

1 **Meta-analysis of high-latitude nitrogen-addition and warming studies implies**
2 **ecological mechanisms overlooked by land models**

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47 **Abstract**

48

49 Accurate representation of ecosystem processes in land models is crucial for
50 reducing predictive uncertainty in energy and greenhouse gas feedbacks with the
51 climate. Here we describe an observational and modeling meta-analysis approach to
52 benchmark land models, and apply the method to the land model CLM4.5 with two
53 versions of belowground biogeochemistry. We focused our analysis on the above
54 and belowground responses to warming and nitrogen addition in high-latitude
55 ecosystems, and identified absent, or poorly parameterized mechanisms in CLM4.5.
56 While the two model versions predicted similar soil carbon stock trajectories
57 following both warming and nitrogen addition, other predicted variables (e.g.,
58 belowground respiration) differed from observations in both magnitude and
59 direction, indicating CLM4.5 has inadequate underlying mechanisms for
60 representing high-latitude ecosystems. On the basis of observational synthesis, we
61 attribute the model-observation differences to missing representations of microbial
62 dynamics, above and belowground coupling, and nutrient cycling, and we use the
63 observational meta-analysis to discuss potential approaches to improving the
64 current models. However, we also urge caution concerning the selection of data sets
65 and experiments for meta-analysis. For example, the concentrations of nitrogen
66 applied in the synthesized field experiments (average = 72 kg ha⁻¹ yr⁻¹) are many
67 times higher than projected soil nitrogen concentrations (from nitrogen deposition
68 and release during mineralization), which precludes a rigorous evaluation of the
69 model responses to likely nitrogen perturbations. Overall, we demonstrate that

70 elucidating ecological mechanisms via meta-analysis can identify deficiencies in
71 ecosystem models and empirical experiments.

72

73 **1 Introduction**

74

75 Northern Hemisphere high latitude soils are among the largest global stores
76 of soil organic matter (SOM) (Grosse et al., 2011). Recent studies have estimated
77 SOM storage within permafrost regions to be ~1700 Pg to 3 m depth (Schuur et al.,
78 2012), representing nearly 50% of global terrestrial organic carbon, or nearly twice
79 that currently in the atmosphere (King et al., 2007). Permafrost SOM is stabilized by
80 cold temperatures, and is therefore vulnerable to the warming that high-latitude
81 regions will experience over the next century (Schuur and Abbott, 2011). However,
82 the response of high-latitude ecosystems to global climate change is complex. Under
83 warming, the active layers of permafrost soils thicken, and may serve as a reservoir
84 of chemically labile organic carbon. Carbon released from these soils (mostly as CO₂
85 or CH₄) may accelerate the rate of warming and form a positive feedback to climate
86 change (Koven et al., 2011). Alternatively, elevated rates of organic matter
87 decomposition release limiting nutrients (e.g., nitrogen) that could stimulate plant
88 productivity, sequestering CO₂ from the atmosphere, serving as a negative feedback
89 on climate change (Shaver et al., 1992).

90 Predictions of how future climate change will alter high-latitude soil carbon
91 are derived mainly from (a) conclusions of in situ field manipulation studies and (b)
92 output of land models either coupled or uncoupled with an atmospheric model. The
93 Earth System Models (ESMs) couple land and atmospheric processes by simulating

94 land biogeochemical and biophysical states and fluxes (including soil carbon
95 dynamics and effluxes) and feedbacks to atmospheric carbon concentrations across
96 decadal, centennial, and millennial time scales (Kaplan et al., 2002; Koven et al.,
97 2011) . Current ESMs have high uncertainty in their predicted magnitude of carbon-
98 climate feedbacks (Arora et al., 2013; Friedlingstein et al., 2006) because of
99 insufficiencies in model structure and parameterization (Bonan et al., 2011; Jung et
100 al., 2007; Piao et al., 2013; Zaehle et al., 2014).

101 Benchmarking the performance of land models has been challenging (Luo et
102 al., 2012) . One approach has been to compare model output against the output of
103 distinct manipulation studies (Thomas et al., 2013b) that acutely perturb
104 ecosystems on short time scales (months to years). However, the broad spatial
105 heterogeneity of high-latitude soils may not be well represented by the
106 concentration of high-latitude field studies within a few sites. Herein, we benchmark
107 the models by compiling data from a range of studies measuring the same variables
108 across spatial gradients. This approach can determine an overall ecosystem
109 response to perturbation, eliminating the weight placed on any one study. Data
110 compilation can also identify important mechanisms that determine the fate of soil
111 carbon but are currently not represented in the land models.

112 In the present study, we examined the fate of high-latitude soil carbon based
113 on conclusions drawn from (1) meta-analyses of high-latitude field studies ($\geq 60^\circ$ N)
114 focusing on ecosystem responses to warming and nitrogen additions and (2) meta-
115 analyses of simulations mimicking the experiments using the land component
116 (CLM4.5) of the Community Earth System Model (CESM). We address four

117 questions: (1) Do the models and synthesized data predict a similar response of
118 carbon and nutrient cycling to ecosystem warming and nitrogen addition? (2) In
119 what areas do the models and experiments diverge? (3) What are the mechanisms,
120 including those absent in the models, the field experiments demonstrate to be
121 important for evaluating the fate of soil C? (4) What types of observationally derived
122 model benchmarks are appropriate for the various ecosystem processes relevant to
123 high-latitude soil C dynamics?

124

125 **2 Materials and Methods**

126

127 **2.1 Literature search**

128 We compiled published observations for replicated field studies from high-
129 latitude ecosystems ($\geq 60^\circ$ N) (Fig. 1) examining responses of belowground
130 biogeochemistry to warming and nitrogen addition. The data were mainly extracted
131 from published figures or tables, or directly from the authors in cases where
132 unpublished results were referenced in a published study. Manipulation studies
133 were located by searching the ISI Web of Knowledge, using the following principal
134 terms: “Arctic”, “Permafrost”, “High-latitude”, paired with: “Manipulation”,
135 “Nitrogen”, “Warming”. Where available, we collected data from control and
136 perturbed soils on microbial (i.e., bacterial + fungal) biomass, fungal biomass,
137 aboveground biomass, belowground respiration, heterotrophic respiration, gross
138 primary productivity (GPP), litter decomposition, soil organic matter content (SOM),

139 net nitrogen-mineralization, and soil and microbial nitrogen and phosphorus
140 concentrations.

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

150 For nitrogen addition, we collected studies that applied nitrogen as either
151 ammonium nitrate (NH_4NO_3) or nitrogen phosphorus potassium fertilizer (NPK).
152 We analyzed over 2,300 entries (i.e., individual measurements of each metric)
153 across 37 nitrogen addition field studies from 14 geographically distinct sites (Table
154 S1). We examined the influence of geography on the response of our data sets by
155 partitioning the data between that collected from European and North American
156 manipulation studies. The data were also temporally disaggregated in a similar
157 manner as described above for the warming experiments.

158 Data were extracted from figures using the Data Thief software (Tummers,
159 2006). Comparison data were standardized to units of “ g m^{-3} ” prior to calculating a
160 response ratio. Bulk density measurements for the different soils were extracted
161 from the published studies or through personal communication with the authors. In

162 the cases where authors could not be contacted, bulk density was estimated using a
163 previously published approach (Calhoun et al., 2001).

164

165 **2.2 Meta analysis**

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

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

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

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

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

178 A mixed model was used to calculate the cumulative differences in the
179 response variables in treatment versus control plots. These cumulative differences
180 were calculated for the overall dataset, and also after constraining the datasets to
181 similar conditions and forcings (e.g., geographic location, magnitude of N added).

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

192

193 **2.3 CLM-BGC spin-up and experimental manipulation scenarios.**

194 We simulated the ecosystem perturbation experiments using the community
195 land model (CLM4.5) with two different representations of belowground
196 biogeochemistry; a vertically resolved belowground module with similar
197 biogeochemistry to the Century model (termed CLM-Century, (Koven et al., 2013),
198 and the Carbon-Nitrogen biogeochemistry module (termed CLM-CN, (Thornton et
199 al., 2007). CLM-Century and CLM-CN share the same formulation of aboveground
200 biogeochemical processes and land biogeophysics, but differ in their representation
201 of belowground carbon turnover and nitrogen cycling. For example, CLM-CN
202 represents the belowground decomposition cascade as four discrete pools with
203 faster turnover times than the three-pool approach used by CLM-Century (Koven et
204 al., 2013). Furthermore, the nitrogen cycle of CLM-CN is much more open (i.e.,

205 higher cycling rates and losses) than that of CLM-Century. Finally, CLM-CN does not
206 resolve the vertical biogeochemical gradients characteristic of CLM-Century. All
207 simulations were run at a spatial resolution of $1.9^\circ \times 2.5^\circ$, using the Qian et al., (Qian
208 et al., 2006) dataset for atmospheric forcing. The models were spun up for 1500
209 years to preindustrial equilibrium following an improved spinup approach (Koven
210 et al., 2013). Simulations were then run from 1850 to 1979 under contemporary
211 climate forcing before the onset of perturbation conditions over the following 21
212 years (from 1980 to 2000). Vegetation cover type was specified as described in
213 Oleson et al., (Oleson et al., 2013). Model simulations were parameterized to
214 replicate the field experiments: the soil was warmed by scaling the aerodynamic
215 resistance by a factor of 10, a value obtained by trial and error to achieve a desired
216 warming of $\sim 1^\circ\text{C}$ (in accordance with the average temperature increase noted for
217 the experimental manipulations, see results section below), while keeping sufficient
218 spatial variability of the warming. CLM forces the soil heat transport process
219 through the residual flux from incoming radiation, latent heat, and sensible heat.
220 Increasing aerodynamic resistance reduces the sensible and latent heat fluxes and
221 warms the soil during the growing season. We tried warming the soil by increasing
222 the surface air temperature (which is a diagnostic variable in CLM), but this
223 approach violated CLM's surface energy budget and was therefore avoided.
224 Furthermore, increasing aerodynamic resistance is more analogous to the approach
225 of installing open-top chambers to warm the soil.

226 Nitrogen was added in the form of NH_4NO_3 at concentrations that replicated
227 the very high concentrations of the nitrogen addition experiments (20, 40, 60, 80,

228 and 100 kg-N ha⁻¹ yr⁻¹). However, for comparison, we also simulated the model
229 response to a range of nitrogen concentrations that reflect more realistic nitrogen
230 deposition scenarios up to 2050 (0.2, 1.0, 2.0, 3.0 kg-N ha⁻¹ yr⁻¹, Galloway et al.,
231 2004). To mimic the approach of most field studies, we began the perturbation
232 (warming or nitrogen addition) when a given model grid was snow free for 7 days
233 (< 1 mm standing stock) and ended after more than 7 days with standing snow (> 1
234 mm standing stock).

235 Model output was collected for each site considered in the meta-analysis (Fig.
236 1) using a 3×3 grid that surrounded the experimental manipulation site at the
237 center. The mean and standard deviation (SD) of predictions from the 9 grid cells
238 were then used to calculate the response ratios from that site. For coastal sites,
239 some modeled grid cells were not on land due to model spatial resolution, and data
240 statistics were therefore scaled with the actual number of data points accordingly.
241 For all sites we took the mean and SD of the grid cells and analyzed the data using
242 the meta-analysis approach applied to the observations and described above. Our
243 model analysis was limited to the output from the surface soil (10 cm for CLM-
244 Century and bulk prediction for CLM-CN, which represents approximately the top
245 20 cm of soil) where the majority of the collected studies focused their
246 measurements.

247

248 **3 Results.**

249 **3.1 Response of belowground C-cycling to warming**

250 On average, experimental warming increased soil temperatures by 1.4°C (\pm
251 0.7°C). Belowground respiration increased significantly under warming by 9% (\pm
252 5%) compared to the controls. This increase in belowground respiration was largely
253 driven by the response of European soils, which increased 33% ($\pm 11\%$) above
254 control soils. Conversely, belowground respiration from North American soils
255 showed a more modest, and non-significant, increase ($2.5\% \pm 6.5\%$; Fig. 2a, S1b). It
256 is unlikely that this spatial difference is due to greater experimental warming of
257 European soils: passive warming increased soil temperatures by $1.4 \pm 0.6^{\circ}\text{C}$ in
258 Europe and $1.3 \pm 0.5^{\circ}\text{C}$ in North American experiments. A transient effect of
259 belowground respiration in high-latitude soils was also noted in the data set. Short
260 term experiments (< 2 years), showed a large significant increase ($34.4\% \pm 16\%$) in
261 belowground respiration, which was not evident in studies lasting 2 – 4 years.
262 However, studies lasting ≥ 5 years also had significant increases in belowground
263 respiration. GPP increased significantly (11.8%) in warmed soils (Fig. 2a) and
264 showed a positive relationship with belowground respiration (Fig. 3).

265 Despite elevated GPP, litter decomposition declined significant by 9% ($\pm 5\%$),
266 while SOM did not change significantly from control values (Fig. 2a). Both microbial
267 and fungal biomass increased non-significantly under warming: microbial biomass
268 increased 3.8% ($\pm 12\%$) while fungal biomass increased by 11.5% ($\pm 19\%$).

269 Under warming, soil nitrogen mineralization and soil nitrogen
270 concentrations both declined non-significantly (nitrogen mineralization: $7.6\% \pm$
271 15% , soil nitrogen: $5.1\% \pm 9\%$) below the control soils. Soil phosphorus increased
272 non-significantly above the control soils ($12.5\% \pm 9\%$, Fig. S1b). Finally, the use of

273 the OTC and OTG to passively warm high-latitude soils significantly lowered soil
274 moisture 8% ($\pm 6\%$), below the control soils (Fig. S1b).

275 Modeled warming experiments increased soil temperature by $1.21\text{ }^{\circ}\text{C} \pm$
276 $0.47\text{ }^{\circ}\text{C}$ in CLM-CN and $0.91\text{ }^{\circ}\text{C} \pm 0.35\text{ }^{\circ}\text{C}$ in CLM-Century. In response, the two
277 models each predicted stronger relative and absolute increases in belowground
278 respiration compared with the observational data. The models predicted higher
279 litter decomposition in response to warming, which is in contrast with the
280 decreasing trend found in the observational data. Both models also predicted
281 increased nitrogen mineralization following warming, contrary to the observational
282 data. The relative changes in SOM under warming were consistent between the
283 model predictions and observations. Soil moisture increased non-significantly in
284 both models (CLM-CN: $38\% \pm 42\%$; CLM-Century: $7\% \pm 33\%$), but with a wide
285 variability. In general, CLM-CN tended to predict a much stronger temperature
286 response than CLM-Century (Fig. 2a).

287

288 **3.2 Response of belowground carbon cycling to nitrogen addition**

289 The field experiments added an average of $72\text{ kg-N ha}^{-1}\text{ yr}^{-1}$ ($\pm 38\text{ kg-N ha}^{-1}$
290 yr^{-1}) of nitrogen to soils, with a range of $1 - 100\text{ kg-N ha}^{-1}\text{ yr}^{-1}$. This additional
291 nitrogen reduced belowground respiration and resulted in a larger sink for SOM,
292 indicating a negative feedback to atmospheric CO_2 concentrations (Fig. 2b).
293 Belowground respiration in soils receiving additional nitrogen (in the form NH_4NO_3)
294 declined $11.8\% (\pm 7\%)$, significantly below control soils (Fig. 2b). This pattern was
295 consistent for the two geographical regions examined and was not dependent on the

296 duration of the experiment. Belowground respiration in European soils declined,
297 non-significantly, by 7% ($\pm 9.5\%$) below control soils (Fig. S1a). Belowground
298 respiration in North American soils also declined significantly by 12.7% ($\pm 9\%$).
299 Belowground respiration showed a negative relationship with increasing soil
300 nitrogen concentration (Fig. 4a). Linear regressions failed to uncover a significant
301 relationship between the response of belowground respiration and climate (MAT,
302 MAP) or experimental factors (experimental duration and magnitude of nitrogen
303 added). Heterotrophic respiration showed no significant change under nitrogen
304 addition; however, the data are highly variable ($\pm 12\%$). Nitrogen addition resulted
305 in a significant decline in litter decomposition (% mass loss yr⁻¹) of 4.8% ($\pm 3\%$),
306 while SOM increased significantly 19.5 % ($\pm 10\%$) in perturbed soils.

307 GPP increased significantly under nitrogen addition ($44.3\% \pm 7.5\%$)
308 compared with the control soils (Fig. 2b). On average, aboveground biomass
309 (vascular + non-vascular plants) non-significantly increased upon nitrogen addition
310 ($15\% \pm 22\%$). Vascular plant biomass increased significantly ($33\% \pm 8\%$) over that
311 of the control soils (Fig. S1b).

312 Overall, a non-significant increase in microbial biomass was observed for
313 experimental soils (Fig. 2b), yet, declined with increasing concentrations of nitrogen
314 added to the soil (Fig. 4b). When factoring in geographical location, microbial
315 biomass in European soils increased significantly above the controls ($17.5\% \pm 9\%$),
316 but decreased non-significantly relative to control soils in North American soils (Fig.
317 S1a). While different forms of nitrogen were applied in the experiments (e.g.,
318 NH_4NO_3 or NPK), the most significant factors, explaining 37 % of the variance in

319 microbial biomass, were site-specific pH and mean annual temperature. Finally,
320 fungal biomass increased significantly by 23% ($\pm 20.5\%$) compared to the control
321 soils.

322 For nitrogen perturbed CLM-CN and CLM-Century simulations we analyzed
323 the relative response of variables complementary to the observational meta-
324 analysis. Under nitrogen addition, the modeled response variables matched
325 observations for only two parameters: GPP and SOM, and only at the lowest
326 nitrogen addition concentrations (i.e., $\leq 1 \text{ kg-N ha}^{-1} \text{ yr}^{-1}$, Fig. S3). Neither model
327 accurately replicated the trend in the observed response of belowground
328 respiration, litter decomposition, and nitrogen mineralization (Fig. 2b), while both
329 models overestimated the response of heterotrophic respiration.

330

331 **4 Discussion**

332 Accurate representation of the processes governing soil carbon cycling in
333 high-latitude soils is crucial for reducing model uncertainty in energy and
334 greenhouse gas feedbacks with climate. By comparing meta-analyses based on
335 model output and observations, we show that two belowground biogeochemical
336 representations in CLM4.5 are unable to adequately represent many of the observed
337 high-latitude ecosystem responses to two important climate change variables:
338 temperature and nitrogen availability. We focus our discussion on the potential
339 reasons for the discrepancies in responses by highlighting: (1) the most important
340 mechanisms currently missing from, or poorly represented in, the models; and (2)
341 instances where deficiencies in the experimental approaches prohibits the data

342 from being used for benchmarking the model. We also recommend further
343 approaches to improve the mechanistic basis of the belowground biogeochemistry
344 representation in ESMs.

345

346 **4.1 Response of belowground carbon cycling to warming**

347 The observational meta-analysis suggests that elevated belowground
348 respiration is balanced by elevated GPP (and associated increases in soil organic
349 matter). We therefore conclude that the coupling of aboveground and belowground
350 processes resulted in these soils being carbon neutral under modest (+ 1.3 °C)
351 warming. The models also predicted no significant changes to belowground SOM
352 content under warming due to concomitant increases in belowground respiration
353 and GPP. However, the magnitude of the modeled fluxes is many times larger than
354 the observed fluxes. Therefore, the net impact of the manipulation on SOM was
355 predicted by the models, but with incorrect mechanisms.

356 As a broader point, we believe this result illustrates a common problem
357 among tests of land model performance, i.e., inferences of model fidelity based on
358 comparisons solely with observations of emergent responses that has low signal to
359 noise ratio. For example, it is insufficient to use net ecosystem exchange (NEE) as a
360 sole model benchmark (Schwalm et al., 2010), because it ignores that: (1) NEE is
361 typically a small difference between ecosystem respiration and assimilation and (2)
362 models separately represent these gross fluxes as being differently controlled by
363 climate and antecedent system states. We contend that representing this type of
364 emergent ecosystem net flux within the observational uncertainty gives little

365 information as to whether the model is accurately representing the underlying
366 mechanisms appropriately.

367

368 *4.1.1 Nitrogen cycling under warming:* Confronting the model outputs with
369 observations showed a consistent overestimation of key variables in the model
370 predictions (Fig. 2a). One potential reason for a larger modeled response is the
371 approaches CLM-CN and CLM-Century take to representing the nitrogen cycle, as
372 modeled nitrogen input, retention, and loss have been shown to have a large impact
373 on ecosystem carbon sequestration (Thomas et al., 2013b; Zaehle and Dalmonech,
374 2011). Moreover, data based modifications to ESM nitrogen cycling mechanisms
375 may further improve the correspondence between observations and model output
376 (Thomas et al., 2013b).

377 CLM-CN predicts much higher rates of nitrogen loss from denitrification, than
378 CLM-Century, and is therefore more responsive to changing nitrogen availability
379 from inputs, mineralization, and losses. Under warming, CLM-CN predicted a
380 significant loss of soil nitrogen not predicted in CLM-Century, which has a more
381 closed nitrogen cycle, possibly more representative of the nitrogen cycle in high-
382 latitude soils (Barsdate and Alexander, 1975), where mineralization is the main
383 source of nitrogen for plant and microbial growth during the growing season
384 (Shaver et al., 1992). Depolymerization of proteinaceous compounds, to amino acids
385 and eventually ammonia (Jones et al., 2009; Schimel and Bennett, 2004) is the
386 critical step in this process and dependent on microbial physiology and subject to

387 the same biotic and abiotic controls of organic matter decomposition (see
388 discussion below).

389 Modeled nitrogen mineralization, however, increases under warming with a
390 concomitant increase in soil nitrogen in the CLM-Century framework. CLM-CN, with
391 its high rates of mineral nitrogen losses shows a very large decline in soil nitrogen,
392 possibly rendering the above- and belowground communities nitrogen limited
393 throughout. In our data analyses, nitrogen mineralization declined as microbial
394 nitrogen (i.e., immobilization) increased. The end result in both cases (i.e., the
395 models and observations) is the potential limitation of plant growth over long time
396 scales. Our data synthesis suggests that the release of nitrogen from increased
397 decomposition is used to meet microbial demands or immobilized. Microbial
398 immobilization is regulated by the stoichiometric imbalance between the substrate
399 being depolymerized and the physiological nutrient demand. While analogous to the
400 CUE, nitrogen use efficiency (NUE), which relates immobilization and mineralization
401 to microbial growth (Mooshammer et al., 2014), is regulated independently in
402 order to maintain cell stoichiometry. Some attempts have been made to incorporate
403 NUE controls into ecosystem models (Manzoni and Porporato, 2009), but further
404 experimental and modeling work is required to understand NUE's plasticity and
405 impacts on soil carbon dynamics.

406

407 *4.1.2 Aboveground dynamics:* The biogeochemical coupling between aboveground
408 and belowground components of the ecosystem is crucial for understanding high-
409 latitude carbon cycling under a changing climate. The meta-analysis of field

410 measurements showed a general stimulation of aboveground activity under
411 warming, while previous field studies have noted a shift in plant community
412 composition with warming, favoring the establishment of deciduous shrubs and
413 graminoids and selecting against mosses and lichens (Schuur et al., 2007; Sistla et al.,
414 2013; Walker et al., 2006). This shift toward more woody plants changes the
415 ecosystem carbon balance and nutrient dynamics (Jackson et al., 2002; Welker et al.,
416 2004), as shrubs tend towards higher internal carbon allocation toward woody
417 tissue, but also may increase belowground carbon allocation (as both litter and
418 exudates) relative to mosses (Street et al., 2013). This change in belowground
419 allocation may result in the observed relationship between GPP and belowground
420 respiration (Fig. 3), indicating a close coupling between these two processes.

421 Current models crudely represent above- and belowground biogeochemical
422 coupling and do not represent some of the crucial roles plants play in soil carbon
423 dynamics (Ostle et al., 2009; Schmidt et al., 2011). Of particular relevance to high-
424 latitude ecosystems is the lack of any representation of cryptogams or bryophytes in
425 CLM4.5. These plants contribute substantially to aboveground biomass and
426 biogeochemical processes in tundra soils (Cornelissen et al., 2007; Elbert et al.,
427 2012) and are clearly important for accurate simulations of tundra carbon dynamics.
428 Few ESM land models (including CLM4.5) include dynamic vegetation, and when it
429 is included, representation tends to be coarse (Ostle et al., 2009). Ongoing work will
430 attempt to address some of these deficiencies, by including representations of
431 aboveground ecosystem demography (Huntingford et al., 2008; Moorcroft et al.,
432 2001), and soil carbon dynamics (Riley et al., 2014; Tang and Riley, 2013).

433 Integration of these approaches into the CLM framework may improve the
434 robustness of long-term tundra soil simulations and reduce uncertainty associated
435 with the aboveground model response.

436

437 *4.1.3 Litter decomposition:* Disagreement between the observations and model
438 predictions was also noted for litter decomposition. Under warming, litter
439 decomposition declined in the observations, possibly contributing to SOM
440 accumulation, but increased in the models. In previous studies, the response of litter
441 decomposition to warming was largely dependent on the method used to increased
442 soil temperature (Aerts, 2006). OTCs tend to warm the soil and reduce soil moisture,
443 limiting litter decomposition by saprotrophic fungi. Soil moisture in the models
444 showed a non-significant increase with warming as the permafrost began to thaw
445 (Fig. 2a). The difference between the observational meta-analysis and the models
446 represents a potentially confounding factor in using this data to benchmark the
447 model. A previous meta-analysis focused solely on litter decomposition in Arctic and
448 Alpine tundra found that warming induced a small increase in decomposition
449 provided sufficient soil moisture (Aerts, 2006). This response was not apparent in
450 our data syntheses, but suggests the model results, while overestimating litter
451 decomposition, were at least in the appropriate direction. Soil moisture is an
452 important controller on decomposition (Aerts, 2006; Hicks Pries et al., 2013).
453 However, changes to surface hydrology during permafrost thaw are dependent on
454 thermokarst formation and topological features of the landscape (Jorgenson and
455 Osterkamp, 2005) and may result in increased or decreased soil moisture. We

456 identify these issues as important for further experimental and modeling work in
457 order to better represent future changes in surface hydrology and the consequences
458 for litter decomposition.

459

460 *4.1.3 Belowground response to warming:* The observational data indicated elevated
461 belowground respiration under warming. The response of microbial heterotrophs
462 to warming can partially be explained by kinetic theory, whereby biochemical
463 reaction rates increase with increasing temperature (Davidson and Janssens, 2006).
464 Hydrolytic and oxidative extracellular enzymes, secreted to depolymerize complex
465 organic matter (Allison et al., 2010), are sensitive to temperature (German et al.,
466 2012). Structural modifications in cold ecosystems maximize their specific activity
467 under in situ temperatures relative to temperate ecosystems (Hochachka and
468 Somero, 2002), which may result in significantly enhanced activity under warming
469 (Koch et al., 2007). This theory fits with the short-term (<2yr) data from the current
470 meta-analysis showing increasing belowground respiration despite no increase in
471 microbial biomass.

472 However, we also identified a drop in belowground respiration in studies
473 lasting longer than 2 years and shorter than 5 years (Fig. S1b). Belowground
474 respiration has consistently been reported to decline under prolonged warming
475 (Rustad et al., 2001) and attributed to substrate limitation (Hartley et al., 2008) or a
476 community-level response of microbial populations to warmer temperatures
477 offsetting the kinetic response of individual microbes (Bradford, 2013; Bradford et
478 al., 2008). Given the increased GPP found in our meta-analysis, belowground

479 communities are unlikely to be substrate limited. Therefore, we hypothesize that the
480 community-level response is likely responsible for the drop in belowground
481 respiration under 2 – 5 years of warming.

482 The subsequent increase in belowground respiration over prolonged
483 warming (> 5 years) could represent either the decomposition of leaf litter driven
484 by changes in microbial community composition, or thawing subsurface organic
485 matter (Dorrepaal et al., 2009). This latter hypothesis is relevant to the long-term
486 fate of high-latitude carbon. In the current analysis, NEE appears balanced, with no
487 change in SOM. However, temporal patterns of vegetation response to warming
488 show a transient effect of warming, with nutrient limitation reducing plant
489 productivity on longer time scales (Arft et al., 1999; Chapin and Shaver, 1996). It is
490 possible, given the large nitrogen immobilization under warming, that belowground
491 respiration may continue longer than productivity, unbalancing NEE and leading to
492 net carbon loss.

493 Temperature is a key factor influencing biogeochemical mechanisms in the
494 model. CLM models belowground respiration using a static Q_{10} and fixed carbon use
495 efficiencies (CUE) for different SOM pools size. This approach may result in the large
496 modeled increase in belowground respiration. In reality, both Q_{10} and CUE vary on
497 spatial and temporal scales, and respond non-linearly to changes in temperature
498 (Janssens & Pilegaard, 2003; Sinsabaugh et al., 2013, Tang & Riley, 2014). Recent
499 microbe-explicit models (MEMs) that consider basic microbial physiology (e.g.,
500 Lawrence et al., 2009) introduce direct biological control over soil carbon cycling
501 and different conclusions on soil carbon pool size and dynamics under warming

502 (Allison et al., 2010; Lawrence et al., 2009; Wieder et al., 2013). For example, by
503 scaling the CUE value with temperature, in accordance with published observations
504 (Luo et al., 2001; Melillo, 2002), the MEMs show a decline in soil carbon turnover
505 under warming (Li et al., 2014; Wieder et al., 2013). Recent work using a MEM with
506 explicit representation of internal physiology, extracellular enzymes, and mineral
507 surfaces (Tang and Riley 2014), demonstrates that both decomposition temperature
508 sensitivity and CUE are hysteretic and cannot easily be represented by a simple
509 function of soil temperature. However, it is also important to note that microbial
510 CUE is not solely temperature-dependent, and other factors, some of which are
511 already present in CLM-CN and CLM-Century (including nutrient and soil moisture
512 limitations), may uncouple growth and respiration and change CUE (Manzoni et al.,
513 2008; Sinsabaugh et al., 2013). The predictions of the microbe-explicit models
514 (MEM) provide further impetus for greater representation of the structure and
515 function of belowground biomass.

516

517 **4.2 Response of belowground carbon cycling to nitrogen addition**

518 Our meta-analysis of field observations found that the addition of inorganic nitrogen
519 to traditionally nitrogen limited ecosystems enhances the carbon sink, consistent
520 with previous studies (Luo et al., 2012; McGuire et al., 2012). Interactions between
521 the carbon and nitrogen cycles resulting in soil carbon accumulation in different
522 ecosystems have been reported previously (Magnani et al., 2007; Thomas et al.,
523 2013b), and have been attributed to an increased carbon allocation to woody tissue
524 (Ciais et al., 2008; Tummers, 2006) and reduction in the SOM decomposition rate

525 (Olsson et al., 2005). Overall, our data-synthesis is largely consistent with the
526 overarching conclusions of previous meta-analyses (Janssens et al., 2010; Knorr et
527 al., 2005).

528 A question remains, however, about the value of the responses synthesized
529 from studies that add fertilizer (NH_4NO_3 or NPK) as a source of nitrogen far in
530 excess of anticipated global change scenarios for high-latitude ecosystems. The
531 average concentration of nitrogen added to the soils in the tundra studies ($\sim 72 \text{ kg}$
532 $\text{ha}^{-1} \text{ yr}^{-1}$) is extremely high when compared with (1) estimates of nitrogen fixation
533 ($< 10 \text{ kg ha}^{-1} \text{ yr}^{-1}$, Cleveland et al., 1999); (2) nitrogen deposition (both current rates
534 of deposition $0.2 - 0.24 \text{ kg ha}^{-1} \text{ yr}^{-1}$, (Jones et al., 2005) and projections of future
535 deposition (Galloway et al., 2004)); and (3) potential nitrogen availability from
536 organic matter mineralization under a warming climate (Harden et al., 2012).
537 Consequentially, we question whether such data lends itself to understanding the
538 response of the ecosystem to realistic chronic incremental changes in nitrogen
539 availability, and the benefit of benchmarking the ecosystem models against such a
540 dataset. On the other hand, if the models include the relevant underlying
541 mechanisms, then they should reproduce the field studies, regardless of the amount
542 of nitrogen added. We give further examples below of where the high nitrogen
543 concentrations may confound the interpretation of the experiments with respect to
544 the model predictions.

545

546 *4.2.1 SOM dynamics:* SOM accumulation under nitrogen addition experiments is a
547 common feature of both the field experiments and the model simulations. However,

548 the underlying mechanisms leading to SOM accumulation are very different, adding
549 uncertainty to the model predicted soil carbon fate over longer timescales. In both
550 versions of CLM, the alleviation of nitrogen limitation stimulates a number of
551 ecosystem processes including aboveground primary productivity, litter
552 decomposition, and organic matter decomposition. The accumulation of SOM
553 indicates the stimulation of GPP and litter decomposition (as a source into the SOM
554 pools) must outweigh losses from increased belowground respiration.

555 The observations, on the other hand, show a significant decline in
556 belowground respiration and litter decomposition under nitrogen addition.
557 Belowground respiration depends on the decomposition and substrate utilization
558 capabilities of the microbial (i.e., bacterial and fungal) community to mineralize root
559 exudates and litter. A drop in belowground respiration may, therefore, be
560 attributable to several mechanisms not included in either version of CLM, including
561 the internal reallocation of carbon in plants and trees that reduces the rate of root
562 exudation to belowground ecosystems (Janssens et al., 2010). Carbon limitation of
563 the microbial community may result in a decline in biomass and belowground
564 respiration (Janssens et al., 2010). Our empirical data shows increased GPP and
565 vascular plant biomass that could indicate the reallocation of newly fixed carbon in
566 vascular plants (Ciais et al., 2008) and drop in belowground exudation.

567

568 *4.2.2 Belowground response to nitrogen addition:* Overall, the current observational
569 meta-analysis found a non-significant increase in microbial biomass (i.e., bacterial
570 and fungal) but a significant increase in fungal biomass under nitrogen addition.

571 This response appears contrary to previous studies that have recorded a drop in
572 microbial biomass under nitrogen addition (Treseder, 2008), but in line with
573 fertilization studies in tundra ecosystems (Clemmensen et al., 2006). We also note
574 that microbial biomass (and belowground respiration) are inversely related to the
575 amount of nitrogen added to the soils (Fig. 4a, b). At low nitrogen concentrations,
576 microbial community activity can be stimulated (Allison et al., 2009) and
577 decomposition elevated, as indicated by the models (Fig. 2b) and some of the
578 observations (Fig. 4b). Elevated nitrogen concentrations, however, have a negative
579 impact on microbial biomass (Treseder, 2008) and decomposition (Janssens et al.,
580 2010). This response can occur through the inhibition of lignin-degrading enzymes
581 produced by saprotrophic fungi (Sinsabaugh et al., 2002; but see Hobbie, 2008), or
582 the increased physical protection of organic matter from decomposition attributed
583 to soil carbon undergoing condensation reactions with high concentrations of
584 inorganic nitrogen (Dijkstra et al., 2004). Therefore, under the high nitrogen inputs
585 used in the present field studies, the coupling between above- and belowground
586 ecosystems can decrease belowground respiration and litter decomposition
587 resulting in an accumulation of SOM.

588 Whereas the warming meta-analysis yielded results that could be used to
589 constrain model mechanisms, the same cannot be concluded for the nitrogen-
590 addition studies due to the uncertainty of how high-latitude soils will respond to
591 lower concentrations of nitrogen. However, we suggest two potential model changes
592 that could rectify the different conclusions derived from the observations and
593 models. (1) A dynamic vegetation approach sensitive to changes in nitrogen

594 inventory could represent compositional changes across the tundra with important
595 ramifications for root biomass, litter quality, and plant exudates that play a
596 significant role in soil carbon dynamics (Aerts et al., 2005). (2) Representation of
597 discrete belowground biomass functional groups (e.g., heterotrophic and fungal
598 decomposers) alongside their dependencies on soil nitrogen may help to constrain
599 the belowground response to nitrogen addition. Finally, while the model
600 mechanisms should ideally be able to reproduce the observed response to high
601 nitrogen loading, we believe that future manipulation studies in high-latitude soils
602 that use realistic nitrogen additions would be more relevant for understanding the
603 tundra soil response. For example, recent studies have added nitrogen to tundra
604 soils at magnitudes one order of magnitude higher than measured concentrations
605 (Lavoie et al., 2011) or guided by soil mineralization rates (Sistla et al., 2012). The
606 ecosystem response is therefore more likely to reflect future responses under
607 anticipated mineralization or deposition scenarios (Galloway et al., 2004).

608

609 **4.3 Barriers and criteria for successful experiment-based model**

610 **benchmarking**

611 While we were able to benchmark some aspects of the model predictions
612 using the observational meta-analysis, we acknowledge several concerns that may
613 have complicated the data-model comparison. First, no general protocol consistent
614 with field experiments is available for setting up model perturbations. Although
615 different land models have different structures and degrees of complexity, a
616 standard approach to establishing perturbations would be beneficial. In our model,

617 atmospheric warming resulted in unrealistic uniform soil warming across the study
618 domain and therefore underestimated the spatial heterogeneity found in passive
619 warming experiments (Bokhorst et al., 2012). On the other hand, solely reducing the
620 wind speed failed to alter the soil thermal regime, indicating a possible problem in
621 the formulation of CLM's surface boundary layer resistance. However, our approach
622 of warming via enhanced aerodynamics resistance is not transferable to models
623 using atmospheric temperature, rather than a surface energy balance scheme, to
624 force soil thermal dynamics.

625 Therefore, criteria need to be established to ensure, regardless of the method
626 used, that the experimental manipulation is reproduced in the model with sufficient
627 fidelity that the predicted and observed responses can be reasonably compared. We
628 consider the criterion used here for the warming experiments (i.e., that the mean
629 predicted manipulation soil temperatures are not significantly different from the
630 observations) to be a minimally acceptable criterion. Ideally, the predicted response
631 of soil temperature, soil moisture, and radiation under warming would emerge in a
632 statistically similar manner to the observations. In the current study, this criterion
633 was not met for soil moisture, where the observations found that soil moisture
634 declined (by $8\% \pm 6\%$) under warming and the model predicted large increases
635 (CLM-CN: $38\% \pm 42\%$; CLM-Century: $7\% \pm 33\%$). This may be an important given
636 the significant impacts moisture has on decomposition and nitrogen cycling.

637 Second, the spatial discrepancy between the model predictions and
638 observational data is large. This mismatch arises from several sources, including
639 uncertainties caused by spatial heterogeneity in the site and experimental

640 manipulation (e.g., unequal heating within the open-top chambers, energy leaking at
641 the boundary with surrounding soil), and uncertainties in the climate and
642 environmental forcing data used to drive the models.

643 Third, while we acknowledge the complexity of interpreting single-factor
644 manipulation experiments, the multifaceted nature of climate change calls for more
645 multifactorial experiments and models that can reproduce any response. The few
646 studies we could find measuring the response of similar variables to combined
647 warming and nitrogen addition (e.g., Shaver et al., 1998) found an even larger
648 warming response than for the single-factor experiments. However, there were too
649 few studies measuring complementary variables to conduct a complete meta-
650 analysis. Previous studies conducted in high-latitude soils have recorded a stronger
651 response of decomposition following perturbation by a combination of drivers (e.g.,
652 elevated temperature and CO₂) than if those factors were considered in isolation
653 (Fenner et al., 2007). In contrast, Leuzinger et al. (Leuzinger et al., 2011) give
654 several examples where the opposite occurs: a combination of multiple drivers
655 lessens the ecological response relative to individual drivers. These contradictory
656 results call for further consideration of the impact of multiple drivers in high-
657 latitude ecosystems that might be used to benchmark model performance.

658

659 **4.4 Overall Recommendations**

660 We have demonstrated here that despite some experimental drawbacks, the
661 underlying biogeochemical mechanisms of CLM-CN and CLM-Century are
662 insufficient to accurately reproduce the observations of a number of high-latitude

663 perturbation experiments. However, we can identify several metrics from the meta-
664 analyses, including nitrogen mineralization and litter decomposition, which may
665 serve as useful indices of model performance. The sign and magnitude of these
666 response ratios were incorrectly predicted by the models in under both warming
667 and nitrogen addition. This error in the sign of the response also occurred for
668 simulated belowground respiration under nitrogen addition, where the model was
669 unable to capture the detrimental impact of very high nitrogen concentrations. In
670 contrast, the SOM response under temperature and nitrogen perturbations appears
671 to be a poor metric to benchmark the models, possibly owing to the large size and
672 undefined composition of the soil organic matter stock.

673 Future development of biogeochemistry representation in CLM should focus
674 on improvements to the nitrogen cycle. Recent work has shown that specific
675 modifications to different nitrogen cycle pathways (e.g., redox cycling, plant-
676 microbial interactions) can improve the correspondence between model predictions
677 and observational data (Thomas et al., 2013a). Development should also may focus
678 on improved kinetics (e.g., equilibrium chemistry approximations, (Tang and Riley,
679 2013) to regulate competition for nutrients between biotic and abiotic sinks (e.g.,
680 plants, microbes, minerals) as an alternative to the current allocation schemes of
681 CLM-CN (Thornton et al., 2007). In addition, the integration of dissolved organic
682 nitrogen cycling as a nutrient source for microbes and plants appears to be an
683 important source of nitrogen in high-latitude soils (Hobbie et al., 2009; Weintraub
684 and Schimel, 2005). However, insufficient data were available to include DON as a
685 response factor in the meta-analysis.

686 The lack of explicit coupling between plant functional types (PFT) and
687 belowground microbial ecosystems in the model fails to capture the importance of
688 this interaction for carbon and nutrients cycling and SOM stability. The PFT concept
689 could be further extended to characterize differential belowground carbon
690 allocation (Street et al., 2013). In addition, symbiotic relationships between
691 different plants and mycorrhizal fungi can increase nutrient acquisition (Hobbie et
692 al., 2009), by facilitating nitrogen fixation (Nasto et al., 2014), and phosphorus
693 acquisition (Smith et al., 2011), thereby increasing photosynthetic rates (Jia et al.,
694 2004). Improving and expanding the definition of the PFT to include these
695 associations may serve to improve coupling between nutrient cycling with
696 belowground biogeochemistry.

697 Finally, while the magnitudes of nitrogen added to tundra soils were very
698 high, the threshold relationship (Fig. 4) that describes the alleviation of nitrogen
699 limitation and stimulation of ecosystem processes at low concentrations from their
700 inhibition at high nitrogen concentrations has support from previous studies (Knorr
701 et al., 2005). However, mechanisms have not yet been integrated in the model to
702 capture this range of responses. The model should be able to reproduce the impact
703 of high nitrogen concentrations associated with agriculture soils, and more work is
704 required to further characterize this threshold effect. It is unlikely, however, that the
705 model-predicted linear relationship between nitrogen availability and ecosystem
706 processes will, in general, be true.

707

708 **5 Summary and conclusions**

709 The use of a meta-analysis to benchmark models has a distinct advantage of
710 aggregating the response of a number of different climate change experiments
711 across spatial and temporal scales to converge upon an average ecosystem or biome
712 response. This aggregation reduces the weight that any one study has on the
713 development of a model benchmark metric. This approach is particularly valuable in
714 ecosystems in which a large number of studies have been performed (e.g.,
715 temperate systems, (Lu et al., 2013). However, we also caution that the field
716 experiments used in a benchmarking meta-analysis must be carefully chosen. We
717 demonstrated the utility of benchmarking land models using studies and
718 measurements that attain a realistic ecosystem response to warming, and the
719 difficulties associated with comparing model performance against nitrogen addition
720 studies that do not replicate conditions under current, or anticipated future climate.

721

722 **Author contribution**

723 NJB and WJR designed the experiment. NJB develop the meta-analysis. JYT
724 developed model perturbation approach and carried out the simulations. NJB
725 analyzed the results and wrote the manuscript with input from WJR and JYT.

726

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734

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1072 Figure 1: Study sites included in the meta-analysis.

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1074 Figure 2: Response ratio of select variables under (a) warming and (b) nitrogen
1075 addition. The figures show the average response to perturbation derived from the
1076 observations (blue circles or squares), CLM-CN (orange squares), and CLM-Century
1077 (red squares). Also shown is the variance either side of the average. Under
1078 circumstances where the variance could not fit on the axis, a numerical value
1079 indicates the limits of variance. In figure 2b, R_B is given as the response to the
1080 average nitrogen concentration and also to lower, more realistic concentrations
1081 (represented by the green square). The modeled response in Figure 2b is the
1082 collated response following the addition of low nitrogen concentrations (i.e., 0.2, 1.0,
1083 2.0 and 3.0 kg-N ha⁻¹ yr⁻¹) and high concentrations (20, 60 and 100 kg-N ha⁻¹ yr⁻¹).
1084 Note the axis change in fig. 2b following the break. The number of individual studies
1085 and data points (in brackets) used in calculating the observation response ratio are
1086 given in blue on the right-hand side of the figure.

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1088 Figure 3: Relationship between GPP and heterotrophic respiration in warmed plots.
1089 Data points from the graph also represent the duration of warming. Each point
1090 represents the effect size expressed as a percentage and the calculated bootstrapped
1091 variance (across the x and y axis).

1092 Figure 4: The effect of increasing N-addition on (a) Belowground respiration, and
1093 (b) microbial (i.e., bacterial + fungal) biomass.

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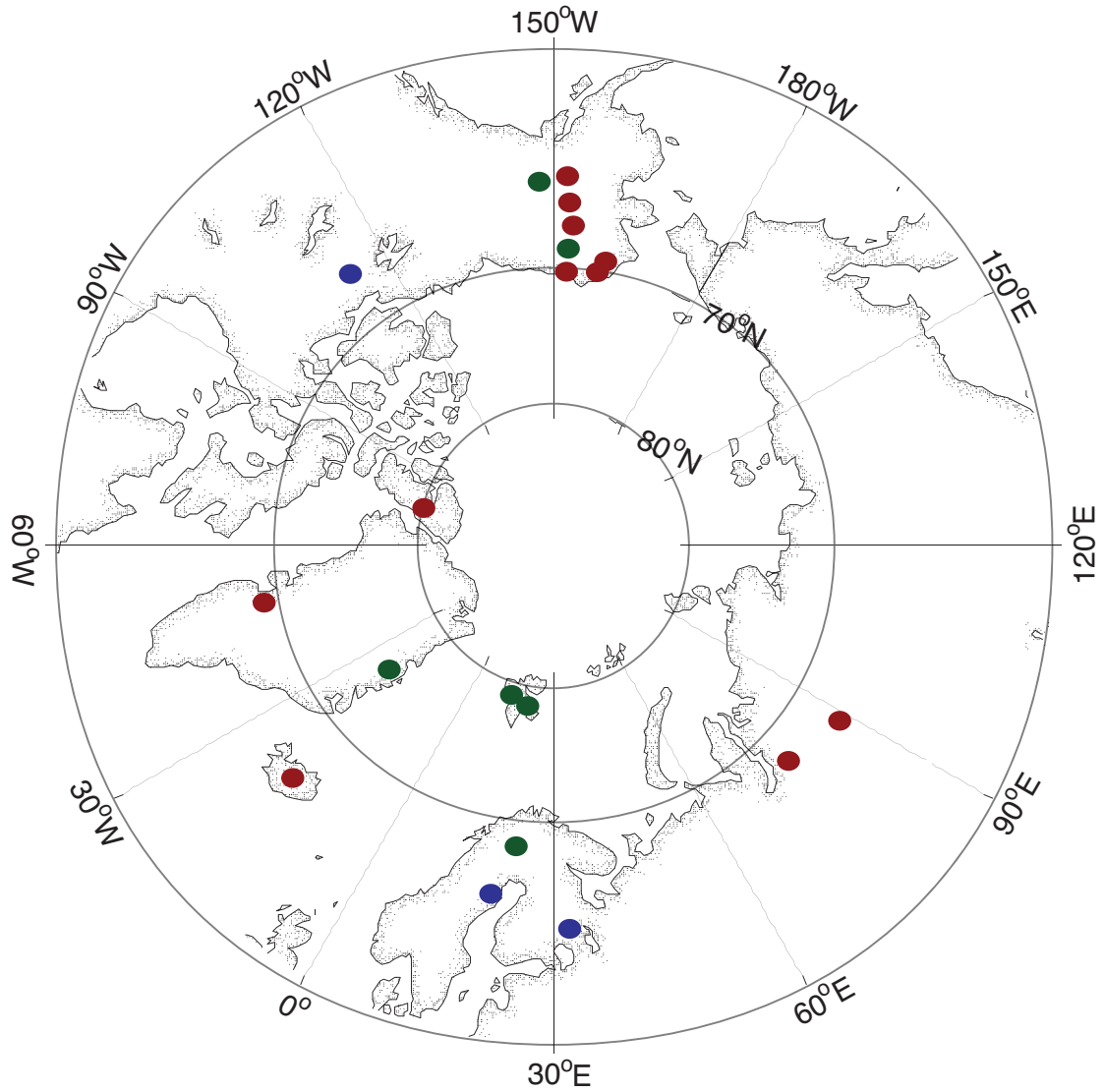
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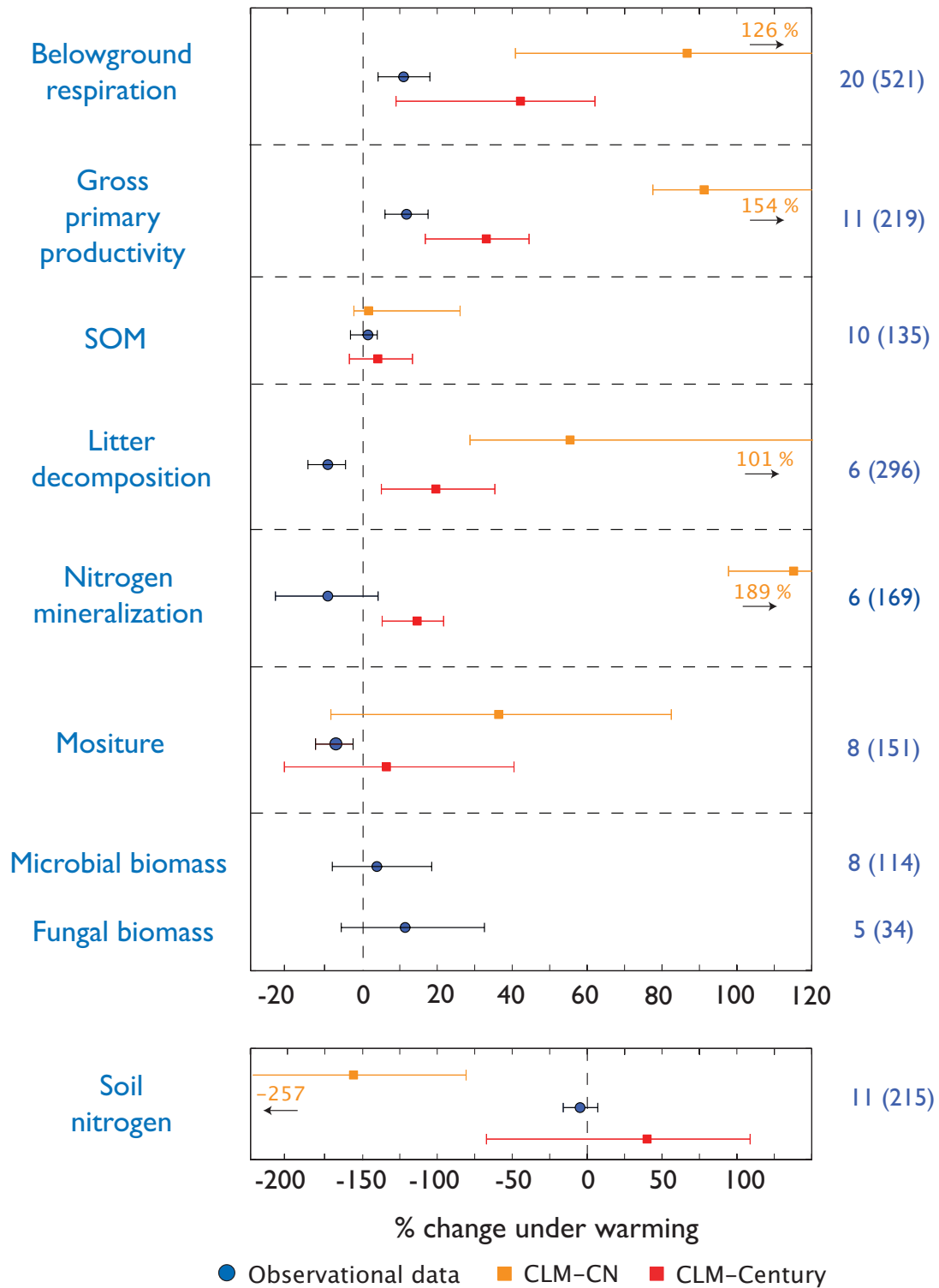


● Nitrogen addition only
 ● Nitrogen addition and warming
 ● Warming experiment only

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Figure 1

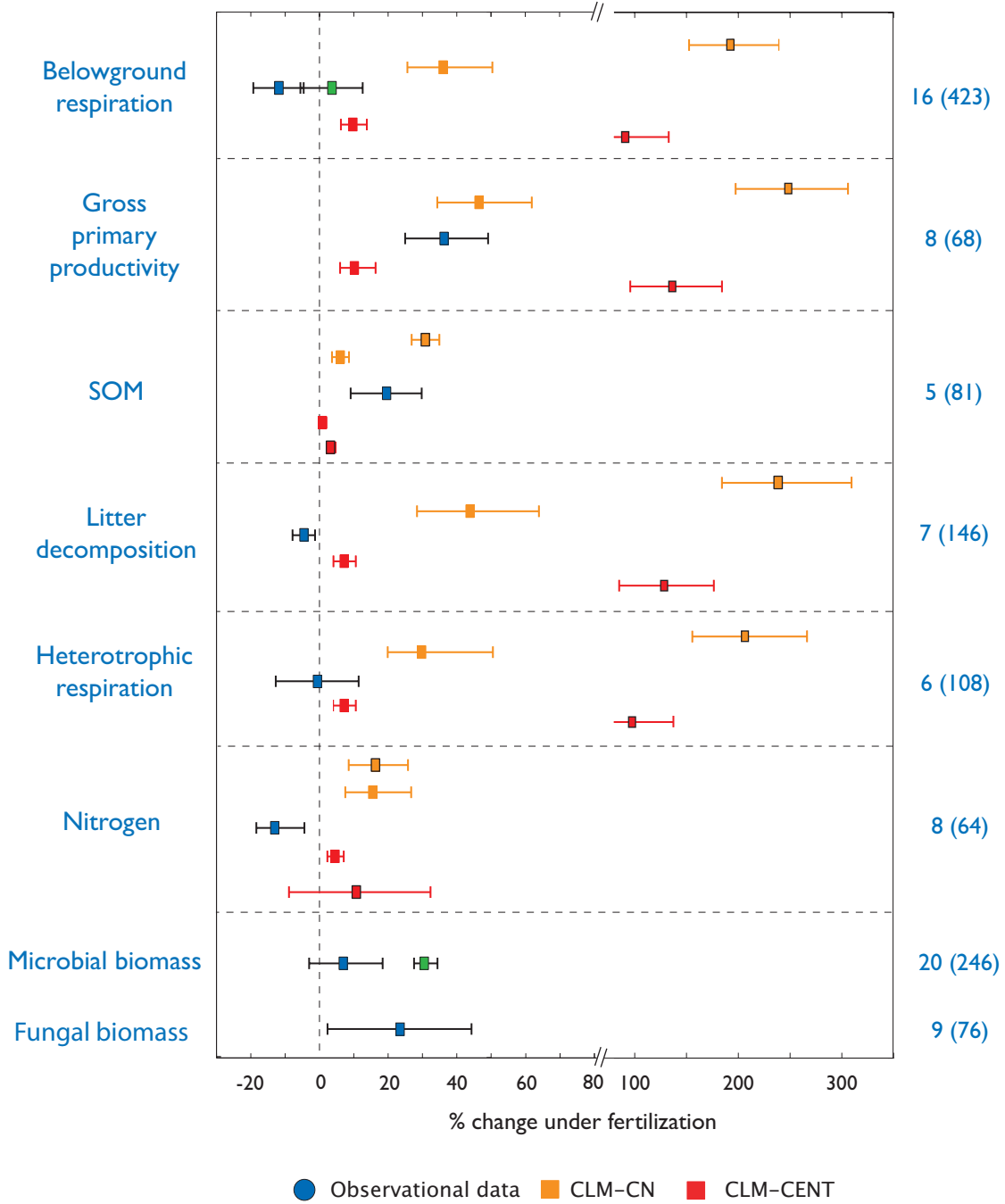
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Figure 2a

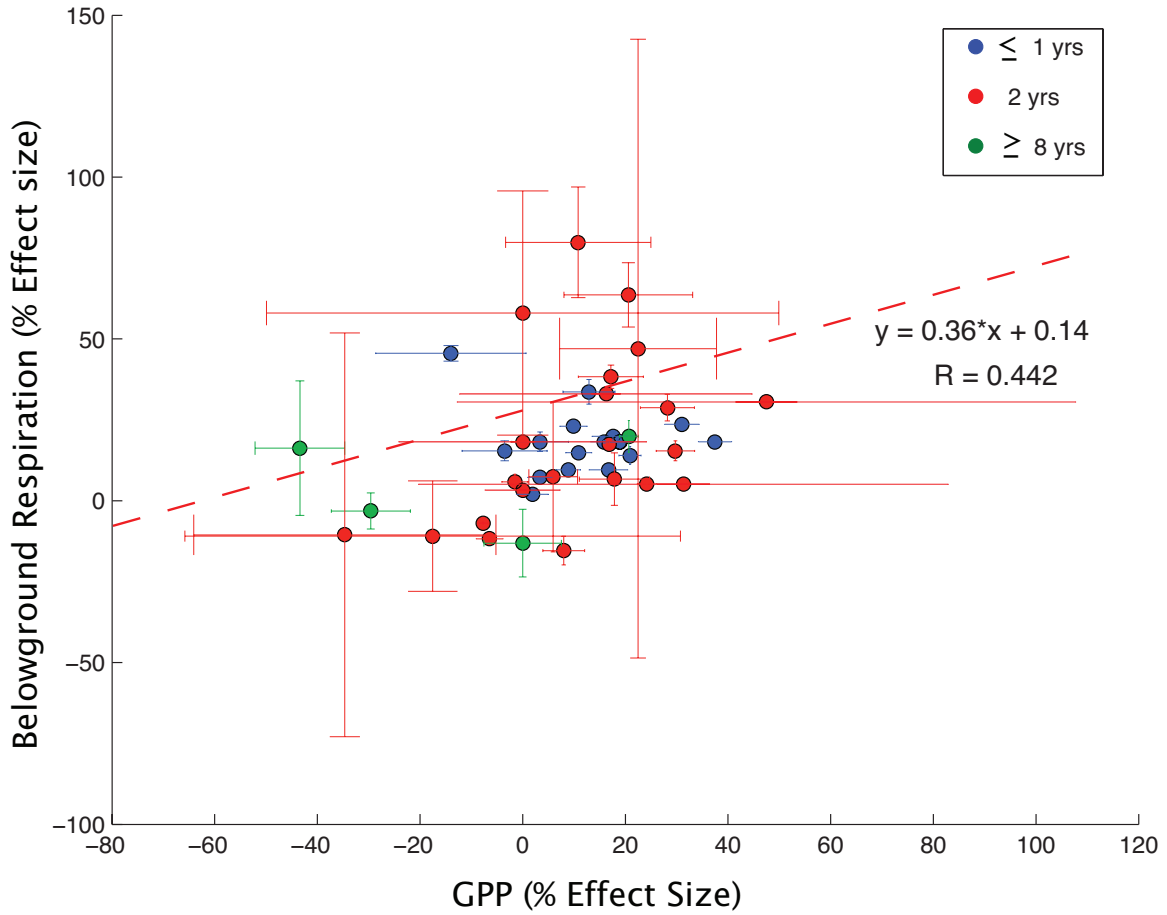
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Figure 2b

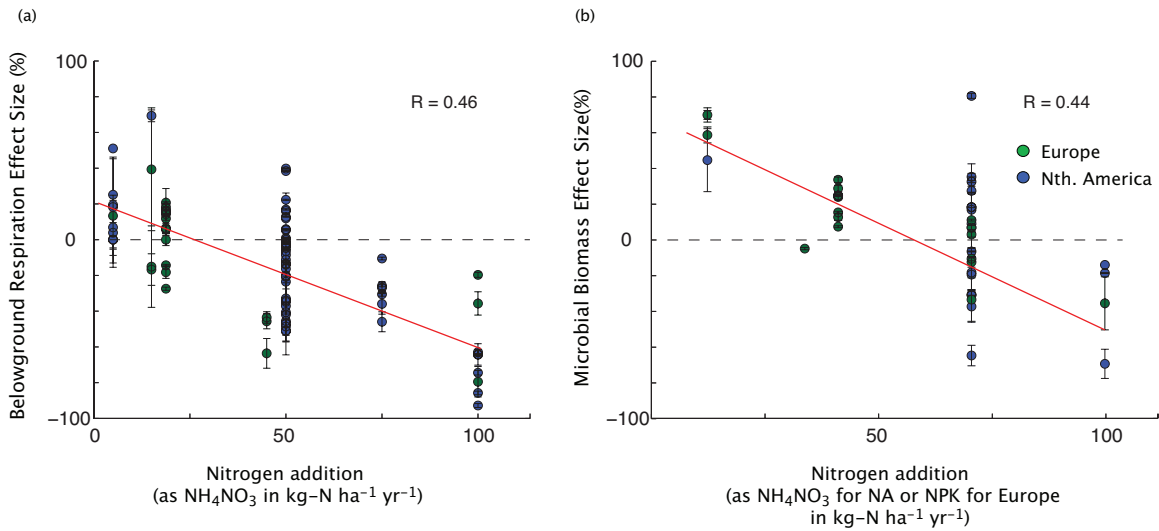
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Figure 3

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Figure 4