

# Inter-annual variability of soil respiration in wet shrublands

Dominguez, Maria; Smith, Andrew; Reinsch, Sabine; Emmett, Bridget

## Ecosystems

DOI: 10.1007/s10021-016-0062-3

Published: 01/06/2017

Peer reviewed version

Cyswllt i'r cyhoeddiad / Link to publication

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA): Dominguez, M., Smith, A., Reinsch, S., & Emmett, B. (2017). Inter-annual variability of soil respiration in wet shrublands: do plants modulate its sensitivity to climate? *Ecosystems*, 20(4), 796-812. https://doi.org/10.1007/s10021-016-0062-3

Hawliau Cyffredinol / General rights Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

· Users may download and print one copy of any publication from the public portal for the purpose of private study or research.

- You may not further distribute the material or use it for any profit-making activity or commercial gain
   You may freely distribute the URL identifying the publication in the public portal ?

#### Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1	Inter-annual variability of soil respiration in wet shrublands: do plants modulate its
2	sensitivity to climate?
3	María T. Domínguez <sup>a,b*</sup> , Andrew R. Smith <sup>c</sup> , Sabine Reinsch <sup>a</sup> , Bridget A. Emmett <sup>a</sup>
4	Affiliations
5	<sup>a</sup> Centre for Ecology and Hydrology Bangor, Natural Environment Research Council.
6	Deiniol Road, Bangor, Gwynedd, LL57 2UW, UK.
7	<sup>b</sup> Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS-CSIC). 10 Reina
8	Mercedes Av, 41012, Sevilla, Spain (present address).
9	<sup>c</sup> School of Environment, Natural Resources and Geography, Bangor University. Deiniol
10	Road, Bangor, Gwynedd, LL57 2UW, UK.
11	*Corresponding author. Email: maitedn@irnase.csic.es; phone number: +34 954624711;
12	fax number: +34 95 462 4002.
13	
14	Author contributions
15	BAE conceived and supervised the experiment. MTD, ARS and SR collected data and
16	contributed to experimental maintenance. MTD led data analysis and wrote the paper.
17	BAE, ARS and SR commented on the manuscript.
18	
19	
20	
21	
	1

#### 22 Abstract

Understanding the response of soil respiration to climate variability is critical to formulate 23 realistic predictions of future carbon (C) fluxes under different climate change scenarios. 24 There is growing evidence that the influence of long-term climate variability in C fluxes 25 from terrestrial ecosystems is modulated by adjustments in the aboveground-26 27 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. 28 We hypothesised that the decline in plant productivity observed over a decade would 29 30 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 31 32 variability in plant productivity, and consequently, in total soil respiration, due to excesswater constraining nutrient availability for plants. As hypothesised, there were parallel 33 decreases between plant productivity and annual and summer CO<sub>2</sub> emissions over the 13-34 35 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 36 decreased from 9.4 to 2.8). Contrary to our second hypothesis, summer maximum air 37 38 temperature rather than rainfall was the climate variable with the greatest influence on 39 aboveground biomass and annual cumulative respiration. Since summer air temperature and rainfall were positively associated, the greatest annual respiration values were 40 recorded during years of high rainfall. The results suggest that adjustments in plant 41 42 productivity might have a critical role in determining the long-term-sensitivity of soil 43 respiration to changing climate conditions.

Keywords: plant productivity; Q<sub>10</sub>; soil C; climate change; drought; heathland; *Calluna vulgaris*

### 46 Introduction

Soil respiration represents a major flux of C to the atmosphere, estimated at 98 Pg C yr<sup>-1</sup> and increasing by 0.1 Pg C yr<sup>-1</sup> 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, longterm data sets containing climate, vegetation and CO<sub>2</sub> flux information are critically needed but generally unavailable due to the limited duration of most of studies.

54 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 55 56 nutrient availability (reviewed in Luo and Zhou 2006). At a global scale, annual soil 57 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 58 drive the annual variability in soil respiration in many ecosystems, including evergreen 59 broadleaf forests, wooded grasslands and open shrublands, where annual soil respiration 60 positively correlates with rainfall (Raich et al 2002). This has been observed at the plot-61 62 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 63 64 2003) which are seasonally exposed to conditions of low water availability. Often absent 65 in these data sets are those ecosystems exposed to seasonal excess-water conditions, 66 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 67 68 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 69 availability, which accelerates SOM decomposition (Fenner and Freeman 2011). Here, 70

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.

74 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 75 76 of C fluxes from terrestrial ecosystems is mediated by adjustments in abovegroundbelowground couplings (Stoy et al 2009; Aanderud et al 2011; Shao et al 2014), which 77 78 suggests that predicting long-term  $CO_2$  fluxes from climate variables alone could lead to 79 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 80 81 demonstrated by a range of tree-girdling (Högberg et al 2001; Jing et al 2015), canopy 82 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 83 84 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 85 respiration over the years across a range of spatial scales, and that the direct effect of plant 86 87 productivity can overrule the influence of climate (Janssens et al 2001; Reichstein et al 88 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 96 or "pure" temperature sensitivity of ecosystem respiration seems to converge across 97 climatic zones and ecosystem types (Mahecha et al 2010), the apparent temperature 98 99 sensitivity of ecosystem or soil respiration spans over a much broader range across 100 ecosystems (Davidson et al 2006; Zhou et al 2009; Mahecha et al 2010). This broader 101 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 102 103 complexity of responses of the respiratory fluxes to temperature depending on site properties. Recently, several works showed that the temperature sensitivity of microbial 104 105 soil respiration is modulated by the supply of fresh C inputs by plants, with decreases in Q<sub>10</sub> correlated to a reduction of labile soil C availability (Curiel-Yuste et al 2010; 106 107 Thiessen et al 2013). Thus, changes in plant productivity over time might play a critical 108 role in the long-term-sensitivity of soil respiration to a changing climate.

109 Wet temperate shrublands are an example of an ecosystem with a marked seasonality, 110 where soil respiration strongly depends on photosynthesis (Larsen et al 2007), and where 111 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 112 113 limit SOM decomposition. These wet shrublands are often characterised by the presence 114 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 115 116 1.96 million ha (Hall et al 2014) and have one of the highest soil C densities across 117 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 118 119 to inter-annual variations in rainfall due to the limited capacity of the soil to buffer drying 120 events, in comparison to peatlands. In order to forecast future CO<sub>2</sub> emissions from these

ecosystems under the different climate change scenarios, it is critical to analyse thecontribution of plant and climate controls to soil respiration.

123 To address this question, we studied the inter-annual variability in total soil respiration from a wet shrubland in North Wales (UK) during 13 years. Previously we have shown, 124 125 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 2015). Here, we analysed the response of soil respiration to ambient fluctuations of 128 temperature, rainfall and plant productivity at a decadal time scale. We analysed the 129 130 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:

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

The study was carried out near Clocaenog Forest at NE Wales, UK (53°03'19"N, 3°27'55"W), situated at 490 m a.s.l. Mean annual air temperature is 8.2 °C and rainfall is 1411 mm (automated weather station located at the site, 2000-2012 period). Inter-annual

variations of air temperature and rainfall are strongly influenced by the North Atlantic 146 Oscillation (NAO), with high winter and spring temperatures and high rainfall during 147 years of high (positive) NAO index and vice versa (Ottersen et al 2001). The ecosystem 148 is an upland Atlantic heathland dominated by Calluna vulgaris (L.) Hull (> 60 % of plant 149 biomass), with Vaccinium myrtilus L., Empetrum nigrum L. and Deschampsia flexuosa 150 (L.) Trin. The ecosystem has remained unmanaged and undisturbed over at least the last 151 25 years, and has moved from a "mature" to "degenerate" phase of heathland succession 152 153 (Gimingham 1972).

The soil at the site can be classified as Ferric stagnopodzol in the Hafren Series in the Soil Survey of England and Wales (Cranfield University, 2014). Organic matter content in the topsoil (0- 10 cm) is 89%, with a C:N ratio of 37.4 and a bulk density of 0.09 g cm<sup>-3</sup>. Soils at 18-20 cm (total depth of the soil) have organic matter content of 37%, and bulk density of 0.41 g cm<sup>-3</sup>. See Robinson et al (2016) for further details on soil properties at 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  $\times$  5 m, which had a 0.5-m buffer strip around the perimeter (Beier et al 2004). These were the control plots in a field-scale experimental manipulation 165 166 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 applied, and thus the plots were under ambient temperature and rainfall conditions. The 168 169 plots were established in 1999, and soil respiration has been monitored from summer 170 1999 to date.

172 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 173 174 the soil. Three collars per plot were used (a total of 9 collars); these collars did not exclude roots, and therefore measurements of CO<sub>2</sub> efflux included both heterotrophic respiration 175 176 from soil microorganisms, as well as autotrophic respiration from roots within the collars. 177 Measurements were taken in the afternoon, between 12:00 and 15:00, using portable 178 infrared gas analysers (EGM-2, PP Systems until 2008 and LI-8100 automated soil CO<sub>2</sub> flux system onwards) coupled to soil respiration chambers. Due to technical limitations, 179 180 during 2005 measurements were restricted to the spring and summer seasons.

181

# 182 Abiotic variables

183 Meteorological conditions (air temperature and humidity, rainfall and wind speed) have 184 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 185 due to technical problems, and climate data for missing dates were gathered from the 186 187 Alwen Dam MET station, located 6 km away from our experimental site (Met Office, 188 2012). Monthly North Atlantic Oscillation (NAO) index values, representing the difference between the normalised sea level pressure over Gibraltar and the normalised 189 sea level pressure over Southwest Iceland (Jones et al 1997) were gathered from a public 190 191 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.

Soil moisture (0–10 cm depth) was measured at every routine visit to the site using a theta
probe (ML-2, Delta-T, Cambridge, UK) and a soil moisture meter (HH2, Delta-T) until
2009. In 2009, TDR probes (CS616, Campbell Scientific, Logan, UT, USA) were inserted
into the soil at 5 cm for a continuous monitoring of soil moisture (hourly recordings).

199

#### 200 Vegetation Data

Plant community composition and biomass were monitored most years, excepting 2004-201 202 2006, at the end of the growing season using the pin-point method. In each plot three permanent  $0.5 \times 0.5 \text{ m}^2$  subplots were established and a grid of 100 pins was lowered 203 204 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 species. 209

All data sets are available from CEH's Environmental Information Platform
(<u>https://eip.ceh.ac.uk/</u>). See Supplementary Material for links to archived data.

212

213 Data analysis

For each date we calculated the number of growing degree days (GDD) from air temperature data, according to Roltsch et al. (1999):  $GDD_i = (Tmax_i + Tmin_i)/2 - T_{low}$ where  $T_{max}$  and  $T_{min}$  are the maximum and minimum air temperatures for each single day i, respectively, and  $T_{low}$  is the lower threshold temperature for plant growth, which was set to 5 °C (Beier et al 2004). Upper threshold temperature for growth ( $T_{high}$ ) was set to 219 25 °C. GDD<sub>i</sub> was set to zero if GDD<sub>i</sub> < 1 or if GDD<sub>i</sub> > ( $T_{high} - T_{low}$ ).

220

221 Annual and seasonal cumulative CO<sub>2</sub> emissions were calculated assuming that the routine measurements taken in the afternoon represented the daily maximum rate of CO<sub>2</sub> efflux, 222 223 as described in Domínguez et al. (2015). Based on a diurnal study conducted in 2002, we calculated the daily average respiration rates as 87% of that maximum. Then, average 224 seasonal rates were calculated, and finally seasonal cumulative CO<sub>2</sub> emissions were 225 226 obtained by multiplying the seasonal rates by the number of days in each season. Annual emissions were calculated as the sum of all the seasonal emissions. Spring, summer, 227 228 autumn and winter seasons correspond to March-May, June-August, September-229 November and December-February, respectively.

230

The apparent temperature sensitivity of soil respiration was assessed for each year using two models (excluding 2005 due to limited respiration data available, and 2007 and 2008 due to incomplete soil temperature data sets). In the first model, respiration data was fitted against soil temperature (at 5 cm depth) using an exponential function:  $SR = ae^{bT}$ , where SR is soil respiration, T is soil temperature, and *a* and *b* are fitted constants. Q<sub>10</sub> values were calculated as: Q<sub>10</sub> =  $e^{10b}$  (Suseela et al 2012).

237

In the second model, the square root of the respiration data was fitted against soil temperature using a lineal relationship:  $SR^{1/2} = a(T-T_{min})$ , where SR is soil respiration, *a* is a fitted constant, T is soil temperature, and  $T_{min}$  is the apparent minimum temperature for microbial activity (Ratwosky et al 1982). This "square-root model" is frequently used to describe microbial activity below the optimum temperature for growth, and it better describes the sensitivity of heterotrophic respiration when the temperature range is below 244 25 °C, 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 period, using the mgcv package in R 3.2.3. Each time series was modelled as a function 251 252 of two smoothing factors as fixed terms. The first term, accounting for annual cycles, was a function of the Julian day of each measurement, and used cyclic penalized cubic 253 regression spline smooth. The second term, accounting for possible decadal time trends, 254 255 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 structure, using restricted maximum likelihood. This model was compared against 259 different alternative models which considered different autocorrelation structures 260 261 (compound symmetry, continuous autocorrelation structure of order 1, moving average correlations of different orders, spherical and exponential correlation). The optimal model 262 was selected based on Akaike Information Criteria (AIC). Validation of the selected 263 264 model included graphical examination of normalised residuals to check for homogeneity and independency. For soil moisture, the 2000-2008 and the 2009-2012 periods were 265 266 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 variables were mutually correlated, we selected some key variables to be used as 272 273 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 air temperatures (highly correlated with annual and spring maximum temperatures, and 275 276 winter minimum air temperatures), 2) spring minimum air temperature, 3) summer rainfall (used as an index of rainfall variability, significantly related to annual and spring 277 278 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.

A PCA was then applied to the selected climate and vegetation variables together with 282 annual soil respiration, summer average soil temperature and summer average soil 283 moisture to explore the patterns of covariation among climate, vegetation and respiration. 284 285 To assess the influence of the selected climate predictors (summer maximum air temperatures, spring minimum temperatures and summer rainfall) on summer and annual 286 287 CO<sub>2</sub> 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.

The model with the best autocorrelation structure was selected based on AIC. Then, we evaluated the optimal structure of the fixed terms, by applying a sequential backwards deletion of the fixed terms included in this model, using the maximum likelihood as fit method. The optimal model was selected based on AIC and refitted using restricted maximum likelihood. Model validation included graphical examination of normalised residuals to check for homogeneity and normality. We verified the independency of predictors included in the final model (variance inflation factor < 2).

299

Similarly, linear mixed models that considered the temporal autocorrelation of vegetation and respiration measurements over the years were applied to check for significant relationships between the number of GDDs in each summer season and the plant productivity variables (total aboveground biomass and *C. vulgaris* C-fixing biomass), as well as to study the relationships between CO<sub>2</sub> emissions, apparent sensitivity of soil respiration to soil temperature and plant productivity.

306

307 **Results** 

#### 308 *Climate and vegetation variability*

Over the 13 years some climate variables followed a significant time trend. The additive 309 310 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 in air temperatures between 2004 and 2006 (1000-2200 days after the start of the study), 313 314 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 following the downward trend of the NAO over that period (lower summer NAO index 316

values, in comparison to the 2000-2005 period, Fig 2a). The additive mixed model for
daily rainfall explained a very limited proportion of its variance (4 %, Table S1), but
suggested some downward trend between 2000 and 2006 (Fig 1d). This trend was more
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 and 3.4 °C, respectively (Fig. 3a). Temperatures were particularly low during the winters 324 325 of 2001, 2010 and 2011, when they remained below 2 °C. 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 moisture records ( $< 0.2 \text{ m}^3 \text{ m}^{-3}$ ) were observed in summer 2006. Since 2010 seasonal 331 differences decreased, soils being wetter during the summer. The fitted additive models 332 333 did not performed well at describing seasonal or long-term trends in soil moisture, in 334 particular for the 2008-2012 period (Table S1).

Aboveground biomass showed a 14% inter-annual variability (average  $\pm$  standard deviation of 3.4  $\pm$  0.48 kg m<sup>-2</sup>), which was closely linked to the variability in summer minimum and maximum temperatures, indicated by the number of growing-degree days (Fig 4a, Table S2). Consequently there was a trend for a reduction in total aboveground biomass at the site between 2006 and 2012. Likewise, the productivity of the plant community, measured by the abundance of C-fixing biomass of dominant *C. vulgaris*, was significantly related to summer air temperatures (Fig 4b, Table S2). When this index was expressed in terms of deviation from the inter-annual average, a clear pattern of
decreased plant productivity at the site was observed over the studied decade, in particular
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 usually lower than 50 mg C m<sup>-2</sup> h<sup>-1</sup> and peaks of >200 mg C m<sup>-2</sup> h<sup>-1</sup> during the summer 348 months (June, July and August) coinciding with the maximum plant phenological 349 350 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 decline in annual emissions, ranging from 904 g C m<sup>-2</sup> in 2000 to 275 g C m<sup>-2</sup> in 2011, 352 with an average of 490 g C m<sup>-2</sup> for the 2000-2012 period and a 42 % inter-annual 353 354 variability (Fig 5c). Summer and autumn respiration accounted for 42 % and 29 % of 355 annual CO<sub>2</sub> emissions, respectively, while spring and winter respiration only represented 18 % and 13 % of annual respiration, respectively. The downward trend in annual 356 357 cumulative respiration was caused by strong declines in spring, summer and autumn respiration rates (Fig 6). The decline in summer respiration was remarkable, being 358 reduced by more than 50 % between 2000 and 2012. This change occurred without a 359 360 concurrent decrease in average soil temperatures during the summer season (Fig 6), which resulted in a decline in *apparent* temperature sensitivity, indicated by the Q<sub>10</sub> values (Fig 361 7a). The two models used to describe apparent temperature sensitivity (the  $Q_{10}$  and the 362 "square-root model") gave similar results, explaining similar percentages of the annual 363 variance of the soil respiration rates and showing similar decreases in apparent 364 temperature sensitivity over time. We therefore used the  $Q_{10}$  model for all further 365 366 analysis.

For those years for which the comparison between plant biomass and temperature sensitivity of soil respiration was possible (8 out of 13 years), we found that *apparent* temperature sensitivity was positively related to aboveground plant biomass (Fig 7b, Table S3). Maximum *apparent* temperature sensitivity ( $Q_{10} > 9$ ) was recorded during the first studied years, when aboveground biomass was greater than 4 kg m<sup>-2</sup>.

372

# 373 Influence of climate on soil respiration

In the multivariate analysis, summer maximum air temperatures and the abundance of *C. vulgaris* C-fixing biomass were closely associated to annual cumulative soil respiration (Fig 8). Interestingly, annual respiration was decoupled from average soil temperature in the summer season. Instead, there was a trend for a positive association between summer soil moisture and annual respiration (Fig 8).

Table 1 shows the results of the mixed models applied to summer and annual cumulative 379 CO<sub>2</sub> emissions, with a selection of climate variables (summer maximum temperatures 380 381 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 °C, 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 predictor for annual cumulative respiration. This model was significant, but had slightly 389 lower empirical support (lower AIC) than the linear mixed model (data not shown). 390

In contrast to one of our initial hypotheses, no pattern of covariation between seasonal or annual respiration and rainfall was detected, neither between plant productivity and rainfall (data not shown). No significant relationship was observed between average soil temperature during the summer season and summer or annual cumulative respiration (data not shown).

As plant productivity was significantly related to summer air temperatures, summer soil respiration was also associated with aboveground plant biomass, although this relationship was marginally significant (p = 0.059, Table 2). The relationship between 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 current predictions of climate change might result in the release of a significant amount 407 of the organic C stored in the soil in these ecosystems. Long-term data sets covering 408 409 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 predictions of potential soil C losses under the projected climate change scenarios. Our 411 412 work provides unique information about the response of soil respiration to climate fluctuations in these ecosystems. 413

Annual fluxes of  $CO_2$  from the soil to the atmosphere ranged from 904 g C m<sup>-2</sup> to 275 g 414 C m<sup>-2</sup>, with an average of 490 g C m<sup>-2</sup> for the 2000-2012 period, and 45 % inter-annual 415 variability. This inter-annual average is equivalent to 13.5 % of the organic C stored in 416 the top 5 cm of the soil at our site (estimated at 3.6 kg C m<sup>-2</sup>). This value is in agreement 417 418 with other studies of CO<sub>2</sub> fluxes in shrubland ecosystems across Europe, estimating that annual soil respiration represents 3-12 % of the soil organic C pool (Beier et al 2009). 419 The relatively high losses of C to the atmosphere through soil respiration are related to 420 421 the size of the soil organic C pool; organo-mineral soils in these wet shrublands contain large organic C stocks, much of which becomes accessible to soil microbes under 422 appropriate temperature and moisture conditions, which leads to high rates of 423 heterotrophic respiration (Beier et al 2009). In addition, in wet (hydric) shrublands the 424 relative belowground C allocation is by far greater than in mesic and dry (xeric) 425 426 shrublands (Beier et al 2009), which results in high root respiration rates. In spite of the size of the respiration fluxes, wet C. vulgaris shrublands are net C sinks, sequestering 427 between 1.26 and 3.50 t C ha<sup>-1</sup> year<sup>-1</sup> (Beier et al 2009; Quin et al 2015), although the 428 429 recurrence of extreme climate events such as summer droughts may turn these ecosystems into C sources (Sowerby et al 2010). 430

431

432 Influence of climate on soil respiration

433

Over the studied period air temperature was determined by a large-scale climatic pattern,
the NAO. Inter-annual variability of soil respiration (both annual and summer emissions)
was significantly related to summer air temperatures, and therefore summer and annual
emissions declined markedly between 2006 and 2012 coinciding with a downward trend
of the NAO. However, the parallel decreases in annual respiration and plant productivity

(Figs 4c and 5c), the positive association between plant biomass and the apparent sensitivity of soil respiration to soil temperature (Fig. 7 b), and the decoupling between summer or annual cumulative respiration and average summer soil temperature over the studied period (Figs 6 and 8) suggest that the climate effect on soil respiration could be 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 activity (Kuzyakov and Gavrishkova 2010), and because heterotrophic microbes may 446 preferably use short-lived C pools (Trumbore 2000), heterotrophic respiration also 447 depends primarily on plant inputs (Högberg et al. 2001; Irvine et al. 2005; Knohl et al. 448 449 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 these wet shrublands. Our results agree with recent findings that suggest that ecosystem 451 452 respiration and net ecosystem exchange strongly respond to environmental variability at short (daily, weekly) time scales, while at longer (annual, decadal) time scales the 453 biological responses to climate variability or ecosystem development (such as changes in 454 plant productivity or functional diversity, and variations in the soil C pools), rather than 455 456 the climate variability per se, determine the C fluxes (Richardson et al. 2007; Stoy et al 2009; Mahecha et al 2010; Marcolla et al 2011; Delpierre et al. 2012; Shao et al 2014; 457 Knapp et al 2015). In any case, our study is merely observational, and therefore the 458 459 observed relationships between plant productivity and respiration might not be causal. 460 Further experimental work (for instance, simultaneous manipulations of air temperatures and plant productivity in a factorial design) would be needed to confirm the role of plant 461 productivity in the response of soil respiration to climate variability at our site. 462

Annual emissions reached their maximum when average maximum summer temperature 463 464 was around 18 °C, with slight decreases at warmer temperatures. Those years with summer maximum temperatures above 18 °C (2003, 2005 and 2006) were anomalous hot 465 466 years, particularly 2003 when the heat and drought caused a Europe-wide reduction in primary productivity (Ciais et al 2005). Instead the studied wet shrubland responded to 467 the heat and drought of 2003 with an increase in biomass and a decrease in litterfall 468 (Peñuelas et al 2007). Given the common positive relationship between litter 469 470 accumulation and soil respiration (Maier and Kress 2000; Sulzman et al 2005; Liu et al 2008), the slight decrease in soil respiration might be caused by a reduction in litter 471 472 accumulation during the warmest years. Soil moisture limitation during these warm years is not likely to be the reason for the this pattern, as experimental manipulation of rainfall 473 474 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).

In contrast to one of our initial hypotheses, we found no pattern of covariation between 477 annual or seasonal rainfall and respiration, despite our experimental manipulation of 478 rainfall showed that summer drought clearly stimulates respiration, with the heterotrophic 479 480 component likely being more responsive to drought (Sowerby et al 2008; Domínguez et al 2015). As climate at our site is determined by the NAO, high winter/spring 481 temperatures and high rainfall values are associated during years of high (positive) NAO 482 index and vice versa. Therefore maximum values of annual soil respiration were recorded 483 484 during years of high precipitation (Fig 8), leading to an apparent disagreement with the results from the experimental climate manipulations at our site, which considered air 485 486 temperature and rainfall as separate factors. Interestingly, there was a decoupling between 487 average summer soil temperatures and summer soil CO<sub>2</sub> emissions. It is likely that during

the warm and wet summers the high soil water content had a thermal buffering effect, soils being less exposed to fluctuations in air temperature. Indeed, soil drying in wet organic soils increases the sensitivity of SOM decomposition to air temperature, and intensifies the losses of soil organic C during drying events (Ise et al, 2008). The frequent positive association between summer temperatures and rainfall at our site might prevent greater losses of soil C through respiration during the summer seasons.

494

# 495 Plant productivity and apparent temperature sensitivity

Annual apparent  $Q_{10}$  values were high, considerably above the range of mean apparent 496 497  $Q_{10}$  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, which confound the "pure" or intrinsic temperature response of microbial respiration. 504 505 High apparent Q<sub>10</sub> 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

in a decline in soil respiration due to a reduction, not only in the autotrophic fraction, but 512 513 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 shortage of fresh C inputs by plants (Curiel-Yuste et al 2010; Thiessen et al 2013), and 518 519 increases in the Q<sub>10</sub> of SOM decomposition by rhizophere priming effects (Zhu and Cheng, 2011). Some theoretical models and soil incubation studies have shown that the 520 521 mineralization of chemically recalcitrant or structurally complex substrates have a higher  $Q_{10}$  than the mineralization of more labile substrates (Knorr et al 2005; Fierer et al 2009), 522 523 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 organic C pools through microbial priming (Bader et al 2007; Dijkstra and Cheng, 2007; 528 529 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 interact to fully understand the response of SOM decomposition to temperature 531 532 (Kirschbaum 2004; Knorr et al 2005).

In addition to the observed decline in maximum summer temperatures between 2006 and 2012, which was linked to a decline in plant productivity, the process of ageing of the plant community could also partly explain the decrease in site productivity over the 13 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 the last 25 years, and has moved from a "mature" to "degenerate" phase of heathland 577 succession, as described by Gimingham (1972). Management of C. vulgaris heathlands 578 579 usually includes grazing and periodical burning and cutting, to maintain a mosaic landscape comprised of C. vulgaris at multiple life stages. These management disturbance 580 regimes are used to maintain a healthy stand for recreational purposes resulting in higher 581 582 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 heathlands the proportion of autotrophic respiration decreases as the ecosystem ages 584 (Koppitke et al 2012), which could partly explain the observed reduction in apparent 585 temperature sensitivity over the years, given the positive relationship between the relative 586 contribution of autotrophic respiration to soil C efflux and apparent temperature 587 588 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 other ecosystems (Tang et al 2006; Yan et al 2009). 590

591

#### 592 **Conclusions**

593

594 Our work showed that annual soil CO<sub>2</sub> 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

respiration to soil temperature suggest that the effect of summer temperatures on soil CO<sub>2</sub> 600 601 efflux is mediated by a strong control of plant productivity on soil respiration. As plant productivity does not depend only on climate conditions, but also on other ecological 602 603 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 productivity to understand long-term variability in soil CO<sub>2</sub> emissions. Further 605 606 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

611

We thank all the CEH staff members who have contributed to the experiment 612 613 establishment and maintenance over the years, in particular Alwyn Sowerby and David 614 Williams. This research was funded by the EU projects CLIMOOR, VULCAN and 615 INCREASE FP7-INFRASTRUCTURE-2008-1 (Grant Agreement no. 227628) - the 616 INCREASE project. M.T.D was supported by two postdoctoral fellowships awarded by 617 the Spanish Government (National Science and Technology Foundation and Juan de la 618 Cierva fellowship). We thank two anonymous reviewers for their suggestions on previous 619 versions of the manuscript.

620

### 621 **References**

Aanderud ZT, Schoolmaster Jr DR, Lennon JT. 2011. Plants mediate the sensitivity of
soil respiration to rainfall variability. Ecosystems 14: 156–67.

624	Bader NE, Cheng W. 2007. Rhizosphere priming effect of Populus fremontii obscures
625	the temperature sensitivity of soil organic carbon respiration. Soil Biology and
626	Biochemistry 39: 600–6.
627	Beier C, Emmett B, Gundersen P, Tietema A, Peñuelas J, Estiarte M, Gordon C, Gorissen
628	A, Llorens L, Roda F, Williams D. 2004. Novel approaches to study climate
629	change effects on terrestrial ecosystems in the field: drought and passive nighttime
630	warming. Ecosystems 7: 583–97.
631	Beier C, Emmett BA, Tietema A, Schmidt IK, Peñuelas J, Láng EK, Duce P, De Angelis
632	P, Gorissen A, Estiarte M, de Dato GD, Sowerby A, Kröel-Dulay G, Lellei-
633	Kovács E, Kull O, Mand P, Petersen H, Gjelstrup P, Spano D. 2009. Carbon and
634	nitrogen balances for six shrublands across Europe. Global Biogeochemical
635	Cycles 23.
636	Benjamini Y, Hochberg Y. 2000. On the adaptive cntrol of the false discovery rate in
637	multiple testing with independent statistics. Journal of Educational and Behavioral
638	Statistics 25: 60–83.
639	Bond-Lamberty B, Thomson A. 2010. Temperature-associated increases in the global soil
640	respiration record. Nature 464: 579-582
641	Ciais P, Reichstein M, Viovy N, Granier A, Ogee J, Allard V, Aubinet M, Buchmann N,
642	Bernhofer C, Carrara A, Chevallier F, De Noblet N, Friend AD, Friedlingstein P,
643	Grunwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G,
644	Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert
645	G, Soussana JF, Sanz MJ, Schulze ED, Vesala T, Valentini R. 2005. Europe-wide

reduction in primary productivity caused by the heat and drought in 2003. Nature437: 529–33.

648 Cranfield University. 2014. The Soils Guide. Available: www.landis.org.uk. Cranfield
649 University, UK.

- 650 (http://www.landis.org.uk/services/soilsguide/series.cfm?serno=755). Last
  651 accessed 18/11/2014.
- Curiel-Yuste J, Janssens IA, Carrara A, Ceulemans R. 2004. Annual Q10 of soil
  respiration reflects plant phenological patterns as well as temperature sensitivity.
  Global Change Biology 10: 161–9.
- Curiel-Yuste J, Ma S, Baldocci DD. Plant-soil interactions and acclimation to temperature
   of microbial-mediated soil respiration may affect predictions of soil CO<sub>2</sub> efflux.
   Biogeochemistry 98: 127–38.
- Davidson EA, Holbrook NM. 2009. Is temporal variation of soil respiration linked to the
  phenology of photosynthesis? In: Noormets A, editor. Phenology of ecosystem
  processes-applications in global change research. New York: Springer-Verlag. pp
  187–99.
- Davidson EA, Janssens IA. 2006 Temperature sensitivity of soil carbon decomposition
  and feedbacks to climate change. Nature 440: 165–73.
- Delpierre N, Soudani K, François C,Le Maire G, Bernhofer C, Kutsch W, Misson L.,
  Rambal S, Vesala T, Dufrêne E. 2012. Quantifying the influence of climate and
  biological drivers on the interannual variability of carbon exchanges in European
  forests through process-based modelling. Agricultural and Forest Meteorology,
  154–155: 99–112.

669	Domínguez M, Sowerby A, Smith A, Robinson D, Van Baarsel S, Mills RE, Marshall M,
670	Koller E, Lebron I, Hall J, Emmett B. 2015. Sustained impact of drought on wet
671	shrublands mediated by soil physical changes. Biogeochemistry 122: 151-63.
672	Dijkstra FA, Cheng W. 2007. Interactions between soil and tree roots accelerate long-
673	term soil carbon decomposition. Ecology Letters 10: 1046–53.
674	Emmett BA, Beier C, Estiarte M, Tietema A, Kristensen HL, Williams D, Peñuelas J,
675	Schmidt I, Sowerby A. 2004. The response of soil processes to climate change:
676	results from manipulation studies of shrublands across an environmental gradient.
677	Ecosystems 7: 625–37.
678	Epron D, Nouvellon Y, Roupsard O, Mouvondy W, Mabiala A, Saint-André L, Joffre R,
679	Jourdan C, Bonnefond J-M, Berbigier P, Hamel O. 2004. Spatial and temporal
680	variations of soil respiration in a Eucalyptus plantation in Congo. Forest Ecology
681	and Management 202: 149–60.
682	Freeman C, Ostle N, Kang H. 2001. An enzymic 'latch' on a global carbon store. Nature
683	409: 149-149.
684	Fenner N, Freeman C. 2011. Drought-induced carbon loss in peatlands. Nature Geosci 4:
685	895-900.
686	Fierer N, Colman BP, Schimel JP, Jackson RB. 2006. Predicting the temperature
687	dependence of microbial respiration in soil: A continental-scale analysis. Global
688	Biogeochemical Cycles 20: GB3026
689	Fontaine S, Barot S, Barre P, Bdioui N, Mary B, Rumpel C. 2007. Stability of organic
690	carbon in deep soil layers controlled by fresh carbon supply. Nature 450: 277–80.

691 Gimingham CH. 1972 Ecology of heathlands. London: Chapman Hall.

- Hall J, Curti C, Dore T, Smith R. 2014. Methods for the calculation of critical loads and
  their exceedances in the UK, draft report to UK Department of Environment and
  Rural Affairs-DEFRA. <u>http://nora.nerc.ac.uk/505595/</u>. Last accessed 7 September
  2015.
- Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Högberg MN, Nyberg G,
  Ottosson-Lofvenius M, Read DJ. 2001. Large-scale forest girdling shows that
  current photosynthesis drives soil respiration. Nature 411: 789–92.
- Irvine J, Law BE, Martin JG, Vickers D. 2008. Interannual variation in soil CO<sub>2</sub> efflux
  and the response of root respiration to climate and canopy gas exchange in mature
  ponderosa pine. Global Change Biology 14: 2848–59.
- 702 Ise T, Dunn AL, Wofsy SC, Moorcroft PR. 2008. High sensitivity of peat decomposition 703 to climate change through water-table feedback. Nature Geosciences 1: 763-766. 704 Janssens IA, Lankreijer H, Matteucci G, Kowalski AS, Buchmann N, Epron D, Pilegaard 705 K, Kutsch W, Longdoz B, Grünwald T, Montagnani L, Dore S, Rebmann C, 706 Moors EJ, Grelle A, Rannik Ü, Morgenstern K, Oltchev S, Clement R, 707 Guðmundsson J, Minerbi S, Berbigier P, Ibrom A, Moncrieff J, Aubinet M, Bernhofer C, Jensen NO, Vesala T, Granier A, Schulze E-D, Lindroth A, Dolman 708 709 AJ, Jarvis PG, Ceulemans R, Valentini R. 2001. Productivity overshadows 710 temperature in determining soil and ecosystem respiration across European 711 forests. Global Change Biology 7:269-78.

712	Jia X, Zhou X, Luo Y, Xue K, Xue X, Xu X, Yang Y, Wu L, Zhou J. 2014. Effects of
713	substrate addition on soil respiratory carbon release under long-term warming and
714	clipping in a tallgrass prairie. PLoS ONE 9:e114203.

- Jing Y, Guan D, Wu J, Wang A, Jin C, Yuan F. 2015. An experimental comparison of
  two methods on photosynthesis driving soil respiration: girdling and defoliation.
  PLoS ONE 10: e0132649.
- Jones PD, Jonsson T, Wheeler D. 1997. Extension to the North Atlantic oscillation using
  early instrumental pressure observations from Gibraltar and south-west Iceland.
  International Journal of Climatology 17: 1433–50.
- Kirschbaum MUF. 2004. Soil respiration under prolonged soil warming: are rate
   reductions caused by acclimation or substrate loss? Global Change Biology 10:
   1870-1877.
- Knohl A, Werner R, Brand W, Buchmann N. 2005. Short-term variations in  $\delta^{13}$ C of ecosystem respiration reveals link between assimilation and respiration in a deciduous forest. Oecologia 142: 70-82.
- Knapp A, Carroll CW, Denton E, La Pierre K, Collins S, Smith, M. 2015. Differential
  sensitivity to regional-scale drought in six central US grasslands. Oecologia 177:
  949–957.
- Kopittke GR, van Loon EE, Tietema A, Asscheman D. 2013. Soil respiration on an aging
  managed heathland: identifying an appropriate empirical model for predictive
  purposes. Biogeosciences 10: 3007–38.
- Knorr W, Prentice IC, House JI, Holland EA. 2005. Long-term sensitivity of soil carbon
  turnover to warming. Nature 433: 298-301.

- Kuzyakov Y, Gavrichkova O. 2010. Time lag between photosynthesis and carbon dioxide
  efflux from soil: a review of mechanisms and controls. Global Change Biology
  16: 3386–406.
- Larsen KS, Ibrom A, Beier C, Jonasson S, Michelsen A. 2007. Ecosystem respiration
  depends strongly on photosynthesis in a temperate heath. Biogeochemistry 85:
  201–13.
- Liu L, King JS, Booker FL, Giardina CP, Lee Allen H, Hu S. 2009. Enhanced litter input
  rather than changes in litter chemistry drive soil carbon and nitrogen cycles under
  elevated CO<sub>2</sub>: a microcosm study. Global Change Biology 15: 441–53.
- Luo Y, Zhou X. 2006. Soil respiration and the environment. Burlington, MA, USA:
  Academic Press.
- Mahecha M, Reichstein M, Carvalhais N, Lasslop G, Lange H, Seneviratne SI, Vargas R,
  Ammann C, Arain MA, Cescatti A, Janssens IA, Migliavacca M, Montagnani L,
  Richardson AD. 2010. Global convergence in the temperature sensitivity of
  respiration at ecosystem level. Science 329: 838–40.
- Maier CA, Kress LW. 2000. Soil CO<sub>2</sub> evolution and root respiration in 11 year-old
  loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient
  availability. Canadian Journal of Forest Research 30: 347–59.
- Marcolla, B., Cescatti, A., Manca, G., Zorer, R., Cavagna, M., Fiora, A., Gianelle, D.,
  Rodeghiero, M., Sottocornola, M., Zampedri, R. 2011. Climatic controls and
  ecosystem responses drive the inter-annual variability of the net ecosystem

- exchange of an alpine meadow. Agricultural and Forest Meteorology 151: 1233–
  1243.
- Met-Office. 2012. Met Office Integrated Data Archive System (MIDAS) Land and
  Marine Surface Stations Data (1853-current). NCAS British Atmospheric Data
  Center.
- 761 Migliavacca, M, Reichstein M, Richardson AD, Colombo R, Sutton MA, Lasslop G, Tomelleri E, Wohlfahrt G, Carvalhais N, Cescatti A, Mahecha, MD, Montagnani 762 L, Papale D, Zaehle S, Arain A, Arneth A, Black TA, Carrara A, Dore S, Gianelle 763 764 D, Helfter C, Hollinger D, Kutsch WL, Lafleur PM, Nouvellon Y, Rebmann C, Da Rocha HR, Rodeghiero M, Roupsard O, Sebastiá MT, Seufert G, Soussana JF, 765 766 Van Der Molen MK. 2011. Semiempirical modeling of abiotic and biotic factors 767 controlling ecosystem respiration across eddy covariance sites. Global Change Biology 17: 390–409. 768
- Ottersen G, Planque B, Belgrano A, Post E, Reid PC, Stenseth NC. 2001. Ecological
  effects of the North Atlantic Oscillation. Oecologia 128: 1–14.
- Peñuelas J, Prieto P, Beier C, Cesaraccio C, De Angelis P, De Dato G, Emmett BA,
  Estiarte M, Garadnai J, Gorissen A, Láng EK, Kröel-Dulay G, Llorens L,
  Pellizzaro G, Riis-Nielsen T, Schmidt IK, Sirca C, Sowerby A, Spano D, Tietema
  A. 2007. Response of plant species richness and primary productivity in
  shrublands along a north–south gradient in Europe to seven years of experimental
  warming and drought: reductions in primary productivity in the heat and drought
  year of 2003. Global Change Biology 13: 2563-2581.

778	Pietikäinen J, Pettersson M, Båath E. 2005. Comparison of temperature effects on soil
779	respiration and bacterial and fungal growth rates. FEMS Microbiology Ecology
780	52: 49–58.

Quin SLO, Artz RRE, Coupar AM, Woodin SJ. 2015. Calluna vulgaris-dominated upland
 heathland sequesters more CO<sub>2</sub> annually than grass-dominated upland heathland.
 Science of The Total Environment 505: 740–7.

Raich JW, Potter CS, Bhagawati D. 2002. Interannual variability in global soil
respiration, 1980–94. Global Change Biology 8: 800–12.

Ratkowsky DA, Olley J, McMeekin TA, Ball A. 1982. Relationship between temperature
and growth rate of bacterial cultures. Journal of Bacteriology 149: 1–5.

- Reichstein M. 2003. Modeling temporal and large-scale spatial variability of soil
   respiration from soil water availability, temperature and vegetation productivity
   indices. Global Biogeochemical Cycles 17: 1104.
- Reynolds B, Chamberlain PM, Poskitt J, Woods C, Scott WA, Rowe EC, Robinson DA,
  Frogbrook ZL, Keith AM, Henrys PA, Black HIJ, Emmett BA. 2013. Countryside
  Survey: National "Soil Change" 1978–2007 for Topsoils in Great Britain—
  Acidity, Carbon, and Total Nitrogen Status. Vadose Zone Journal 12.

Richardson AD, Hollinger DY, Aber JD, Ollinger SV, Braswell BH. 2007.
Environmental variation is directly responsible for short- but not long-term
variation in forest-atmosphere carbon exchange. Global Change Biology 13: 788–
803.

- Rinnan R, Rousk J, Yergeau E, Kowalchuk GA, Bååth E. 2009. Temperature adaptation
  of soil bacterial communities along an Antarctic climate gradient: predicting
  responses to climate warming. Global Change Biology 15: 2615–25.
- Rinnan R, Michelsen A, Bååth E. 2011. Long-term warming of a subarctic heath
  decreases soil bacterial community growth but has no effects on its temperature
  adaptation. Applied Soil Ecology 47: 217–20.
- Robinson DA, Jones SB, Lebron I, Reinsch S, Domínguez MT, Smith AR, Jones DL,
  Marshall MR, Emmett BA. 2016. Experimental evidence for drought induced
  alternative stable states of soil moisture. Scientific Reports 6:20018.
- Sampson DA, Janssens IA, Curiel-Yuste J, Ceulemans R. 2007. Basal rates of soil
  respiration are correlated with photosynthesis in a mixed temperate forest. Global
  Change Biology 13: 2008–17.
- Scott-Denton LE, Sparks KL, Monson RK. 2003. Spatial and temporal controls of soil
  respiration rate in a high-elevation, subalpine forest. Soil Biology and
  Biochemistry 35: 525–34.
- Shao J, Zhou X, He H, Yu G, Wang H, Luo Yi, Chen J, Gu L, Li B. 2014. Partitioning
  climatic and biotic effects on interannual variability of ecosystem carbon
  exchange in three ecosystems. Ecosystems 17: 1186–201.
- Stoy PC, Richardson AD, Baldocchi DD, Katul GG, Stanovick J, Mahecha MD,
  Reichstein M, Detto M, Law BE, Wohlfahrt G, Arriga N, Campos J, McCaughey
  JH, Montagnani L, Paw U KT, Sevanto S, Williams M. 2009. Biosphere-

- 820 atmosphere exchange of  $CO_2$  in relation to climate: a cross-biome analysis across 821 multiple time scales. Biogeosciences 6: 2297–312.
- Sowerby A, Emmett BA, Williams D, Beier C, Evans CD. 2010. The response of
  dissolved organic carbon (DOC) and the ecosystem carbon balance to
  experimental drought in a temperate shrubland. European Journal of Soil Science
  61: 697-709.
- Sulzman EW, Brant JB, Bowden RD, Lajtha K. 2005. Contribution of aboveground litter,
  belowground litter, and rhizosphere respiration to total soil CO<sub>2</sub> efflux in an old
  growth coniferous forest. Biogeochemistry 73: 231-256.
- Suseela V, Conant RT, Wallenstein MD, Dukes JS. 2012. Effects of soil moisture on the
  temperature sensitivity of heterotrophic respiration vary seasonally in an old-field
  climate change experiment. Global Change Biology 18: 336-348.
- Tang X-L, Zhou G-Y, Liu S-G, Zhang D-Q, Liu S-Z, Li J, Zhou C-Y. 2006. Dependence
  of soil Respiration on soil Temperature and soil moisture in successional forests
  in Southern China. Journal of Integrative Plant Biology 48: 654–63.
- Thiessen S, Gleixner G, Wutzler T, Reichstein M. 2013. Both priming and temperature
  sensitivity of soil organic matter decomposition depend on microbial biomass –
  An incubation study. Soil Biology and Biochemistry 57: 739–48.
- Thomas CK, Law BE, Irvine J, Martin JG, Pettijohn JC, Davis KJ. 2009. Seasonal
  hydrology explains interannual and seasonal variation in carbon and water
  exchange in a semiarid mature ponderosa pine forest in central Oregon. Journal of
  Geophysical Research: Biogeosciences 114.

842	Trumbore S. 2000. Age of soil organic matter and soil respiration: radiocarbon constraints
843	on belowground C dynamics. Ecological Applications 10: 399–411.
844	Wan S, Luo Y. 2003. Substrate regulation of soil respiration in a tallgrass prairie: Results
845	of a clipping and shading experiment. Global Biogeochemical Cycles 17.
846	Wang X, Piao S, Ciais P, Janssens IA, Reichstein M, Peng S, Wang T. 2010. Are
847	ecological gradients in seasonal $Q_{10}$ of soil respiration explained by climate or by
848	vegetation seasonality? Soil Biology and Biochemistry 42: 1728–34.
849	Wang Y, Li Q, Wang H, Wen X, Yang F, Ma Z, Liu Y, Sun X, Yu G. 2011. Precipitation
850	frequency controls interannual variation of soil respiration by affecting soil
851	moisture in a subtropical forest plantation. Canadian Journal of Forest Research
852	41: 1897–906.
853	Wei W, Weile C, Shaopeng W. 2010. Forest soil respiration and its heterotrophic and
854	autotrophic components: Global patterns and responses to temperature and
855	precipitation. Soil Biology and Biochemistry 42: 1236–1244.
856	Yan J, Zhang D, Zhou G, Liu J. 2009. Soil respiration associated with forest succession
857	in subtropical forests in Dinghushan Biosphere Reserve. Soil Biology and
858	Biochemistry 41: 991–9.
859	Zhou T, Shi P, Hui D, Luo Y. 2009. Global pattern of temperature sensitivity of soil
860	heterotrophic respiration $(Q_{10})$ and its implications for carbon-climate feedback.
861	Journal of Geophysical Research: Biogeosciences 114.

Zhu B, Cheng W. 2011. Rhizosphere priming effect increases the temperature sensitivity
of soil organic matter decomposition. Global Change Biology 17: 2172–83.

864	Zuur A, Ieno EN, Walker N, Saveliev A, Smith GM. 2009. Mixed Effects Models and
865	extensions in Ecology with R. New York, USA: Springer-Verlag.
866	
867	
868	
869	
870	
871	
872	
873	
874	
875	
876	
877	
878	
879	
880	
000	
001	
882	
883	
884	
885	Tables
886	
887	Table 1. Results of the selected linear mixed models applied to summer and annual
888	cumulative CO <sub>2</sub> emissions as response variables, and a selection of climate variables as

predictors. Both models included a spherical autocorrelation structure term to account for temporal autocorrelation. The model for summer emissions also included a variance covariate term (dependent on summer maximum temperatures), needed to improve the structure of model residuals. The increase in goodness of fit (decrease in AIC values) from null models (which assume no influence of any climate predictors on summer or annual emissions) is indicated. Summer Tmax: average of daily maximum temperatures during the summer season.

- 896
- 897

Response Variable	AIC	ΔΑΙϹ	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
Table 2. Results of the linear mixed models applied to summer and annual cumulative								
CO <sub>2</sub> emissions as response variables, and aboveground plant biomass as predictor. Both								
models included a spherical autocorrelation structure term to account for temporal								

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.
- 914

	Response Variable	AIC	ΔAIC	Intercept	Predictor	Estimated	St. error	t-value	p-value	
	Summer CO <sub>2</sub>				Aboveground	purumeter				
	emissions	303.87	-1.21	63.85	biomass	0.038	0.019	1.97	0.0592	
	Annual CO <sub>2</sub> emmisions	325.68	0.62	286.62	Aboveground biomass	0.043	0.027	1.64	0.114	
915										
916										
917										
918										
919										
920										
921										
922										
923										
924										
925										
926										
927										
928										
929										
930	Figure caption	S								
931	Fig 1. Smooth functions resulting from the application of additive mixed models to air									

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

smoothing terms. The first term, accounting for annual cycles, was a function of the Julian
day of each measurement (a, c), and used cyclic penalized cubic regression spline smooth.
The second term, accounting for possible decadal time trends, was a function of the
cumulative number of days since the date of the first measurement (January 2000), using
plate regression spline or cubic regression spline smooths (b, d). See Table S1 for a
summary of model results.

939

Fig. 2. a) Variation in summer air temperatures (average of daily maximum values) and
the North Atlantic Oscillation Index (NAO index) of the summer seasons for the 20002012 period. Annual and winter rainfall is also shown (b).

943

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 model to soil temperature time series. The first smoother (b), accounting for annual 947 cycles, was a function of the Julian day of each measurement, and used cyclic penalized 948 cubic regression spline smooth. The second smoother (c), accounting for possible decadal 949 time trends, was a function of the cumulative number of days since the date of the first 950 951 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 depth, mean of three plots). 953

954

955 Fig. 4. a) Aboveground biomass of the plant community over the 2000-2012 period 956 (symbols, mean  $\pm$  standard error, left axis), and number of growing-degree days (GDD) during the summer seasons (grey line, right axis). b) C-fixing biomass of the dominant 957 958 plant species (*Calluna vulgaris*) over the studied period (symbols, mean ± standard error, left axis), and number of growing-degree days (GDD) during the summer seasons (grey 959 line, right axis). In both graphs p-values correspond to the linear positive relationship 960 961 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 an autocorrelation structure term to account for repeated measures of plant productivity 963 964 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 of model results. c) Relative changes in C. vulgaris C-fixing biomass (index of plant 966 967 productivity) over the 2000-2012 period (percentage of change from inter-annual average). C-fixing biomass estimated by pin-point calibration, from the number of hits of 968 969 green C. vulgaris leaves.

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 trends, was a function of the cumulative number of days since the date of the first 976 977 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  $\pm$  standard error for three plots) for the 2000-2012 period. Inter-annual average is indicated. 979

Fig. 6. Seasonal soil respiration rates for the 2000-2012 period (mean ± standard error).
Average soil temperatures (0-5 cm depth) during the seasons are also shown (grey line,
right-axis).

984

985 Fig. 7. a) Apparent sensitivity of soil respiration to soil temperature (indicated by apparent  $Q_{10}$  values) over the study period (average  $\pm$  standard error of the three 986 987 experimental plots for each year). b) Relationship between apparent temperature sensitivity and aboveground plant biomass (individual plots). P-value corresponds to the 988 linear positive relationship between apparent temperature sensitivity and total 989 aboveground plant biomass. This linear mixed model included an autocorrelation 990 991 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 °C.

994

Fig. 8. Result of a principal components analysis applied to the inter-annual variations of 995 annual soil respiration (R<sub>vear</sub>) and a selection of climate and vegetation variables. The 996 997 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. vulgaris), as an index of plant productivity; Su. Tmax: average of daily maximum 999 1000 temperatures during the summer season. Su. Soil M: average soil moisture during the summer season; Su. Soil T: average soil temperature during the summer season; Sp. 1001 1002 Tmin: average of daily minimum temperatures during the spring season.

Fig. 9. Summer (a) and annual (b) cumulative respiration predicted by the linear mixed 1004 models applied to CO<sub>2</sub> emissions, with average of summer daily maximum temperatures 1005 as climate predictor (black lines). 95% confidence intervals (grey lines) and p-values are 1006 also shown. These linear mixed models included an autocorrelation structure term to 1007 1008 account for repeated measures of soil respiration on the same plots over the 13-year period (spherical autocorrelation). See Table 1 for a summary of model results. Measured 1009 1010 summer and annual cumulative respiration is also shown (symbols, average  $\pm$  standard error of the three experimental plots for each year). 1011