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Discussions

Meta-analysis of high-latitude nitrogen-addition and warming studies imply ecological mechanisms overlooked by land models

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Abstract

Accurate representation of ecosystem processes in land models is crucial for reducing predictive uncertainty in energy and greenhouse gas feedbacks with the atmosphere. Here we describe an observational and modeling meta-analysis approach to benchmark land models, and apply the method to the land model CLM4.5 with two versions of belowground biogeochemistry. We focused our analysis on the above and belowground high-latitude ecosystem responses to warming and nitrogen addition, and identified mechanisms absent, or poorly parameterized in CLM4.5. While the two model versions predicted similar trajectories for soil carbon stocks following both types of perturbation, other variables (e.g., belowground respiration) differed from the observations in both magnitude and direction, indicating the underlying mechanisms are inadequate for representing high-latitude ecosystems. The observational synthesis attribute these differences to missing representations of microbial dynamics, characterization of above and belowground functional processes, and nutrient competition. We use the observational meta-analyses to discuss potential approaches to improving the current models (e.g., the inclusion of dynamic vegetation or different microbial functional guilds), however, we also raise a cautionary note on the selection of data sets and experiments to be included in a meta-analysis. For example, the concentrations of nitrogen applied in the synthesized field experiments (average $= 72\,\mathrm{kg\,ha^{-1}\,yr^{-1}}$) are many times higher than projected soil nitrogen concentrations (from nitrogen deposition and release during mineralization), which preclude a rigorous evaluation of the model responses to nitrogen perturbation. Overall, we demonstrate here that elucidating ecological mechanisms via meta-analysis can identify deficiencies in both ecosystem models and empirical experiments.

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1 Introduction

Northern Hemisphere high latitude soils are among the largest global stores of soil organic matter (SOM) (Grosse et al., 2011). Recent studies have estimated SOM storage within permafrost regions to be ∼ 1700 Pg to 3 m depth (Schuur et al., 2012), representing nearly 50 % of global terrestrial organic carbon, or nearly twice that currently in the atmosphere (King et al., 2007). Permafrost SOM is stabilized by cold temperatures, and is therefore vulnerable to the warming that high-latitude regions will experience over the next century (Schuur and Abbott, 2011). However, the response of high-latitude ecosystems to global climate change is complex. Under warming, the active layers of permafrost soils thicken, and may serve as a reservoir of chemically labile organic carbon. Carbon released from these soils (mostly as CO_2 or CH_4) may accelerate the rate of warming and form a positive feedback to climate change (Koven et al., 2011). Alternatively, elevated rates of organic matter decomposition could stimulate plant productivity, sequestering CO_2 from the atmosphere, serving as a negative feedback on climate change (Shaver et al., 1992).

Predictions of how future climate change will alter high-latitude soil carbon are derived mainly from (a) conclusions of in situ field manipulation studies and (b) output of land models either coupled or uncoupled with an atmospheric model. The coupled Earth System Models (ESMs) simulate biogeochemical and biophysical states and fluxes (including soil carbon dynamics and effluxes) and feedbacks to atmospheric carbon concentrations across decadal, centennial, and millennial time scales (Kaplan et al., 2002; Koven et al., 2011). Current ESMs have high uncertainty in their predicted magnitude of carbon-climate feedbacks (Arora et al., 2013; Friedlingstein et al., 2006) because of insufficiencies in model structure and parameterization (Bonan et al., 2011; Jung et al., 2007; Zaehle et al., 2005).

Consequentially, benchmarking the performance of these models has been challenging (Luo et al., 2012). One approach has been to compare model output against the output of manipulation studies (Thomas et al., 2013b) that acutely perturb ecosys-

tems on short time scales (months to years). However, field experiments with short experimental timeframes (months to years) and high rates of perturbation may not be representative of the long-term (decadal to centennial), and chronic nature of anthropogenic climate change. Furthermore, the broad spatial heterogeneity of high-latitude soils may not be well represented by the concentration of high-latitude field studies within a few sites. Herein, we benchmark the models by compiling data from a range of studies measuring the same variables across spatial gradients. This approach can determine an overall ecosystem response to perturbation, eliminating the weight placed on any one study. Data compilation can also identify important mechanisms that determine the fate of soil carbon but are currently not represented in the land models.

In the present study, we examined the fate of high-latitude soil carbon based on conclusions drawn from (1) meta-analyses of high-latitude field studies ($\geq 60°$ N) focusing on ecosystem responses to temperature and nitrogen perturbations and (2) meta-analyses of simulations mimicking the experiments using the land component (CLM4.5) of the Community Earth System Model (CESM). We address four questions: (1) Do the models and synthesized data predict a similar response of carbon and nutrient cycling to ecosystem perturbation? (2) In what areas do the models and experiments diverge? (3) What are the mechanisms, including those absent in the models, the field experiments demonstrate to be important for evaluating the fate of soil C? (4) What types of observationally derived model benchmarks are appropriate for the various ecosystem processes relevant to high-latitude soil C dynamics?

2 Materials and methods

2.1 Literature search

We compiled published observations for replicated field studies from high-latitude ecosystems ($\geq 60°$ N) (Fig. 1) examining responses of belowground biogeochemistry to warming and nitrogen addition. The data were mainly extracted from published figures

or tables, or directly from the authors in cases where unpublished results were referenced in a published study. Manipulation studies were located by searching the ISI Web of Knowledge, using the following principal terms: "Arctic", "Permafrost", "High-latitude", paired with: "Manipulation", "Nitrogen", "Warming". Where available, we collected data
5 from control and perturbed soils on microbial (i.e., bacterial + fungal) biomass (MB), fungal biomass (FB), aboveground biomass (AGB), belowground respiration (R_B), heterotrophic respiration (R_H), gross primary productivity (GPP), litter decomposition (LD), soil organic matter content (SOM), net nitrogen-mineralization (N_{min}), and soil and microbial nitrogen and phosphorus (P) concentrations.

10 To characterize the response of high-latitude soils to warming we collected data from studies that passively warmed soil using open top chambers (OTC) or greenhouses (OTG) and snow manipulation studies. We also collected data from studies that used incubations to increase temperature. We collected more than 2800 entries from 53 field studies across 17 different high-latitude ecosystems. We presented the data as
15 a response ratio across all of the studies. We also sought to understand the influence of duration on certain responses, and where appropriate, data was further partitioned by experimental duration: short-term ($< 2\,yr$), long-term ($> 5\,yr$) and intermediate (2–4 yr).

For nitrogen addition, we collected studies that applied nitrogen as either ammonium
20 nitrate (NH_4NO_3) or nitrogen phosphorus potassium fertilizer (NPK). We analyzed over 2300 entries (i.e., individual measurements of each metric (MB, R_H, etc.)) across 37 nitrogen addition field studies from 14 geographically distinct sites (Table S1). We examined the influence of geography on the response of our data sets by partitioning the data between that collected from European and North American manipulation studies.
25 The data was also temporally disaggregated in a similar manner as described above for the warming experiments.

Data were extracted from figures using the Data Thief software (Tummers, 2006). Comparison data were standardized to units of "$g\,m^{-3}$" prior to calculating a response ratio. Bulk density measurements for the different soils were extracted from the pub-

lished studies or through personal communication with the authors. In the cases where authors could not be contacted, bulk density was estimated using a previously published approach (Calhoun et al., 2001).

2.2 Meta analysis

Data were analyzed using the MetaWin 2.2 software package (Rosenberg et al., 2000), using the standard deviation (SD) reported from each individual observation. In the majority of cases, SD was calculated from the reported standard error and number of replicates. A response metric was calculated as the natural log of treatment group relative to a control:

$$\ln R = \ln \left(\frac{\overline{X}^{\mathrm{T}}}{\overline{X}^{\mathrm{A}}} \right)$$

Where $\overline{X}^{\mathrm{T}}$ and $\overline{X}^{\mathrm{A}}$ are the mean values for the treatment and ambient response variable, respectively. The sampling variance ($V_{\ln R}$) was calculated as:

$$V_{\ln R} = \frac{(s^{\mathrm{T}})^2}{N^{\mathrm{T}}(\overline{X}^{\mathrm{T}})^2} + \frac{(s^{\mathrm{A}})^2}{N^{\mathrm{A}}(\overline{X}^{\mathrm{A}})^2}$$

Where s^{T} and s^{A} represent the normalized standard deviations around the mean values and N^{T} and N^{A} are the number of replicate studies from treatment and ambient experiments, respectively. The effect size for different response metrics was subsequently calculated using a weighted average value, where the weight for the ith study is the reciprocal of its sampling variance.

A mixed model was used to calculate the cumulative differences in the response variables in treatment vs. control plots. These cumulative differences were calculated for the overall dataset, and also after constraining the datasets to similar conditions

and forcings (e.g., geographic location, magnitude of N added). When an effect size was drawn from a low number of contributing studies (< 15), the data was resampled (using 2500 iterations) by bootstrapping to give a conservative estimate of the confidence interval (CI). Data was also gathered on climate conditions (mean annual air temperature (MAT) and precipitation (MAP), and growing season mean air temperature (GSMT)) and experimental conditions (experimental duration and magnitude of warming or nitrogen added) for each site sampled. We used a regression analysis to examine whether variability in response variables (e.g., belowground respiration (R_B) and microbial biomass (MB)) was due to spatial differences in climate or due to experimental manipulation (e.g., warming or nitrogen added).

2.3 CLM-BGC spin-up and experimental manipulation scenarios

We simulated the ecosystem perturbation experiments using the community land model (CLM4.5) with two different representations of belowground biogeochemistry; a vertically resolved belowground module with similar biogeochemistry to the Century model (termed CLM-Century, Koven et al., 2013), and the Carbon–Nitrogen biogeochemistry module (termed CLM-CN, Thornton et al., 2007). CLM-Century and CLM-CN share the same formulation of aboveground biogeochemical processes and land biogeophysics, but differ in their representation of belowground carbon turnover and nitrogen cycling. For example, CLM-CN represents the belowground decomposition cascade as four discrete pools with faster turnover times than the three-pool approach used by CLM-Century (Koven et al., 2013). Furthermore, the nitrogen cycle of CLM-CN is much more open (i.e., higher cycling rates and losses) than that of CLM-Century. Finally, CLM-CN does not resolve the vertical biogeochemical gradients characteristic of CLM-Century. The models were spun up for 1500 yr to preindustrial equilibrium, and then run from 1850 to 1979 under contemporary climate forcing before the onset of perturbation conditions over the following 21 yr (from 1980 to 2000). Model simulations were parameterized to replicate the field experiments: the soil was warmed by scaling the aerodynamic resistance by a factor of 10, a value obtained by trial and error

to achieve a desired warming of $\sim 1\,°C$, while keeping sufficient spatial variability of the warming. CLM forces the soil heat transport process through the residual flux from incoming radiation, latent heat, and sensible heat. Increasing aerodynamic resistance reduces the sensible and latent heat fluxes and warms the soil during the growing season. We tried warming the soil by increasing the surface air temperature (which is a diagnostic variable in CLM), but this approach violated CLM's surface energy budget and was therefore avoided. Furthermore, increasing aerodynamic resistance is more analogous to the approach of installing open-top chambers to warm the soil.

Nitrogen was added in the form of NH_4NO_3 at concentrations that replicated the very high concentrations of the nitrogen addition experiments (20, 40, 60, 80 and 100 kg N ha^{-1} yr^{-1}). However, for comparison, we also simulated the model response to a range of nitrogen concentrations that reflect more realistic nitrogen deposition scenarios up to 2050 (0.2, 1.0, 2.0, 3.0 kg N ha^{-1} yr^{-1}, (Galloway et al., 2004). To mimic the approach of most field studies, we began the perturbation (warming or nitrogen addition) when a given model grid was snow free for 7 days (< 1 mm standing stock) and ended after more than 7 days with standing snow (> 1 mm standing stock).

Model output was collected for each site considered in the meta-analysis (Fig. 1) using a 3×3 grid that surrounded the experimental manipulation site at the center. The mean and standard deviation (SD) of predictions from the 9 grid cells were then used to calculate the response ratios from that site. For coastal sites, some modeled grid cells were not on land due to model spatial resolution, and data statistics were therefore scaled with the actual number of data points accordingly. For all sites we took the mean and SD of the grid cells and analyzed the data using the meta-analysis approach applied to the observations and described above. Our model analysis was limited to the output from the surface soil (10 cm for CLM-Century and bulk prediction for CLM-CN, which represents approximately the top 20 cm of soil) where the majority of the collected studies focused their measurements.

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3   Results

3.1   Response of belowground C-cycling to warming

On average, experimental warming increased soil temperatures by 1.4 °C (±0.7 °C). R_B increased significantly under warming by 9 % (±5 %) compared to the controls. However, this increase was largely driven by the response of European soils, where R_B increased 33 % (±11 %) above control soils. Conversely, R_B from North American soils showed a more modest, and non-significant, increase (2.5 %±6.5 %; Figs. 2a and S1b). It is unlikely that this difference is due to greater experimental warming of European soils: passive warming increased soil temperatures by 1.4 °C ± 0.6 °C in Europe and 1.3 °C ± 0.5 °C in North American experiments. A transient effect of R_B in high-latitude soils was also noted in the data set. Short term experiments (< 2 yr), showed a large significant increase (34.4 % ± 16 %) in R_B, which was not evident in studies lasting 2–4 yr. However, studies lasting ≥ 5 yr also had significant increases in R_B. GPP increased significantly (11.8 %) in warmed soils (Fig. 2a) and showed a positive relationship with R_B (Fig. 3).

Despite elevated GPP, litter decomposition (LD) declined significant by 9 % (±5 %), while SOM did not change significantly from control values (Fig. 2a). Both microbial (MB) and fungal (FB) biomass increased non-significantly under warming: MB increased 3.8 % (±12 %) while FB increased by 11.5 % (±19 %).

Under warming, soil nitrogen mineralization and soil nitrogen concentrations both declined non-significantly (N_{MIN}: 7.6 % ± 15 %, soil N = 5.1 % ± 9 %) below the control soils. Soil P increased non-significantly above the control soils (12.5 %±9 %, Fig. S1b). Finally, the use of the OTC and OTG to passively warm high-latitude soils significantly lowered soil moisture 6 % below the control soils (Fig. S1b).

Modeled warming experiments increased soil temperature by 1.21 °C ± 0.47 °C in CLM-CN and 0.91 °C ± 0.35 °C in CLM-Century. In response the two models predicted a stronger relative and absolute increase of R_B compared with the observational data. The models predicted higher LD in response to warming, which is in contrast with the

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decreasing trend found in the observational data. Both models also predicted increased N_{MIN} following warming, contrary to the observational data. The relative changes in SOM under warming were consistent between the model predictions and observations. In general, CLM-CN tended to predict a much stronger temperature response than CLM-Century (Fig. 2a).

3.2 Response of belowground carbon cycling to nitrogen addition

The field experiments added an average of $72\,kg\,N\,ha^{-1}\,yr^{-1}$ ($\pm 38\,kg\,N\,ha^{-1}\,yr^{-1}$) of nitrogen to soils, with a range of 1–$100\,kg\,N\,ha^{-1}\,yr^{-1}$. This additional N reduced belowground respiration (R_B) and resulted in a larger sink for SOM, indicating a negative feedback to atmospheric CO_2 concentrations (Fig. 2b). R_B in soils receiving additional N (in the form NH_4NO_3) declined 11.8% ($\pm 7\%$), significantly below control soils (Fig. 2b). This pattern was consistent for the two geographical regions examined and was not dependent on the duration of the experiment. R_B in European soils declined, non-significantly, by 7% ($\pm 9.5\%$) below control soils (Fig. S1a). R_B in North American soils also declined significantly by 12.7% ($\pm 9\%$). R_B showed a negative relationship with increasing soil nitrogen concentration (Fig. 4a). Linear regressions failed to uncover a significant relationship between the response of R_B and climate (MAT, MAP) or experimental factors (experimental duration and magnitude of nitrogen added). R_H showed no significant change under nitrogen addition; however, the data are highly variable ($\pm 12\%$). Nitrogen addition resulted in a significant decline in LD (% mass loss yr^{-1}) of 4.8% ($\pm 3\%$), while SOM increased significantly 19.5% ($\pm 10\%$) in perturbed soils.

GPP increased significantly under nitrogen addition ($44.3\% \pm 7.5\%$) compared with the control soils (Fig. 2b). On average, aboveground biomass (vascular + non-vascular plants) non-significantly increased upon nitrogen addition ($15\% \pm 22\%$). Vascular plant biomass increased significantly ($33\% \pm 8\%$) over that of the control soils (Fig. S1b).

Overall, a non-significant increase in MB was observed for experimental soils (Fig. 2b), yet, declined with increasing concentrations of nitrogen added to the soil

(Fig. 4b). When factoring in geographical location, microbial biomass in European soils increased significantly above the controls (17.5 % ± 9 %), but decreased non-significantly relative to control soils in North American soils (Fig. S1a). While different forms of nitrogen were applied in the experiments (e.g., NH_4NO_3 or NPK), the most significant factors, explaining 37 % of the variance in microbial biomass, were site-specific pH and mean annual temperature. Finally, fungal biomass increased significantly by 23 % (±20.5 %) compared to the control soils.

For nitrogen perturbed CLM-CN and CLM-Century simulations we analyzed the relative response of variables complementary to the observational meta-analysis. Under nitrogen addition, the modeled response variables matched observations for only two parameters: GPP and SOM, and only at the lowest nitrogen addition concentrations (i.e., $\leq 1\,kg\,N\,ha^{-1}\,yr^{-1}$, Fig. S3). Neither model accurately replicated the trend in the observed response of R_B, LD, and N_{MIN} (Fig. 2b), while both models overestimated the response of R_H.

4 Discussion

Accurate representation of the processes governing soil carbon cycling in high-latitude soils is crucial for reducing model uncertainty in energy and greenhouse gas feedbacks with climate. By comparing meta-analyses based on model output and observations, we show that the current large-scale ecosystems models are unable to adequately represent many of the observed high-latitude ecosystem responses to global change. We focus our discussion on the potential reasons for the discrepancies in responses by highlighting: (1) the most important mechanisms currently missing from, or poorly represented in, the models; and (2) instances where deficiencies in the experimental approaches prohibits the data from being used for benchmarking the model. We also recommend further approaches to improve the mechanistic basis of the belowground biogeochemistry representation in ESMs.

4.1 Response of belowground carbon cycling to warming

The observational meta-analysis suggests that elevated belowground respiration is balanced by elevated GPP (and associated increases in soil organic matter). We therefore conclude that the coupling of aboveground and belowground processes resulted in these soils being carbon neutral under modest (+1.3 °C) warming. This result is contrary to conclusions from previous experimental manipulations (Hobbie et al., 2000) and model analyses (Burke et al., 2013; Koven et al., 2011), which have concluded that warming will increase SOM turnover and C loss of permafrost soils, but is supported by recent manipulation experiments (Natali et al., 2011), studies performed across temperature gradients (Lavoie et al., 2011), and meta-analyses across diverse terrestrial ecosystems (Lu et al., 2013). This disparity in reported SOM change in response to warming likely stems from the interdependent mechanisms affecting carbon stabilization under a warming climate (e.g., nutrient dynamics, oxygen penetration, nutrient limitations and mineral-organic matter complexation). Similarly, the models also predicted no significant changes to belowground SOM content under warming due to concomitant increases in R_B and GPP. However, the magnitude of the modeled fluxes is many times larger than the observed fluxes. Therefore, the net impact of the manipulation was predicted by the models, but for different reasons.

As a broader point, we believe this result illustrates a common problem among tests of land model performance, i.e., inferences of model fidelity based on comparisons solely with observations or emergent responses. The problem can be particularly acute when the emergent response is a relatively small difference between two large fluxes. As another example, the use of net ecosystem exchange (NEE) as a sole model benchmark (Schwalm et al., 2010) ignores that: (1) NEE is typically a small difference between ecosystem respiration and assimilation and (2) models separately represent these gross fluxes as being differently controlled by climate and antecedent system states. We contend that accurately representing this type of emergent ecosystem prop-

erty of flux gives little information as to whether the model is accurately representing the underlying mechanisms appropriately.

The coupling between aboveground and belowground components of the ecosystem is crucial for understanding high-latitude carbon cycling under a changing climate. The meta-analysis of field measurements showed a general stimulation of aboveground activity under warming. Previous field studies have noted that warming in high-latitude ecosystems drives a shift in plant community composition, favoring the establishment of deciduous shrubs and graminoids and selecting against mosses and lichens (Schuur et al., 2007; Sistla et al., 2013; Walker et al., 2006). This shift toward more woody plants changes the ecosystem carbon balance and nutrient dynamics (Jackson et al., 2002; Welker et al., 2004), as shrubs tend towards higher internal carbon allocation toward woody tissue, but also may increase higher belowground carbon allocation (as both litter and exudates) relative to mosses (Hobbie, 1996; Street et al., 2013). This belowground allocation may results in the observed relationship between GPP and R_B (Fig. 3), indicating a close coupling between these two processes. This relationship may develop either due to higher rates of belowground labile root exudation, which may be respired directly by the plants themselves (Luo, 2007), or by the priming of the microbial community and elevation of overall SOM decomposition rates (Fontaine et al., 2004). Our data cannot directly distinguish between the two pathways, however, the observed decline in litter decomposition rates indicate that the elevated belowground respiration rates principally reflect the priming mechanism, as the mineralization of plant exudates spurs the degradation of older soil organic matter (Hartley et al., 2012); however, more data (e.g., radiocarbon measurements) are required to verify this conclusion.

Current models crudely represent above- and belowground biogeochemical coupling and do not represent some of the crucial roles plants play in soil carbon dynamics (Ostle et al., 2009; Schmidt et al., 2011). A comparison of the observational and modeled response to warming shows an overestimation by the models for a number of variables, and the opposite response sign for others (e.g., nitrogen mineralization). Be-

low, we identify several areas of aboveground biogeochemistry that could constrain above and belowground responses to warming in high-latitude ecosystems.

Of particular relevance to high-latitude ecosystems is the models' lack of any representation of cryptogams or bryophytes. These plants contribute substantially to above-
ground biomass and biogeochemical processes in tundra soils (Cornelissen et al., 2007; Elbert et al., 2012) and are clearly important for accurate simulations of tundra carbon dynamics. Few ESM land models (including CLM4.5) include dynamic vegetation, and when it is included, representation tends to be coarse (Ostle et al., 2009). The lack of vegetation dynamics precludes the impact of community shifts under a chang-
ing climate, and the resultant feedbacks to decomposition rates due to changes in litter quality or root depth (Cornwell et al., 2008). In addition, the models do not represent root exudates, which precludes the representation of priming of belowground communities preceding the decomposition of more chemically complex organic matter (Cheng et al., 2013; Fontaine et al., 2007). Significant progress has been made toward a more
detailed inclusion of plant dynamics that include updated mechanisms governing the size and aging structure of aboveground ecosystem demography (Huntingford et al., 2008; Moorcroft et al., 2001), soil carbon dynamics (Riley et al., 2014), and nitrogen cycling (Fisher et al., 2010). Integration of these approaches into the CLM framework may improve the robustness of long-term tundra soil simulations and reduce uncer-
tainty associated with the aboveground model response.

The observational data indicated elevated R_B under warming. The response of microbial heterotrophs to warming can partially be explained by kinetic theory, whereby biochemical reaction rates increase with increasing temperature (Davidson and Janssens, 2006). Hydrolytic and oxidative extracellular enzymes, secreted to de-
polymerize complex organic matter (Allison et al., 2010), are sensitive to temperature (German et al., 2012). Structural modifications in cold ecosystems maximize their specific activity under in situ temperatures relative to temperate ecosystems (Hochachka and Somero, 2002), and this acclimation can result in significantly enhanced activity under warming (Koch et al., 2007). This theory fits with the short-term (< 2 yr) data

from the current meta-analysis showing increasing belowground respiration despite no increase in microbial biomass.

However, we also identified a drop in R_B in studies lasting longer than 2 yr and shorter than 5 yr (Fig. S1b). R_B has consistently been reported to decline under prolonged warming (Rustad et al., 2001) and attributed to substrate limitation (Hartley et al., 2008) or the adaptation of microbial populations to warmer temperatures offsetting the kinetic response of individual microbes (Bradford, 2013; Bradford et al., 2008). Given the increased GPP found in our meta-analysis, belowground communities are unlikely to be substrate limited. Therefore, we hypothesize that community acclimation is likely responsible for the drop in R_B under longer warming. Thermal respiratory acclimation has been demonstrated experimentally for plants (Atkin, 2003), fungi (Crowther and Bradford, 2013; Malcolm et al., 2008), and bacteria (Bradford et al., 2008). However, the physiological acclimation of individuals in an endemic community is likely to be outpaced by the rate of community turnover in soils undergoing experimental warming (Deslippe et al., 2012; Rinnan et al., 2008; Sistla et al., 2013). The ecological consequences of microbial community turnover are complex, but can alter the functional potential of soils, which in turn may alter the rate of organic matter breakdown and nutrient cycling.

The subsequent increase in R_B over prolonged warming (> 5 yr) could represent either the decomposition of leaf litter driven by changes in microbial community composition, or thawing subsurface organic matter (Dorrepaal et al., 2009). This is an important point with regards to the long-term fate of high-latitude carbon. In the current analysis, NEE appears balanced, with no change in SOM. However, temporal patterns of vegetation response to warming show a transient response to warming, with nutrient limitation reducing plant productivity on longer time scales (Arft et al., 1999; Chapin and Shaver, 1996). It is possible, given the large nitrogen immobilization under warming, that R_B may continue longer than productivity, unbalancing NEE and leading to net carbon loss. The long-term nature of above- and belowground response to warming is, therefore, an important research priority for future studies.

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Temperature is a key factor influencing biogeochemical mechanisms in the model. CLM models R_B using a static Q_{10} and carbon use efficiency (CUE) that varies as a function of the SOM pool size. This may result in the large predicted increase in modeled R_B. In reality, both Q_{10} and CUE vary on spatial and temporal scales, and
5 respond non-linearly to changes in temperature (Janssens and Pilegaard, 2003; Sinsabaugh et al., 2013). Recent microbe-explicit models (MEMs) that consider basic microbial physiology (e.g., Lawrence et al., 2009) introduce direct biological control over soil carbon cycling and different conclusions on soil carbon pool size and dynamics under warming (Allison et al., 2010; Wieder et al., 2013). For example, by scaling the
10 CUE value with temperature, in accordance with publish observations (Luo et al., 2001; Melillo, 2002), the MEMs show a decline in soil carbon turnover under warming (Li et al., 2014; Wieder et al., 2013). However, it is also important to note that microbial CUE is not solely temperature-dependent, and other factors, some of which are already present in both CLM-CN and CLM-Century (including nutrient limitation, and soil mois-
15 ture), may uncouple growth and respiration, impacting on CUE (Manzoni et al., 2008; Sinsabaugh et al., 2013). The predictions of the microbe-explicit models (MEM) provide further impetus for greater representation of the structure and function of belowground biomass.

Further aspects of belowground ecology in high-latitude tundra that are not included
20 in the models can have a significant impact on the stability of soil carbon (also see discussion below on barriers to benchmarking). For example, while there is little evidence that fungal: bacterial ratios are altered by warming, either in our observational meta-analysis or in previous work (Strickland and Rousk, 2010), the community composition may change without altering fungal: bacterial ratios (Strickland and Rousk,
25 2010). Therefore it is still important to differentiate the two main decomposing groups with respect to certain physiological traits that could influence R_B (Six et al., 2006). Traits such as biomass stoichiometry, nutrient use efficiency (NUE; see discussion below), substrate utilization and response to environmental variables (e.g., temperature or soil moisture) can bring about changes in the activity of decomposing guilds and the

significance should be tested in MEMs and potentially incorporated in ESMs. These factors are arguably more important than climate when modeling decomposition at local and regional scales (Bradford et al., 2014).

Further disagreement between the observations and models was also found for litter decomposition. Under warming, LD declined in the observations, possibly contributing to SOM accumulation, but was stimulated in the models. In previous studies, the response of LD to warming was largely dependent on the method used to increased soil temperature (Aerts, 2006). OTCs tend to warm the soil and reduce soil moisture, limiting litter decomposition by saprotrophic fungi. Soil moisture in the models showed a non-significant increase with warming as the permafrost began to thaw (Fig. 2a). The difference between the observational meta-analysis and the models represents a potentially confounding factor in using this data to benchmark the model. A more comprehensive meta-analysis of litter decomposition in Arctic and Alpine tundra found that warming induced a small increase in decomposition provided sufficient soil moisture (Aerts, 2006). This response was not apparent in our data syntheses, but suggests the model results, while overestimating LD, were at least in the appropriate direction. Soil moisture is an important controller on decomposition (Aerts, 2006; Hicks Pries et al., 2013). However, changes to surface hydrology during permafrost thaw are dependent on thermokarst formation and topological features of the landscape (Jorgenson and Osterkamp, 2005) and may result in increased or decreased soil moisture. We identify these issues as important for further experimental and modeling work in order to better represent future changes in surface hydrology and the consequences for LD.

Confronting the model outputs with observations showed a consistent overestimation of key variables in the models (Fig. 2a). One potential reason for a larger modeled response is the approaches CLM-CN and CLM-Century take to representing the nitrogen cycle. The inclusion of nitrogen cycling in coupled carbon-nitrogen climate models is consistent with the idea that nitrogen is a significant determinant of carbon cycling in many ecosystems (Hungate, 2003; Vitousek and Howarth, 1991), and modeled nitrogen input, retention, and loss have been shown to have a large impact on ecosystem

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carbon sequestration (Thomas et al., 2013b; Zaehle and Dalmonech, 2011). Moreover, data based modifications to ESM nitrogen cycling mechanisms may further improve the correspondence between observations and model output (Thomas et al., 2013a).

CLM-CN parameterizes high rates of nitrogen loss from volatilization and nitrate leaching, and is therefore more responsive than CLM-Century to changing nitrogen availability from inputs, mineralization, and loss. Under warming CLM-CN predicted a significant loss of soil nitrogen not predicted in CLM-Century, which has a more closed nitrogen cycle, possibly more representative of the nitrogen cycle in high-latitude soils (Barsdate and Alexander, 1975). Rates of nitrogen fixation, deposition and redox cycling (i.e., nitrification and denitrification) are low at high latitudes (Cleveland et al., 1999; Giblin et al., 1991), and hydrological loss of nitrogen at the beginning of the growing season is relatively large (Harms and Jones, 2012; Jones et al., 2005). Mineralization is, therefore, the main source of nitrogen for plant and microbial growth (Shaver et al., 1992).

Mineralization rates are controlled by the depolymerization of proteinaceous substrates that are the dominant nitrogen-containing compounds in soils (Jones et al., 2009; Schulten and Schnitzer, 1997). Mineralization leads to the release of amino acids (Schimel and Bennett, 2004) that are rapidly utilized by both plants and microbes (Kielland, 1994; Weintraub and Schimel, 2005). Ammonia is then released during turnover of the dead biomass. Depolymerization is the critical step in this process and, like organic matter decomposition, is dependent on microbial physiology and subject to the biotic and abiotic controls described above. The balance between the release of nitrogen and immobilization is represented by the microbial nitrogen use efficiency (NUE) (Mooshammer et al., 2014). The NUE is thus an important concept for high-latitude ecosystems, as a carbon sink will only be maintained under sufficient nitrogen availability (Shaver et al., 1992). The models represent nitrogen mineralization as a rate for each belowground SOM pool and there is no consideration for the complexity of nitrogenous compounds (Schulten and Schnitzer, 1997) or the NUE of belowground communities controlling the depolymerization of nitrogenous compounds. Therefore,

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modeled N-mineralization increases under warming with a concomitant increase in soil nitrogen in the CLM-Century framework. CLM-CN, with its high rates of mineral nitrogen losses shows a very large decline in soil nitrogen, possibly rendering the above- and belowground communities nitrogen limited throughout. In our data analyses, nitrogen mineralization declined as microbial nitrogen (i.e., immobilization) increases. The end result in both cases (i.e., the models and observations) is the potential limitation of plant growth over long time scales. Our data synthesis suggests that the release of nitrogen from increased decomposition is used to meet microbial demands or immobilized. Immobilization is regulated by the stoichiometric imbalance between the substrate being depolymerized and the physiological nutrient demand. While analogous to the CUE, NUE is regulated independently in order to maintain cell stoichiometry. Some attempts have been made to incorporate NUE controls into ecosystem models (Manzoni and Porporato, 2009), but further experimental and modeling work is required to understand NUE's plasticity and impacts on soil carbon dynamics.

4.2   Response of belowground carbon cycling to nitrogen addition

Our meta-analysis of field observations found that the addition of inorganic nitrogen to traditionally nitrogen limited ecosystems enhances the carbon sink, consistent with previous studies (Luo et al., 2012; McGuire et al., 2012). Interactions between the carbon and nitrogen cycles resulting in soil carbon accumulation in different ecosystems have been reported previously (Magnani et al., 2007; Thomas et al., 2013b), and have been attributed to an increased carbon allocation to woody tissue (Ciais et al., 2008; Tummers, 2006) and reduction in the SOM decomposition rate (Olsson et al., 2005). Overall, our data-synthesis is largely consistent with the overarching conclusions of previous meta-analyses (Janssens et al., 2010; Knorr et al., 2005).

A question remains, however, about the value of the responses synthesized from studies adding extremely high amounts of nitrogen. The average concentration of nitrogen added to the soils in the tundra studies ($\sim 72\,\text{kg ha}^{-1}\,\text{yr}^{-1}$) is extremely high when compared with (1) estimates of nitrogen fixation ($< 10\,\text{kg ha}^{-1}\,\text{yr}^{-1}$, (Cleveland et al.,

1999); (2) nitrogen deposition (both current rates of deposition 0.2–0.24 kg ha^{-1} yr^{-1}, (Jones et al., 2005) and projections of future deposition (Galloway et al., 2004)); and (3) potential nitrogen availability from organic matter mineralization under a warming climate (Harden et al., 2012). Consequentially, we question whether such data lends itself to understanding the response of the ecosystem to realistic chronic incremental changes in nitrogen availability, and the benefit of benchmarking the ecosystem models against such a dataset. We give further examples below of where the high nitrogen concentrations may confound the interpretation of the experiments with respect to the model predictions.

SOM accumulation under nitrogen addition experiments is a common feature of both the field experiments and the model simulations. However, the underlying mechanisms leading to SOM accumulation are very different, adding uncertainty to the model predicted soil carbon fate over longer timescales. In both versions of CLM, the alleviation of nitrogen limitation stimulates a number of ecosystem processes including aboveground primary productivity, litter decomposition, and organic matter decomposition (R_B). The accumulation of SOM indicates the stimulation of GPP and LD (the carbon cascade simulates the decomposition of litter into the SOM pools) must outweigh losses from increased R_B.

The observations, on the other hand, show a significant decline in R_B and LD under nitrogen addition. R_B depends on the decomposition and substrate utilization capabilities of the microbial (i.e., bacterial and fungal) community to mineralize root exudates and litter. A drop in R_B may, therefore, be attributable to several mechanisms not included in either version of CLM. A recent meta-analysis examined the response of Boreal forest ecosystems to added nitrogen (Janssens et al., 2010), and concluded that the internal reallocation of carbon in plants and trees reduced the rate of exudation to belowground ecosystems, resulting in microbial biomass becoming carbon limited with a concomitant decline in both biomass and R_B (Janssens et al., 2010). Our empirical data shows increased GPP and vascular plant biomass, possibly indicating

a reallocation of newly fixed carbon in vascular plants (Ciais et al., 2008) and a drop in belowground exudation.

Overall, the current observational meta-analysis found a non-significant increase in microbial biomass (i.e., bacterial and fungal) but a significant increase in fungal biomass under nitrogen addition. This response appears contrary to previous studies that have recorded a drop in microbial biomass under nitrogen addition (Treseder, 2008), but in line with fertilization studies in tundra ecosystems (Clemmensen et al., 2006). We also note that microbial biomass (and R_B) are inversely related to the amount of nitrogen added to the soils (Fig. 4a and b). At low nitrogen concentrations microbial community activity can be stimulated (Allison et al., 2009) and decomposition elevated, as captured by the models (Fig. 2b), and some of the observations (Fig. 4b). Elevated nitrogen concentrations, however, have a negative impact on microbial biomass (Treseder, 2008) and decomposition (Janssens et al., 2010). This response can occur through the inhibition of lignin-degrading enzymes produced by saprotrophic fungi (Sinsabaugh et al., 2002; but see Hobbie, 2008). Alternatively, the addition of inorganic N can increase the chemical recalcitrance of soil carbon through condensation reactions with soil organic matter (Dijkstra et al., 2004) increasing the physical protection of organic matter from decomposition. Therefore, under the high nitrogen inputs used in the present field studies, the coupling between above- and belowground ecosystems can decrease R_B and LD resulting in an accumulation in SOM.

The relatively open (CLM-CN) or closed (CLM-Century) modeled nitrogen cycles do not appear responsible for the discrepancy between the observations and model results. Both representations of belowground biogeochemistry assume nitrogen limitation and show a non-asymptotic relationship between ecosystem processes and nitrogen availability, such that adding more nitrogen increases the rate of all nitrogen-dependent processes. Therefore, while the high nitrogen concentrations associated with the field experiments preclude the identification of specific mechanisms that might be missing in the current models under realistic nitrogen perturbation levels, they nonetheless sug-

gest that the models do not contain the mechanisms needed to capture the nonlinear relationship between nitrogen availability and soil carbon dynamics.

Whereas the warming meta-analysis yielded results that could be used to constrain model mechanisms, the same cannot be concluded for the nitrogen-addition studies due to the uncertainty of how high-latitude soils will respond to lower concentrations of nitrogen. However, while bearing in mind the difficulties associated with interpreting the observational meta-analysis, we suggest two modifications to the model to address the different conclusions derived from the two data sets (observations and models). (1) Tundra plant communities are sensitive to changes in nitrogen inventory leading to compositional changes the models do not currently capture, but which have important ramifications for root biomass, litter quality, and plant exudates that play a significant role in soil carbon dynamics (Aerts et al., 2005). (2) Representation of discrete belowground biomass functional groups (e.g., heterotrophic and fungal decomposers) alongside their individual dependencies on soil nitrogen can help to constrain the belowground response to nitrogen addition.

4.3 Barriers for successful experiment-based model benchmarking

While we were able to benchmark some aspects of the model predictions using the observational meta-analysis, we acknowledge several concerns that may have complicated the data-model comparison. First, the spatial discrepancy between the model output and observational data is large. This mismatch arises from several sources, including: (1) the uncertainties in the climate and environmental forcing data used to drive the models; (2) insufficient spatial resolution in the models preventing the representation of all field sites, particularly those in coastal regions (e.g., the Greenland sites); and (3) the lack of a simulation protocol determining the onset and completion of the growing season in the models.

Second, no general protocol consistent with field perturbations is available for setting up model perturbations. While we acknowledge that different land models have different structures and degrees of complexity, a standard approach to establishing perturba-

tions would be beneficial. In our model perturbation experiments, atmospheric warming resulted in uniform soil warming everywhere and therefore underestimated the spatial heterogeneity found in passive warming experiments (Bokhorst et al., 2012). On the other hand, simply reducing the wind speed failed to alter the soil thermal regime, in-
dicating a deficit in the formulation of atmospheric boundary layer dynamics. However, our approach of warming via enhanced aerodynamics resistance is not transferable to models using atmospheric temperature, rather than a surface energy balance scheme, to force soil thermal dynamics.

Third, the high-latitude nitrogen cycle is strongly regulated by the rate of mineraliza-
tion and immobilization (see warming discussion above). However, both organic nitro-
gen and nitrogen fixation are important nitrogen sources contributing to the productivity of high-latitude ecosystems (Chapin et al., 1993). Organic nitrogen is rarely measured in high-latitude field experiments, and ESMs do not presently consider it as an available nitrogen source for plants. We did not explicitly evaluate the role of organic nitrogen dur-
ing perturbation, however, our observational meta-analysis indicated a drop in nitrogen mineralization and soil nitrogen, and elevated immobilization of nitrogen into microbial biomass. Increased immobilization under warming may limit plant nitrogen uptake on long time scales. Organic nitrogen may, therefore, be an important bridge sustaining plant GPP under a warming climate through associations between mycorrhizal fungi and vascular plant roots (Hobbie et al., 2009). If tundra becomes increasing dominated by shrubs under a warming climate, as predicted (Schuur et al., 2007), this mechanism of nitrogen acquisition may become increasingly important.

Nitrogen fixation is currently represent in CLM as a function of the previous years NPP distributed throughout the year, which neglects the role cryptogamic crusts play in fixing nitrogen (Elbert et al., 2012) and the importance of environmental factors (e.g., light intensity, temperature or nutrient concentrations) in determining the rate at which nitrogen is fixed (Liengen and Olsen, 1997).

Fourth, while we acknowledge the complexity of interpreting single-factor manipu-
lation experiments, the multifaceted nature of climate change calls for more multifac-

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torial experiments. The few studies we could find measuring the response of similar variables to combined warming and nitrogen addition found an exacerbation of the reported warming response. However, there were too few studies measuring complementary variables to conduct a meta-analysis. Previous studies conduced in high-latitude soils have recorded a stronger response of decomposition following perturbation by a combination of drivers (e.g., elevated temperature and CO_2) than if those factors were considered in isolation (Fenner et al., 2007). On the other hand, (Leuzinger et al., 2011) give several examples where the opposite is the case: a combination of multiple drivers lessen the responses compared to when the individual drivers are examined alone. These contradictory results call for further consideration of the impact of multiple drivers in high-latitude ecosystems.

Fifth, a greater consideration of small-scale observations in parameterizing ESMs is warranted. The inclusion of the phosphorus cycle may also improve the long-term response of ecosystem models to a changing climate, if increasing soil nitrogen exacerbates phosphorus limitation (Vitousek et al., 2010).

Finally, the field observational data lacks sufficient spatial coverage to characterize high-latitude spatial heterogeneity accurately. There are many studies that cluster in a few regions, represented in the model by only a few grid cells. While we obtained some insights into the deficiencies of the model from this benchmarking exercise, we still lack confidence as to how representative our conclusions might be given the spatial heterogeneity of high-latitude ecosystems.

5 Conclusions

We have shown here that certain mechanisms poorly represented in land models, as highlighted by ecological meta-analysis, can undermine conclusions regarding the stability of high-latitude soil carbon. We found that two versions of CLM (1) poorly replicate coupling of the aboveground and belowground components of the carbon cycle;

(2) poorly represent nitrogen cycling; (3) do not distinguish discrete belowground functional processes, and (4) insufficiently represent plant community dynamics.

We further caution that the field experiments used in a benchmarking meta-analysis must be carefully chosen. We demonstrate the utility of benchmarking land models us-
5 ing studies and measurements that attain a realistic ecosystem response to warming, and the difficulties associated with comparing model performance against field studies that do not simulate the chronic nature of future climate change.

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Testing model performance via meta-analysis

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Figure 1. Study sites included in the meta-analysis.

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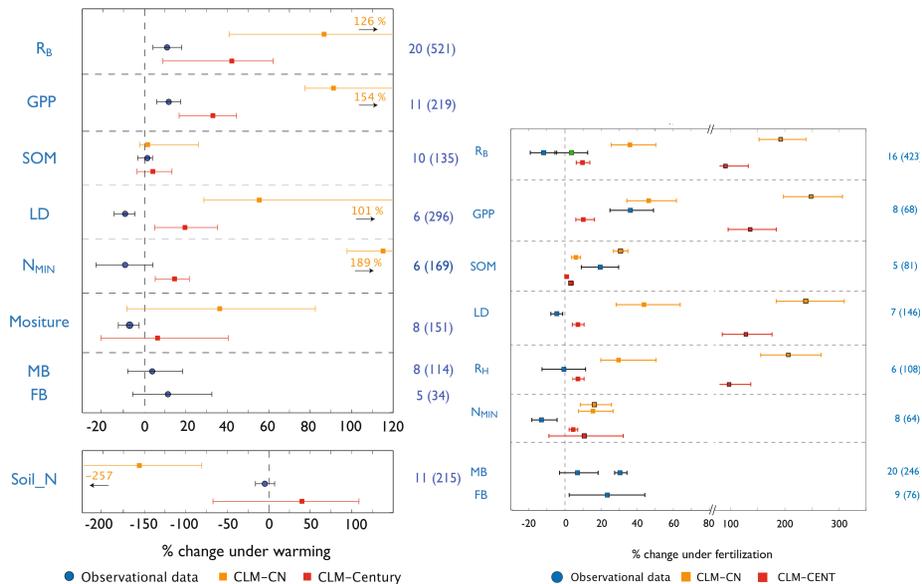
Figure 2. Response ratio of select variables under **(a)** warming and **(b)** nitrogen addition. The figures show the average response to perturbation derived from the observations (shown as blue circles), or the model runs, CLM-CN (orange squares) or CLM-Century (CLM-Century). The error bars around the average denote the variance. In the case of several data points where the variance does not fit onto the x axis a numerical value indicates the limits of the variance. In Fig. 2b, the observational values of B is given in two forms: the average nitrogen concentration (i.e. $72 \, \text{kg ha}^{-1} \, \text{yr}^{-1}$), and also to lower, more realistic concentrations ($< 30 \, \text{kg ha}^{-1} \, \text{yr}^{-1}$ represented by a green square). The modeled response in Fig. 2b is the collated response representing the addition of low nitrogen concentrations (i.e. 0.2, 1.0, 2.0 and $3.0 \, \text{kg N ha}^{-1} \, \text{yr}^{-1}$) and high concentrations (20, 60 and $100 \, \text{kg N ha}^{-1} \, \text{yr}^{-1}$). Note in Fig. 2b the axis changes after the break point. The number of individual studies and data points (in brackets) used in calculating the observational response ratio are given in blue on the right-hand side of the figure.

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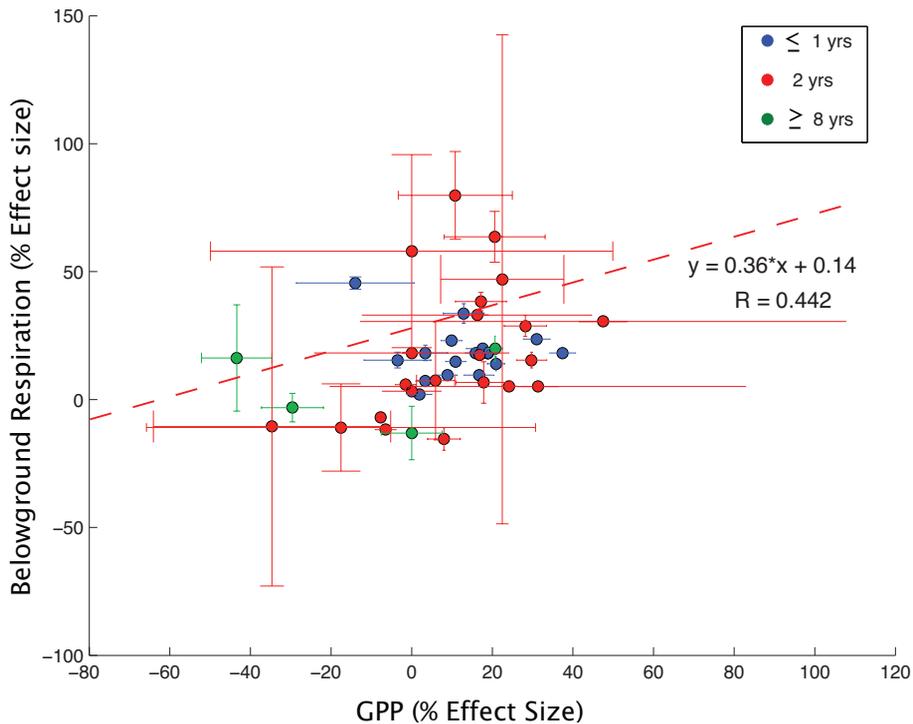Printer-friendly Version

Interactive Discussion

Figure 3. Relationship between GEP and heterotrophic respiration in warmed plots. Data points from the graph also represent the duration of warming. Each point represents the effect size expressed as a percentage and the calculated bootstrapped variance (across the *x* and *y* axis).
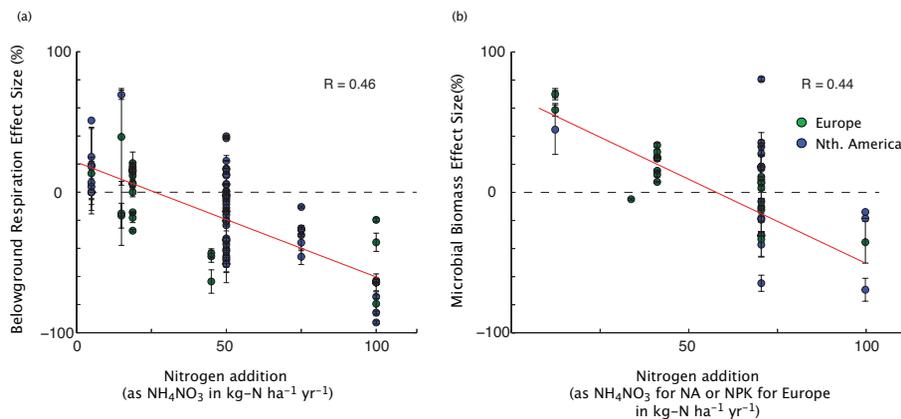
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Interactive Discussion

Figure 4. The effect of increasing N-addition on **(a)** belowground respiration, and **(b)** microbial (i.e., bacterial + fungal) biomass.