



Diminished soil functions occur under simulated climate change in a sup-alpine pasture, but heterotrophic temperature sensitivity indicates microbial resilience



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HIGHLIGHTS

- Climate change threatens sustainable use of mountain pastures by disturbing nutrient and carbon cycling.
- We simulated climate change through transplantation of intact pasture turfs along an elevation gradient.
- Moisture removed in situ temperature sensitivity of respiration.
- Respiration showed variable recovery after wetting, but comparable Q_{10} values among sites.
- Changes to soil function were seen after crossing a model-realistic climate threshold.

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ABSTRACT

The pressure of climate change is disproportionately high in mountainous regions, and small changes may push ecosystem processes beyond sensitivity thresholds, creating new dynamics of carbon and nutrient cycling. Given that the rate of organic matter decomposition is strongly dependent upon temperature and soil moisture, the sensitivity of soil respiration to both metrics is highly relevant when considering soil–atmosphere feedbacks under a changing climate. To assess the effects of changing climate in a mountain pasture system, we transplanted turfs along an elevation gradient, monitored in situ soil respiration, incubated collected top-soils to determine legacy effects on temperature sensitivity, and analysed soil organic matter (SOM) to detect changes in quality and quantity of SOM fractions. In situ transplantation down-slope reduced soil moisture and increased soil temperature, with concurrent reductions in soil respiration. Soil moisture acted as an overriding constraint to soil respiration, and significantly reduced the sensitivity to temperature. Under controlled laboratory conditions, removal of the moisture constraint to heterotrophic respiration led to a significant respiration-temperature response. However, despite lower respiration rates down-slope, the response function was comparable among sites, and therefore unaffected by antecedent conditions. We found shifts in the SOM quality, especially of the light fraction, indicating changes to the dynamics of decomposition of recently deposited material. Our findings highlighted the resilience of the microbial community to severe climatic perturbations, but also that soil moisture stress during the growing season can significantly reduce soil function in addition to direct effects on plant productivity. This demonstrated the sensitivity of subalpine pastures under climate change, and possible implications for sustainable use given reductions in organic matter turnover and consequent feedbacks to nutrient cycling.

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1. Introduction

Through altering temperature and precipitation regimes, climate change is projected to place increasing pressure on the sustainable use and productivity of semi-natural grassland systems. This is thought to be especially so for mountain grasslands such as those in the alpine

and sub-alpine zones (Dunne et al., 2003). Elevated growing-season temperatures and more frequent occurrence of drought periods have the capacity to alter carbon (C) and nutrient cycling at the ecosystem level (Walther et al., 2002), with potential for significant soil–plant feedbacks (Melillo et al., 2002). Higher temperatures may lead to enhanced C losses from soils (Bond-Lamberty and Thomson, 2010; Kirschbaum, 1995) and faster nutrient cycling (Shaw and Harte, 2001; Ineson et al., 1998; Zhang et al., 2012), yet these increases may be offset, or even reversed by the effect of reduced moisture status (Davidson and Janssens, 2006). Whilst dependent upon antecedent conditions and biological community adaptation, moisture stress, especially during the growing season, can lead to considerable reductions in C fixation, and rates of C and nutrient cycling. This is of particular concern given that soil respiration is the second largest annual flux (after photosynthesis) of C between the atmosphere and terrestrial systems (Houghton, 2007). It is therefore highly relevant to assess change in soil respiration under a changing climate. Soil respiration represents a useful and logistically simple measure of general soil function, as it encapsulates the end product of a range of metabolic processes involved in C and nutrient cycling, as well as organism activity. This is particularly important given that the long-term sustainability of ecosystems depends upon maintaining soil function; therefore respiration provides a broad yet sensitive indicator of change.

The fundamental metabolic dependence upon temperature suggests that rate should increase with temperature according to a simple response function (Arrhenius, 1889). In the case of soil respiration, this must assume that all other constraining factors are not limiting, but in situ, this is rarely the case over any significant spatial or temporal scale. Therefore, when measured in the field, the observed response to temperature is in fact the ‘apparent’ sensitivity, and recognises the myriad drivers that exist. The sensitivity to temperature is often encapsulated by the Q_{10} function, which essentially describes the change in rate over a 10 °C change in temperature. This function carries the benefit of being simple and comparable among systems, but is influenced by the statistical model used to derive the temperature–respiration fit (Lloyd and Taylor, 1994). Soil moisture also strongly constrains ecosystem function, and its effect on soil respiration, as well as the interaction with temperature, has been the subject of research for a considerable time (Orchard and Cook, 1983; Flanagan and Johnson, 2005; Yuste et al., 2007; Davidson et al., 2000; Xu et al., 2004; Sjögersten et al., 2012). The conceptual moisture–respiration model of Suseela et al. (2012) serves to summarise the occurrence of a moisture optimum, which approximately coincides with field capacity. The broad applicability of such a model, especially along gradients of drying from optimum, is evident (e.g. Chen et al., 2008), and such a relationship provides a basis for modelling dependencies. However, the interaction of soil moisture with temperature requires consideration of multi-factor approaches, and this dual-driving of function by moisture and temperature has been the focus of a substantial research effort (e.g. Davidson et al., 2000; Raich and Tufekciogul, 2000; Janssens and Pilegaard, 2003). This interaction becomes especially apparent when considering how moving away from soil moisture optima can strongly reduce the temperature sensitivity of soil respiration (Suseela et al., 2012; Lellei-Kovács et al., 2011; Sowerby et al., 2008). To assess the intrinsic temperature sensitivity of soil respiration, incubations of soil cores across temperature manipulations (Yuste et al., 2007; Fang and Moncrieff, 2001) can be used. This approach could also provide information on whether apparent sensitivity in situ is the product of real changes to intrinsic sensitivity, or more a function of other constraining factors.

Investigating change in soil function, and its sensitivity to moisture and temperature can be contextualised by considering changes to soil organic matter (SOM) quality and quantity, primarily as an indicator of any trajectories in C accumulation or loss. Whilst SOM is an inherently complex material that exists along a decomposition continuum, fractions of SOM that reflect early stages of decomposition can be separated

to serve as a more sensitive indicator to short-term change than bulk SOM. This is usually carried out by density separation, where a light fraction organic matter is separated (Sollins et al., 1984; Leifeld and Kögel-Knabner, 2005; Schindlbacher et al., 2010), and is assumed to be relatively available due to a lack of mineral interactions or aggregate occlusions. Not only does this fraction serve as a sensitive indicator of change, but the quality of the light fraction could also be related to temperature sensitivity (Schindlbacher et al., 2010). This relationship can be used to explore whether changes in temperature sensitivity of soil respiration are related to so-called ‘thermal acclimation’ (Bradford et al., 2008), or to changes in substrate quality (Fierer et al., 2005), which is central to respiration–temperature debate (Subke and Bahn, 2010).

Much experimental work to consider the role of climate change on soil and plant function has been based on in situ manipulations, yet natural climate gradients can also be used to study spatial variation in ecosystem processes (Emmett et al., 2004; Zhang et al., 2012). Using the established natural gradient of mean annual temperature (MAT) decrease and a precipitation (MAP) increase with higher elevation in mountain regions, one can conveniently substitute space for time in ecological climate change research (Körner, 2007). Soil monolith transplantation from high to low elevations has been shown to effectively simulate a warmer climate in various studies (see Hart and Perry, 1999; Ineson et al., 1998; Link et al., 2003; Olofsson, 2001; Sebastia, 2007), and across much larger spatial scales in general climate change contexts (Breeuwer et al., 2010). Such an approach provides a natural year-round experimental warming, which also accounts for associated changes in precipitation, snow-to-rain ratio, snowmelt, and length of the vegetation growing-season. Transplantation also allows combined temperature and moisture (multi-factor) treatments to be incorporated without possible issues relating to infrastructure effects and uneven treatment effect throughout the year (Carlyle et al., 2011).

To assess the impact of experimental climate change on soil respiration and SOM in sub-alpine pastures, we used an existing mesocosm transplantation experiment in the Swiss Jura Mountains (Gavazov et al., 2013a) where soil and vegetation were transplanted to four elevations representing a climate gradient in moisture and temperature. Soil respiration was measured in situ during the growing season of 2011, and we explored the relationships to moisture and temperature, and the apparent temperature sensitivity. To assess the intrinsic temperature sensitivity of the heterotrophic component of soil respiration, we sampled the uppermost organic layer of the soil and carried out a laboratory incubation across a temperature range. We also considered change to chemical characteristics of the soil organic matter, which we assessed on bulk soil, and on a light fraction of SOM separated by density. The transplantation approach used in this study spans the whole range of scenarios outlined by Meehl et al. (2007) and incorporates expected changes to precipitation for Switzerland (Frei et al., 2006). This set-up allowed for the detection of thresholds in response parameters, i.e. tipping points (see Lenton, 2011), which when reached, can trigger rapid changes in ecosystem function, with feedbacks to ecosystem resilience and sustainable use.

Given the observation of changes in community composition and productivity (Gavazov et al., 2013b), and the established driving of soil respiration by moisture, we first hypothesised that respiration would be reduced at transplantation sites as a function of soil moisture. Secondly, soil temperature was expected to have a control over soil respiration, but the strength of the relationship was hypothesised to reduce down the transplantation gradient in response to increasing moisture stress. For the laboratory incubations, we expected that removal of moisture constraints would establish temperature sensitivities among all soils, and that the strength of this relationship might vary as a function of in situ conditions. Finally, we assumed that lower productivity down-slope would result in lower abundance of light fraction organic matter,

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