of heathland

578 succession, as described by Gimingham (1972). Management of *C. vulgaris* heathlands

579 usually includes grazing and periodical burning and cutting, to maintain a mosaic

580 landscape comprised of *C. vulgaris* at multiple life stages. These management disturbance

581 regimes are used to maintain a healthy stand for recreational purposes resulting in higher

582 productivity than in mature or degenerate stands. The interruption of these practices has

583 a pronounced impact on the ecosystem C balance over time (Quin et al 2015). In mesic

584 heathlands the proportion of autotrophic respiration decreases as the ecosystem ages

585 (Koppitke et al 2012), which could partly explain the observed reduction in apparent

586 temperature sensitivity over the years, given the positive relationship between the relative

587 contribution of autotrophic respiration to soil C efflux and apparent temperature

588 sensitivity, detected at global-scales for forest ecosystems (Wei et al. 2010). Similar

589 reductions in temperature sensitivity during secondary succession have been observed in

590 other ecosystems (Tang et al 2006; Yan et al 2009).

591

592 **Conclusions**

593

594 Our work showed that annual soil CO_2 emissions and plant productivity from wet

595 shrublands are highly variable in a decadal time-scale, and that they are tightly coupled

596 to summer air temperatures, with a limited influence of rainfall variability on these

597 variables. The decoupling between summer soil temperature and respiration inter-annual

598 variabilities, the parallel declines in soil respiration and plant productivity, and the

599 positive association between plant productivity and the apparent sensitivity of soil

600 respiration to soil temperature suggest that the effect of summer temperatures on soil CO_2

601 efflux is mediated by a strong control of plant productivity on soil respiration. As plant

602 productivity does not depend only on climate conditions, but also on other ecological

603 factors (such as land management, stage during the processes of ecosystem development

604 or secondary succession), it seems essential to consider some measurements of plant

605 productivity to understand long-term variability in soil CO_2 emissions. Further

606 experimental work, however, would be needed to confirm whether plant productivity has

607 such key role in the response of soil respiration to climate variability, as suggested by our

608 observational study.

609

610 **Acknowledgements**

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885 **Tables**

886

887 Table 1. Results of the selected linear mixed models applied to summer and annual

888 cumulative CO_2 emissions as response variables, and a selection of climate variables as

889   predictors. Both models included a spherical autocorrelation structure term to account for

890   temporal autocorrelation. The model for summer emissions also included a variance

891   covariate term (dependent on summer maximum temperatures), needed to improve the

892   structure of model residuals. The increase in goodness of fit (decrease in AIC values)

893   from null models (which assume no influence of any climate predictors on summer or

894   annual emissions) is indicated. Summer Tmax: average of daily maximum temperatures

895   during the summer season.

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Response Variable	AIC	ΔAIC	Intercept	Predictors	Estimated parameter	St. error	t-value	p-value
Summer CO2 emissions	405.5	-9.12	-392.08	Summer Tmax.	36.56	9.44	3.87	0.0004
Annual CO2 emmisions	466.5	-8.92	-274.88	Summer Tmax.	43.47	12.58	3.45	0.0015

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908   Table 2. Results of the linear mixed models applied to summer and annual cumulative

909   CO_2 emissions as response variables, and aboveground plant biomass as predictor. Both

910   models included a spherical autocorrelation structure term to account for temporal

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911   autocorrelation. The increase in goodness of fit (decrease in AIC values) from null models

912   (which assume no influence of plant biomass on summer or annual emissions) is

913   indicated.

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Response Variable	AIC	ΔAIC	Intercept	Predictor	Estimated parameter	St. error	t-value	p-value
Summer CO_2 emissions	303.87	-1.21	63.85	Aboveground biomass	0.038	0.019	1.97	0.0592
Annual CO_2 emmisions	325.68	0.62	286.62	Aboveground biomass	0.043	0.027	1.64	0.114

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930   **Figure captions**

931   Fig 1. Smooth functions resulting from the application of additive mixed models to air

932   temperature and rainfall time series. Each time series was modelled as a function of two

933 smoothing terms. The first term, accounting for annual cycles, was a function of the Julian

934 day of each measurement (**a**, **c**), and used cyclic penalized cubic regression spline smooth.

935 The second term, accounting for possible decadal time trends, was a function of the

936 cumulative number of days since the date of the first measurement (January 2000), using

937 plate regression spline or cubic regression spline smooths (**b**, **d**). See Table S1 for a

938 summary of model results.

939

940 Fig. 2. **a**) Variation in summer air temperatures (average of daily maximum values) and

941 the North Atlantic Oscillation Index (NAO index) of the summer seasons for the 2000-

942 2012 period. Annual and winter rainfall is also shown (**b**).

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944 Fig. 3. **a**) Soil temperature over the course of the study (0-5 cm soil depth, daily average,

945 mean of three plots). Inter-annual winter and summer average values are indicated for

946 reference. **b, c**) Smooth functions resulting from the application of an additive mixed

947 model to soil temperature time series. The first smoother (**b**), accounting for annual

948 cycles, was a function of the Julian day of each measurement, and used cyclic penalized

949 cubic regression spline smooth. The second smoother (**c**), accounting for possible decadal

950 time trends, was a function of the cumulative number of days since the date of the first

951 measurement (January 2000), using cubic regression spline smooth. See Table S1 for a

952 summary of model results. **d**) Soil moisture over the course of the study (0-5 cm soil

953 depth, mean of three plots).

954

955   Fig. 4. **a)** Aboveground biomass of the plant community over the 2000-2012 period

956   (symbols, mean ± standard error, left axis), and number of growing-degree days (GDD)

957   during the summer seasons (grey line, right axis). **b)** C-fixing biomass of the dominant

958   plant species (*Calluna vulgaris*) over the studied period (symbols, mean ± standard error,

959   left axis), and number of growing-degree days (GDD) during the summer seasons (grey

960   line, right axis). In both graphs p-values correspond to the linear positive relationship

961   between total aboveground plant biomass or *C. vulgaris* C-fixing biomass, and summer

962   season cumulative Growing-Degree-Days (GDD). These linear mixed models included

963   an autocorrelation structure term to account for repeated measures of plant productivity

964   on the same plots over the 13-year period (autoregressive order 1 for total biomass; plot

965   identity as random factor for *C.vulgaris* C-fixing biomass). See Table S2 for a summary

966   of model results. **c)** Relative changes in *C. vulgaris* C-fixing biomass (index of plant

967   productivity) over the 2000-2012 period (percentage of change from inter-annual

968   average). C-fixing biomass estimated by pin-point calibration, from the number of hits of

969   green *C. vulgaris* leaves.

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971   Fig. 5. **a**) Soil respiration rates (average of the three experimental plots for each date, N

972   = 3 per plot). **b, c**) Smooth functions resulting from the application of an additive mixed

973   model to soil respiration time series. The first smoother, accounting for annual cycles (**b**),

974   was a function of the Julian day of each measurement, and used cyclic penalized cubic

975   regression spline smooth. The second smoother (**c**), accounting for possible decadal time

976   trends, was a function of the cumulative number of days since the date of the first

977   measurement (January 2000), using thin-plate regression spline smooth. See Table S1 for

978   a summary of model results. **d**) Cumulative annual soil respiration (R_{year}, mean ± standard

979   error for three plots) for the 2000-2012 period. Inter-annual average is indicated.

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981   Fig. 6. Seasonal soil respiration rates for the 2000-2012 period (mean ± standard error).

982   Average soil temperatures (0-5 cm depth) during the seasons are also shown (grey line,

983   right-axis).

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985   Fig. 7. **a**) *Apparent* sensitivity of soil respiration to soil temperature (indicated by

986   *apparent* Q_{10} values) over the study period (average ± standard error of the three

987   experimental plots for each year). **b**) Relationship between *apparent* temperature

988   sensitivity and aboveground plant biomass (individual plots). P-value corresponds to the

989   linear positive relationship between apparent temperature sensitivity and total

990   aboveground plant biomass. This linear mixed model included an autocorrelation

991   structure term to account for repeated measures of plant productivity on the same plots

992   over the 13-year period (spherical autocorrelation). See Table S3 for a summary of model

993   results. Soil temperature ranged from 1.2 to 15.6 ℃.

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995   Fig. 8. Result of a principal components analysis applied to the inter-annual variations of

996   annual soil respiration (R_{year}) and a selection of climate and vegetation variables. The

997   percentage of variance explained by each factor is indicated in their axes. Biomass:

998   abundance of C-fixing biomass of the dominant plant species in the community (*C.*

999   *vulgaris*), as an index of plant productivity; Su. Tmax: average of daily maximum

1000   temperatures during the summer season. Su. Soil M: average soil moisture during the

1001   summer season; Su. Soil T: average soil temperature during the summer season; Sp.

1002   Tmin: average of daily minimum temperatures during the spring season.

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1004   Fig. 9. Summer (**a**) and annual (**b**) cumulative respiration predicted by the linear mixed

1005   models applied to CO_2 emissions, with average of summer daily maximum temperatures

1006   as climate predictor (black lines). 95% confidence intervals (grey lines) and p-values are

1007   also shown. These linear mixed models included an autocorrelation structure term to

1008   account for repeated measures of soil respiration on the same plots over the 13-year period

1009   (spherical autocorrelation). See Table 1 for a summary of model results. Measured

1010   summer and annual cumulative respiration is also shown (symbols, average ± standard

1011   error of the three experimental plots for each year).