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How well can we predict soil respiration with climate indicators, now and in the future?

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Abstract

Soils contain the largest terrestrial store of carbon; three times greater than present atmospheric concentrations, whilst the annual soil-atmosphere exchange of carbon is an order of magnitude larger than all anthropogenic effluxes. Quantifying future pool sizes and fluxes is therefore sensitive to small methodological errors, yet unfortunately remains the second largest area of uncertainty in Intergovernmental Panel on Climate Change projections.

The flux of carbon from heterotrophic decomposition of soil organic matter is parameterized as a rate constant. This parameter is calculated from observed total soil carbon efflux and contemporaneously observed temperature and soil moisture. This metric is then used to simulate future rates of heterotrophic respiration, as driven by the projections of future climate- temperature and precipitation. We examine two underlying assumptions: how well current climate (mean temperature and precipitation) can account for contemporary soil respiration, and whether an observational parameter derived from this data will be valid in the future.

We find mean climate values to be of some use in capturing total soil respiration to the 95 % confidence interval, but note an inability to distinguish between subtropical and Mediterranean fluxes, or wetland-grassland and wetland-forest fluxes.

Regarding the future, we present a collection of CO_2 enrichment studies demonstrating a strong agreement in soil respiration response (a 25 % increase) independent of changes in temperature and moisture, however these data are spatially limited to the northern mid-latitudes.

In order to "future-proof" simple statistical parameters used to calculate the output from heterotrophic soil respiration, we propose a correction factor derived from empirical observations, but note the spatial and temporal limitations.

In conclusion, there seems to be no sound basis to assume that models with the best fit to contemporary data will produce the best estimates of future fluxes, given the methods, future dynamics and the nature of the observational constraints. Only

through long-term field observations and appropriate, perhaps novel, data collection can we improve statistical respiration modelling, without adding mechanistic details at a computational cost.

1 Introduction

5 The future response of the terrestrial carbon cycle is the second largest contributor to climate prediction uncertainty (Bodman et al., 2013). The terrestrial carbon balance is the product of net primary production (NPP) minus effluxes through heterotrophic respiration (Arneth et al., 2010), and complicated through natural (e.g. fire and herbivory) and anthropogenic (land use change and biogeochemical cycle alterations) dis-
10 turbance processes. Resolved globally, recent estimates suggest a terrestrial carbon sink of $2.2 \pm 0.4\,\mathrm{Pg\,C\,yr^{-1}}$ (Le Quére et al., 2009), largely due to increases in productivity associated with recent aforestation, reforestation, abandonment of farmland and, to a lesser extent, CO_2 and nitrogen enrichment (Pan et al., 2011). The first signs of sink saturation in European forests are postulated by Nabuurs et al. (2013), and future
15 dynamics are not only dependent on productivity efficacy, but also the sensitivity of soil respiration to changes in climate.

Microbial decomposition of soil organic carbon (SOC) and leaf litter is enzyme-mediated, and as such is a strongly temperature sensitive process (Lloyd and Taylor, 1994; Knorr et al., 2005). It is therefore anticipated that higher soil temperatures, in the
20 presence of adequate water, will increase microbial activity and thus the heterotrophic respiration (Rh) component of the carbon cycle (Cox et al., 2000), leading to a large positive climate-carbon cycle feedback. Of particular concern then, are the large estimates of stored carbon in the world's soils, the decomposition of which is susceptible to increases in temperature: Jobbágy and Jackson (2000) estimated 2344 Pg C to 3 m
25 depth; nearly four times the amount of C in plant biomass and three times greater than atmospheric CO_2. This implies that the flux of soil respiration to the atmosphere can continue unabated, even if above-ground inputs of new, labile carbon are reduced.

These stores are highly dynamic: the annual flux of respired carbon to the atmosphere is an order of magnitude higher than all annual anthropogenic emissions (Field and Raupach, 2004). Clearly, even small changes in this flux could have huge ramifications for the atmospheric CO_2 pool and any associated feedbacks. Under future climate scenarios, it is feared that soil respiration will exceed net primary production and the currently observable, globally averaged carbon sink will become a source.

The current modeling methodology, used in all coupled global climate models in the latest Intergovernmental Panel on Climate Change report (Todd-Brown et al., 2012; IPCC, 2013), is to derive heterotrophic soil carbon efflux values by up-scaling a first order decay parameter observable at the site-scale over the worldwide, estimated, soil pools. The global applicability and conservancy of intrinsic rates of decomposition have been called into question (Davidson and Janssens, 2006). Chiefly, this method relies singularly on an interpolated rate constant, derived from temperature–efflux correlations at the site-scale, which is then extrapolated to spatial and, critically, temporal ranges far outside the boundary conditions of its' formulation. Such a statistical parameter is not appropriate to forecast how a complex, process-based system will behave under conditions different to those occurring when the parameter is derived, i.e. conditions not observed when the regression between temperature and efflux is interpolated. Additionally, the temperature and moisture values used by the decay parameter are calculated in the future by predicted temperature and precipitation, another key source of uncertainty. Regardless, there is still much support from both theory and observations: for example, Litton et al. (2011) show a strong positive linear relationship between mean annual temperature and respiration in Hawaiian tropical montane wet forests.

We use meta-analysis to test the assumptions that climate indicators can estimate soil carbon efflux now and in the future, on a macro scale analogous to the coarse scale of climate models.

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2   Methods

Using the publicly available dataset of Bond-Lamberty and Thomson (2010), all site data that contains soil respiration (Rs), mean annual precipitation (MAP) and mean annual temperature (MAP) is collated. Additionally, data pertaining to gross primary productivity (GPP), net ecosystem productivity (NEP) and estimates of the heterotrophic to autotrophic ratio of soil respiration is also considered.

To avoid pseudoreplication, the data is examined on a per paper basis. If a paper reports respiration measurements taken at the same site over a number of years with the same MAT and MAP throughout, then the average total soil respiration (Rs) is used, as time-series do not represent independent statistical replicates (Crawley, 2010). Likewise, papers providing Rs data that is not spatially independent are also averaged to arrive at one value for the reported MAP and MAT (the climate) and location.

With papers that sought to study the artificial manipulation of soil respiration as a proxy for climate change, i.e. through CO_2 fertilization, temperature modifications or soil moisture manipulations, the control study values are used, unless otherwise stated. In studies that reported the same MAP and MAT values, but provided separate Rs values for different aboveground species cover or stand age, are also averaged and considered representative of a heterogeneous landscape within the respective prevailing climatic means. The only further manipulation of data is the removal/separation of especially high altitude sites (> 2000 m) when a two-tailed t test confirms the mean of these data as statistically different from the greater population.

3   Results and discussion

3.1   Contemporary fluxes

The distribution of all known field observations of total soil respiration (Rs) is plotted on Fig. 1. Even at a glance, a distribution bias is obvious. Less than 11 % are in high north-

ern latitudes: in other words, roughly 27 independent sites to represent 14.7 million km^2 of boreal forest, covering 11 % of the Earth's land area (Bonan and Shugart, 1989), and tundra, a further 6 % (Oechel and Vourlitis, 1994), totaling some 25 (Gorham, 1991) to > 50 % (Hobbie et al., 2000; Tarnocai et al., 2009) of the global carbon pool. Addition-

5   ally, there appears to be a bias towards coastal sites, probably reflecting natural population trends (Fig. 1 inset). A recent field study by Berridge et al. (2013) shows a strong increase in summer soil respiration with distance inland. If this observation pertains to a consistent mechanism, then the current distribution of field sites may well be yielding misleading meta-trends. The size of the circles in Fig. 1 is a product of the observed

10 magnitude of total soil respiration. Globally, the assumption that warmer mean annual temperatures (MAT) and mean annual precipitation (MAP) produce higher respiration is confirmed as significant, but weakly ($r^2 = 0.19$ $p < 0.001$ and $r^2 = 0.11$ $p < 0.001$, respectively).

    Tukey's Honest Significance Difference Test (HSD) calculates the significance of pair-

15 wise differences in sample means. Figure 2 uses HSD to illustrate the mean differences between terrestrial biomes in total soil respiration (Rs), and the corresponding mean annual temperature (MAT) and precipitation (MAP) where the respiration data was observed. Whenever the horizontal bar does not cross zero, there is a significant difference in mean value; the ninety five per cent confidence interval is proportional to the

20 length of the bars. At a glance, the climate drivers accord with the values of total soil carbon efflux at the ecosystem and biome scale, suggesting that the differences in MAT and MAP that determine the biome classification are sufficient to also estimate soil respiration. However, no significant difference is observable between subtropical–Mediterranean respiration and temperate–subtropical respiration, in the presence of

25 a statistically significant difference in both mean annual temperature and precipitation for these biomes. Likewise, there is a statistically significant difference between wetland–grassland and wetland–forest respiration, in the absence of a commensurate difference in MAP and MAT (Supplement 1). This reveals that processes and conditions within a climate zone, such as porosity, soil organic matter and phenology (Raich and

Tufekcioglu, 2000), are strong enough to exert a control on total soil respiration greater than can be inferred from climatic averages alone. Importantly, fallacious climate-based soil carbon flux estimates, particularly in carbon-rich arctic wetlands, will accumulate into erroneous predictions of the terrestrial carbon cycle feedback. This is perhaps

5   prevalent in the mid-latitudes (30–60° N and S: Fig. 1; inset), where mean annual temperature (MAT) and mean annual precipitation (MAP) are poor explanatory variables of total soil respiration ($r^2 = 0.07$ $p < 0.001$, $r^2 = 0.014$ $p = 0.05$; MAP and MAT, respectively). The site-specific variation is such that simple temperature–moisture parameterizations in these regions are unlikely to capture reality, and subsequently carry forward

10 significant uncertainty in bottom-up estimates of regional and global soil respiration rates.

Taking this further, Fig. 3 shows mid-latitude soil respiration in relation to the two primary climatic drivers: temperature and precipitation. The data is discretized into ranges, where each increment in mean annual precipitation (MAP) shows a commen-

15 surate increase in the median respiration value and upper quartiles (Fig. 3a), up until the highest MAP range. This points to a general increase in respiration facilitated by increased precipitation. The dip at the uppermost extreme (2000–3000 mm) is likely due to the drawbacks of using MAP as a proxy for bio-available water: with high precipitation, run-off becomes a more important component of the hydrological balance,

20 allowing water to bypass infiltration, thence levels of evapotranspiration tend to remain relatively constant in sites experiencing > 1500 mm of MAP (Schulze, 2005). Additionally, several sample sites within the highest precipitation box-plot (Fig. 3a) are at high-altitude where, despite receiving large amounts of water, infiltration into the soil is inhibited by seasonally frozen grounds and snow cover (Indeed, an F test shows the

25 mean of the high altitude sites to be statistically independent).

Conversely, the box-plots of respiration within incremental mean annual temperature (MAT) ranges proffer little obvious average trend (Fig. 3c), a finding that runs counter to the well-documented site-scale dependency of respiration on temperature (Kirschbaum, 1995; Fang and Moncrieff, 2001; Karhu et al., 2010). One consistent

pattern in Fig. 2c is the increase in the upper range of respiration in concert with in-creasing temperature, coinciding with a relatively stable lower range (the "whiskers" of the box-plots). One interpretation is, in line with Arrhenius kinetics of decomposition and experimental observations (Davidson et al., 1998; Tuomi et al., 2008; Zanchi et al.,

5 2012), that increases in temperature stimulate metabolic activity of soil microbes and thus increase the maximum respired carbon. Remembering Liebig's law of the Mini-mum (Von Liebig, 1840), this can only be realized when there are no other limitations. In this case, increased respiration with higher mean annual temperature is only real-ized when there is a transport medium of sufficient quality to bring nutrients of sufficient

10 abundance (Fleischer et al., 2013) and extract waste from metabolically active sites, i.e. bio-available soil moisture. In the absence of limiting nutrients, substrates and their locomotion, respiration will be constrained regardless of any temperature increases, hence the constant lowest extremes in the ranges of respiration observed across the box-plots of Fig. 3c.

15 Interestingly, if one correlates the corresponding MAP with the respiration values used in each temperature range as presented in Fig. 3c, statistically significant asso-ciations can be found (Fig. 3d; data taken from 9–12 °C range within Fig. 2c; $r = 0.74$, $p < 0.001$). This has the coarse effect of controlling for the influence of temperature on respiration in order to better assess the control that precipitation alone exerts. When

20 this process is repeated for temperature, by plotting the respiration data within the discrete MAP brackets with their corresponding MAT as the independent variable, no significant correlations are found (Fig. 3b). This is despite the data presented within Fig. 3 arriving from papers frequently reporting far stronger relationships between tem-perature and respiration than with moisture at the site-scale. Evidently, this correlation

25 thus rather brakes down during inter-site comparisons.

To address the problems in using MAP as a proxy for bio-available soil moisture, we utilized MODIS satellite estimates of annual precipitation and potential evapotran-spiration for the relevant years and locations of study sites. MODIS potential evapo-transpiration (PET) correlated very well with MAT ($r^2 = 0.8$), suggesting the proxies are

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comparable. A principal component analysis (PCA) resolving for the following variables: soil respiration, mean annual temperature, mean annual precipitation, MODIS precipitation estimate for measurement year, MODIS estimate of potential evapotranspiration and latitude, unambiguously places mean and MODIS precipitation in the same plane as total soil respiration (Supplement 2). Potential evapotranspiration is tightly aligned with temperature, as expected, but not with Rs. This supports the above supposition that moisture emerges as the key cross-site constraint of soil respiration in the mid-latitudes, with little association to temperature, on annual timescales.

As discussed above, emissions from the decomposition of terrestrial carbon by heterotrophic respiration are often calculated as the product of a temperature sensitive decay rate acted upon the carbon pool. In other words, temperature and moisture can only facilitate decomposition if there is something to decompose, and total soil respiration is also sensitive to ambient soil carbon content. Surprisingly then, there is no obvious association between soil texture and soil respiration at this scale (Supplement 3), as might be expected given the strong association between soil texture and chemical and physical protection of soil organic matter to decay (Baldock and Skjemstad, 2000).

3.2 Soil Respiration in the Future

A fundamental limitation in the statistical parameterization of heterotrophic respiration is the lack of dynamism. Optimum biological functioning is a constant, but the realization of the optimum, as discussed above, is dynamic and will respond to numerous changes. One way to help "future-proof" the oft-used decay constant (typically from Lloyd and Taylor, 1994) is to incorporate a correction factor that accommodates anticipated change. Figure 5 shows the effect of artificially increased atmospheric carbon dioxide on soil respiration from independent observations, all but one of which show an increase ($n = 20$). This response is likely due to root-microbial interactions (Phillips, 2007), whereby CO_2 enrichment allows more photosynthesis, so long as soil biota can cycle nutrients faster within the soil. In symbiotic plants, this demand is met by a com-

mensurate stimulation of arbuscular mycorrhizal fungi root colonization and rhizobacte-
rial communities (Büscher et al., 2012), and observed as an increase in soil respiration
following increased carbon allocation to root symbionts (Fig. 4). Non-symbiotic plants
on the other hand benefit from a general promotion of plant growth promoting bacterial
species, such as *Pseudomonas* sp. (Marilley et al., 1999). However, the exact explana-
tion may be very site-specific, and in some instances can be due to a single bacterium
(*Pseudomonas mendocina* promotes lettuce growth under elevated CO_2; Kohler et al.,
2009). Additionally, the response of bacterial and fungal groups are disparate and de-
pendent on both soil nutrient status and plant type; both of which are also dynamic
(Drigo et al., 2009). The length of the CO_2 enrichment studies should also be noted as,
in the long-term following successional changes, plant-soil interactions can reduce the
digestibility of, for example, shortgrass steppe vegetation (Morgan et al., 2004), feeding
back into reduced litter respiration (Fig. 4)

Despite these myriad complications, the response is fairly constant and has a small
standard error (24.71 ± 1.94 %). As none of the vegetation modules of the global cir-
culation models used in the most recent IPCC report (Todd-Brown et al., 2012) have
any mechanisms representing belowground biota or their symbiosis with above-ground
communities, such a coarse correction factor is within the prevailing error. This does
not improve the fundamental method, but is an appealing low-hanging fruit. We note
a caveat (Supplement 4): the stated average carbon efflux increase of ~ 25 % is not
static, but depends on the initial efflux. The increase is higher when the initial flux is
higher, but not in relative terms (a log-decrease with higher initial soil respiration of
$r^2 = 0.2$).

3.3 Limitations of the data

MAT and MAP as proxies for soil temperature and bio-available soil moisture are not the
actual, exact conditions experienced at the site when respiration is being measured,
and they will seldom be realized in any given year. This was also a necessary source of
error, however, as data containing study temperature and precipitation is too meager to

be statistically meaningful in meta-analysis. We would be quick to point out that, despite these flaws in using MAP as a surrogate for bio-available water, as well as being blind to other co-variables (such as hysteresis within the system, herbivore grazing, microbial community structure and aboveground floral type and abundance; Fig. 4) there are still
5   strong associations evident between annual soil respiration and MAP, in the absence of comparable correlation with MAT for mid-latitudes (Fig. 3).

However, as previously mentioned, Litton et al. (2011) were able to show a strong association between MAT and annual soil respiration in Hawaiian tropical montane forests. The location of their study could be telling; the tropics are not moisture limited,
10   so increases in productivity and respiration with temperature are likely, and first-order temperature-dependent statistical modeling of soil respiration may be quite relevant. Throughout the mid-latitudes, however, it seems that the same temperature dynamics run secondarily to other forcings (Fig. 3). A promising emerging solution is to include a microbial biomass step in the temperature–respiration equation that can respond to
15   site-specific secondary drivers (Wieder et al., 2013).

Perhaps more importantly, human influence may be such that the climate conditions alone may be incapable of predicting reality, and intensity and history of human settlement will have overriding controls on ecosystems (Ellis et al., 2010 and Fig. 4).

Perhaps most importantly, the soil respiration data used herein is annual values, and
20   is better described as "total soil carbon efflux", as the exact process that bore the carbon (autotrophic, heterotrophic or inorganic) is unknown in most studies. The relative contribution of heterotrophic vs. autotrophic is not constant spatially or temporally, so using in situ total carbon efflux to parameterize the heterotrophic component carries errors pertaining to the unknown origin and age of carbon (and therefore decomposi-
25   tion temperature), which is in practice parameterizing predictions of the unknown with the immeasurable (Subke and Bahn, 2010).

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4 Conclusions

Resolving the heterotrophic respiration component of the carbon balance as a static function based on temperature and moisture is unchanged in the history of IPCC reporting (Todd-Brown et al., 2012). This can generally capture the broad patterns at the biome level, within the spatially limited data, but there is little justification to use this to predict future fluxes. There have been advancements in our ability to separate respective sources of soil carbon effluxes (Vargas et al., 2012), observations of multi-factor effects (Larsen et al., 2011; Dieleman et al., 2012), and some sound reasoning (Davidson et al., 2006; Subke and Bahn, 2010) that suggest this appealingly simplistic approach may be found lacking. Our observations and interpretations are in accordance with such views, however we do offer a correction factor for the effects of CO_2 fertilization on soil carbon efflux, but note caution.

Supplementary material related to this article is available online at http://www.biogeosciences-discuss.net/11/1977/2014/ bgd-11-1977-2014-supplement.pdf.

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Interactive Discussion

Distribution of all soil respiration field measurements, 1961-2010
n = 423

>3500   3000   2000   1000   500   <500

Highest soil respiration ever recorded in the field: 3821 g C m⁻², Mexico (Vargas et al., 2008)

Figure 1

Global distribution of all known soil respiration measuremnets taken in the field (Bond-Lamberty & Thomson, 2010).
Size of the circles is proportional to annual flux of total carbon dioxide. There is no differentiation or correction for the method used to estimate soil respiration.

Field sites USA only

Soil respiration g C m⁻² yr⁻¹

>2000   >1500   >1000   >500   <500
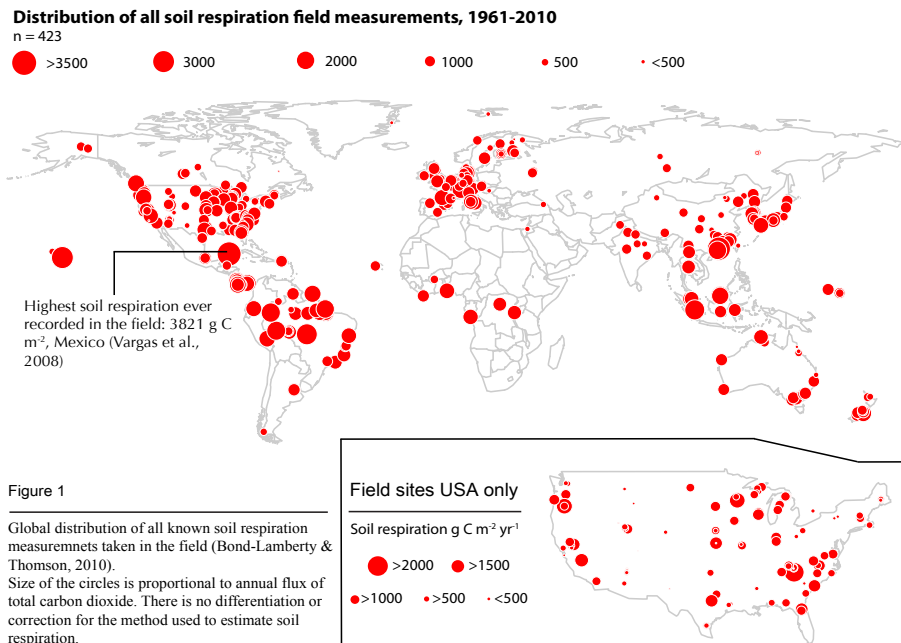
Fig. 1. Distribution of all known soil respiration studies between 1961 and 2010. The magnitude of observed soil respiration is represented by the size of the circles ($\mathrm{g\,C\,m^{-2}\,yr^{-1}}$).
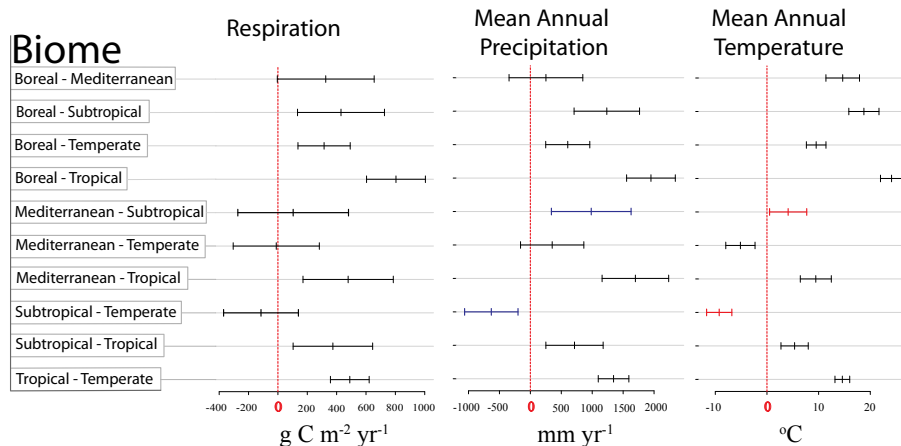
Fig. 2. Tukey's Honest Significance Difference Test (HSD) demonstrating the pairwise differences in sample means for respiration and mean annual precipitation and temperature for terrestrial biomes. Whenever the horizontal bar does not cross zero, there is a significant difference in mean value; the ninety five per cent confidence interval is proportional to the length of the bars.
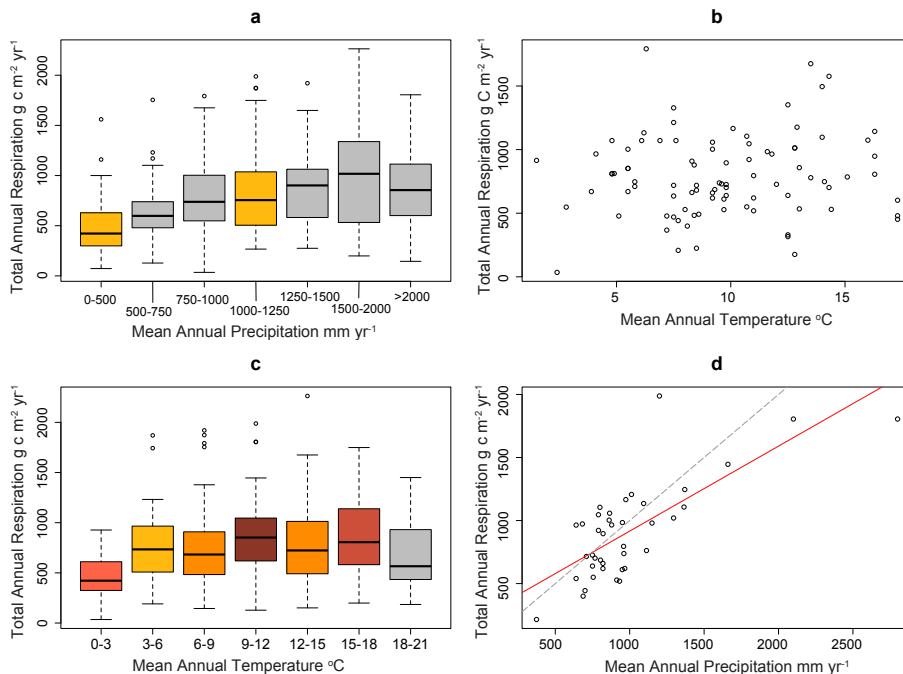
Fig. 3. (a) Box-plots showing the median, range and upper and lower quartiles of the respi-ration data as divided by discrete precipitation ranges. Note that the median value of respira-tion increases linearly with each increment in precipitation, until the uppermost increment. **(b)** The scatter plot of the respiration data contained within the 750–1000 mm range in **(a)** plot-ted against the corresponding mean annual temperature values as the independent variable. **(c)** Akin to **(a)**, but with the same data categorized by mean annual temperature instead of by mean annual precipitation. **(d)** Akin to **(b)**, this scatter plot is the respiration data taken from the 9–12°C range in **(c)** plotted against the corresponding mean annual precipitation values as the independent variable; $r = 0.744$, $p < 0.001$, $n = 40$; grey dashed line is 1 : 1 line.

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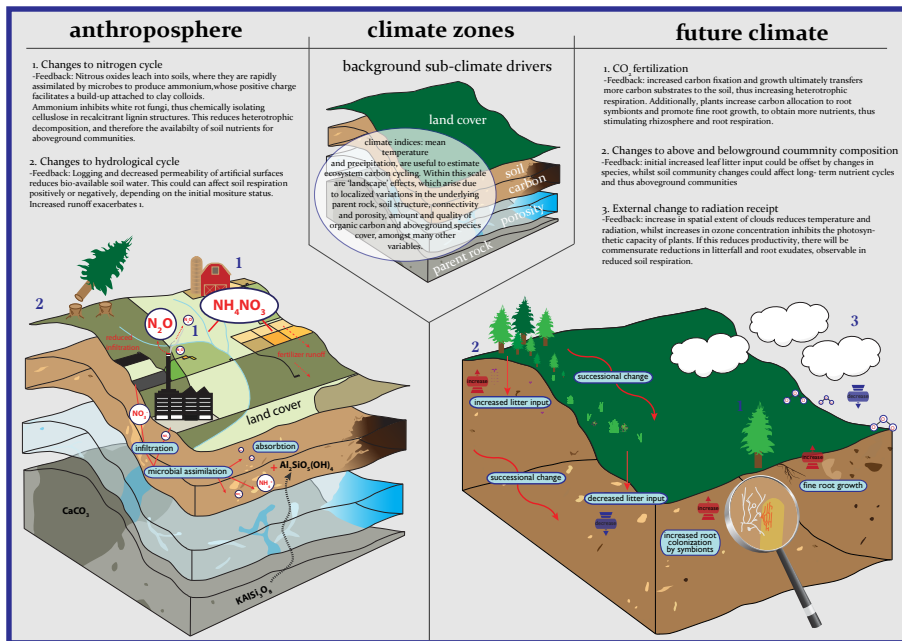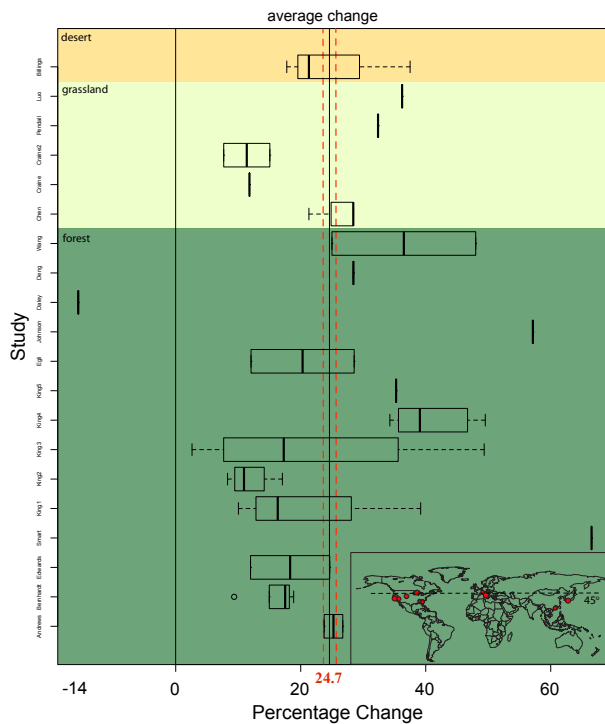Printer-friendly Version

Interactive Discussion

Fig. 4. Diagram illustrating important variations within climate zones (middle), the reality of human interference (left) and future potential future changes within climate zones (right).

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Interactive Discussion

Fig. 5. Spread of effects of artificially elevated atmospheric CO_2 on soil respiration for 20 independent studies, data from: King et al. (2001); King et al. (2004); Deng et al. (2010); Billings et al. (2004); Egil et al. (2001); Craine et al. (2001a, b); Edwards and Norby (1999); Bernhardt et al. (2006); Andrews and Schlesinger (2001); Daley et al. (2009); Luo et al. (1996); Pendall et al. (2003); Johnson et al. (1994); Smart and Peñuelas (2005); Chen et al. (2012); Wang et al. (2012). Average change: 24.71 ± 1.94 %. Relative change (percent increase) log-decreases with higher initial soil respiration (r^2 = 0.2, Supplement 4).