1 **Meta-analysis of high-latitude nitrogen-addition and warming studies implies**
2 **ecological mechanisms overlooked by land models**
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10 **Running title:** Testing model performance via meta-analysis
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47   **Abstract**
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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.

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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 CO_2

85   or CH_4) 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 CO_2 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 (≥ 60° 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 ($\geq 60°$ 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:

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

171   Where $\overline{X}^T$ and $\overline{X}^A$ are the mean values for the treatment and ambient response

172   variable, respectively. The sampling variance ($V_{\ln R}$) was calculated as:

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

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 ith 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° × 2.5°, 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). Model vegetation was specified according to the MODIS

213   vegetation continuous fields (Oleson et al., 2013). Model simulations were

214   parameterized to replicate the field experiments: the soil was warmed by scaling the

215   aerodynamic resistance by a factor of 10, a value obtained by trial and error to

216   achieve a desired warming of ~1 °C (in accordance with the average temperature

217   increase noted for the experimental manipulations, see results section below), while

218   keeping sufficient spatial variability of the warming. CLM forces the soil heat

219   transport process through the residual flux from incoming radiation, latent heat,

220   and sensible heat. Increasing aerodynamic resistance reduces the sensible and

221   latent heat fluxes and warms the soil during the growing season. We tried warming

222   the soil by increasing the surface air temperature (which is a diagnostic variable in

223   CLM), but this approach violated CLM's surface energy budget and was therefore

224   avoided. Furthermore, increasing aerodynamic resistance is more analogous to the

225   approach 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 (±

251   0.7°C). Belowground respiration increased significantly under warming by 9% (±

252   5%) compared to the controls. This increase in belowground respiration was largely

253   driven by the response of European soils, which increased 33% (± 11%) above

254   control soils. Conversely, belowground respiration from North American soils

255   showed a more modest, and non-significant, increase (2.5% ± 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 ± 0.6 °C in

258   Europe and 1.3 ± 0.5 °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% ±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% (± 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% (± 12%) while fungal biomass increased by 11.5% (± 19%).

269   Under warming, soil nitrogen mineralization and soil nitrogen

270   concentrations both declined non-significantly (nitrogen mineralization: 7.6% ±

271   15%, soil nitrogen: 5.1% ± 9%) below the control soils. Soil phosphorus increased

272   non-significantly above the control soils (12.5% ± 9%, Fig. S1b). Finally, the use of

273   the OTC and OTG to passively warm high-latitude soils significantly lowered soil

274   moisture 8% (± 6%,) below the control soils (Fig. S1b).

275   Modeled warming experiments increased soil temperature by 1.21 °C ±

276   0.47 °C in CLM-CN and 0.91 °C ± 0.35 °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% ± 42%; CLM-Century: 7% ± 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 kg-N ha^{-1} yr^{-1} (± 38 kg-N ha^{-1}

290   yr^{-1}) of nitrogen to soils, with a range of 1 – 100 kg-N ha^{-1} 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% (± 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% (± 9.5%) below control soils (Fig. S1a). Belowground

298   respiration in North American soils also declined significantly by 12.7% (± 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 (± 12%). Nitrogen addition resulted

305   in a significant decline in litter decomposition (% mass loss yr^{-1}) of 4.8% (± 3%),

306   while SOM increased significantly 19.5 % (± 10 %) in perturbed soils.

307   GPP increased significantly under nitrogen addition (44.3% ± 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% ± 22%). Vascular plant biomass increased significantly (33 % ± 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% ± 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% (± 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., ≤ 1 kg-N ha^{-1} 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. The

372   inclusion of nitrogen cycling in coupled carbon-nitrogen climate models is

373   consistent with the idea that nitrogen is a significant determinant of carbon cycling

374   in many ecosystems (Hungate, 2003; Vitousek and Howarth, 1991), and modeled

375   nitrogen input, retention, and loss have been shown to have a large impact on

376   ecosystem carbon sequestration (Thomas et al., 2013b; Zaehle and Dalmonech,

377   2011). Moreover, data based modifications to ESM nitrogen cycling mechanisms

378   may further improve the correspondence between observations and model output

379   (Thomas et al., 2013b).

380   CLM-CN predicts much higher rates of nitrogen loss from denitrification, than

381   CLM-Century, and is therefore more responsive to changing nitrogen availability

382   from inputs, mineralization, and losses. Under warming, CLM-CN predicted a

383   significant loss of soil nitrogen not predicted in CLM-Century, which has a more

384   closed nitrogen cycle, possibly more representative of the nitrogen cycle in high-

385   latitude soils (Barsdate and Alexander, 1975). Rates of nitrogen fixation, deposition

386   and redox cycling (i.e., nitrification and denitrification) are low at high latitudes

387   (Cleveland et al., 1999; Giblin et al., 1991), and hydrological loss of nitrogen at the

16

388   beginning of the growing season has been reported to be relatively large (Harms

389   and Jones, 2012; Jones et al., 2005). Mineralization is, therefore, the main source of

390   nitrogen for plant and microbial growth (Shaver et al., 1992).

391   Mineralization rates are controlled by the depolymerization of proteinaceous

392   compounds (Jones et al., 2009; Schulten and Schnitzer, 1997), leading to the release

393   of amino acids (Schimel and Bennett, 2004) that are rapidly utilized by plants and

394   microbes (Kielland, 1994; Weintraub and Schimel, 2005). Ammonia is then released

395   during turnover of the dead microbial biomass. Depolymerization is the critical step

396   in this process and, like organic matter decomposition, is dependent on microbial

397   physiology and subject to the biotic and abiotic controls described above. Modeled

398   nitrogen mineralization, however, increases under warming with a concomitant

399   increase in soil nitrogen in the CLM-Century framework. CLM-CN, with its high rates

400   of mineral nitrogen losses shows a very large decline in soil nitrogen, possibly

401   rendering the above- and belowground communities nitrogen limited throughout.

402   In our data analyses, nitrogen mineralization declined as microbial nitrogen (i.e.,

403   immobilization) increased. The end result in both cases (i.e., the models and

404   observations) is the potential limitation of plant growth over long time scales. Our

405   data synthesis suggests that the release of nitrogen from increased decomposition is

406   used to meet microbial demands or immobilized. Microbial immobilization is

407   regulated by the stoichiometric imbalance between the substrate being

408   depolymerized and the physiological nutrient demand. While analogous to the CUE,

409   nitrogen use efficiency (NUE), which relates immobilization and mineralization to

410   microbial growth (Mooshammer et al., 2014), is regulated independently in order

411   to maintain cell stoichiometry. Some attempts have been made to incorporate NUE

412   controls into ecosystem models (Manzoni and Porporato, 2009), but further

413   experimental and modeling work is required to understand NUE's plasticity and

414   impacts on soil carbon dynamics.

415

416   *4.1.2 Aboveground dynamics:* The biogeochemical coupling between aboveground

417   and belowground components of the ecosystem is crucial for understanding high-

418   latitude carbon cycling under a changing climate. The meta-analysis of field

419   measurements showed a general stimulation of aboveground activity under

420   warming, while previous field studies have noted a shift in plant community

421   composition with warming, favoring the establishment of deciduous shrubs and

422   graminoids and selecting against mosses and lichens (Schuur et al., 2007; Sistla et al.,

423   2013; Walker et al., 2006). This shift toward more woody plants changes the

424   ecosystem carbon balance and nutrient dynamics (Jackson et al., 2002; Welker et al.,

425   2004), as shrubs tend towards higher internal carbon allocation toward woody

426   tissue, but also may increase belowground carbon allocation (as both litter and

427   exudates) relative to mosses (Street et al., 2013). This change in belowground

428   allocation may result in the observed relationship between GPP and belowground

429   respiration (Fig. 3), indicating a close coupling between these two processes. This

430   positive relationship may develop due to higher rates of belowground labile root

431   exudation, which may be respired directly by the plants themselves (Luo, 2007), or

432   'prime' the microbial community leading to the destabilization and decomposition

433   of chemically complex SOM (Fontaine et al., 2004). Our data analysis cannot directly

434   distinguish between the two pathways, although an observed drop in litter

435   decomposition rates could indicate that the mineralization of plant exudates spurs

436   the degradation of older SOM (Hartley et al., 2012), resulting in elevated

437   belowground respiration rates. Further field studies and more data (e.g.,

438   radiocarbon measurements) are required to verify this conclusion.

439   Current models crudely represent above- and belowground biogeochemical

440   coupling and do not represent some of the crucial roles plants play in soil carbon

441   dynamics (Ostle et al., 2009; Schmidt et al., 2011). Of particular relevance to high-

442   latitude ecosystems is the lack of any representation of cryptogams or bryophytes in

443   CLM4.5. These plants contribute substantially to aboveground biomass and

444   biogeochemical processes in tundra soils (Cornelissen et al., 2007; Elbert et al.,

445   2012) and are clearly important for accurate simulations of tundra carbon dynamics.

446   Few ESM land models (including CLM4.5) include dynamic vegetation, and when it

447   is included, representation tends to be coarse (Ostle et al., 2009). Ongoing work will

448   attempt to address some of these deficiencies, by including representations of

449   aboveground ecosystem demography (Huntingford et al., 2008; Moorcroft et al.,

450   2001), and soil carbon dynamics (Riley et al., 2014; Tang and Riley, 2013).

451   Integration of these approaches into the CLM framework may improve the

452   robustness of long-term tundra soil simulations and reduce uncertainty associated

453   with the aboveground model response.

454

455   *4.1.3 Litter Decomposition:* Disagreement between the observations and model

456   predictions was also noted for litter decomposition. Under warming, litter

457   decomposition declined in the observations, possibly contributing to SOM

458   accumulation, but increased in the models. In previous studies, the response of litter

459   decomposition to warming was largely dependent on the method used to increased

460   soil temperature (Aerts, 2006). OTCs tend to warm the soil and reduce soil moisture,

461   limiting litter decomposition by saprotrophic fungi. Soil moisture in the models

462   showed a non-significant increase with warming as the permafrost began to thaw

463   (Fig. 2a). The difference between the observational meta-analysis and the models

464   represents a potentially confounding factor in using this data to benchmark the

465   model. A previous meta-analysis focused solely on litter decomposition in Arctic and

466   Alpine tundra found that warming induced a small increase in decomposition

467   provided sufficient soil moisture (Aerts, 2006). This response was not apparent in

468   our data syntheses, but suggests the model results, while overestimating litter

469   decomposition, were at least in the appropriate direction. Soil moisture is an

470   important controller on decomposition (Aerts, 2006; Hicks Pries et al., 2013).

471   However, changes to surface hydrology during permafrost thaw are dependent on

472   thermokarst formation and topological features of the landscape (Jorgenson and

473   Osterkamp, 2005) and may result in increased or decreased soil moisture. We

474   identify these issues as important for further experimental and modeling work in

475   order to better represent future changes in surface hydrology and the consequences

476   for litter decomposition.

477

478   *4.1.3 Belowground Ecology:* The observational data indicated elevated belowground

479   respiration under warming. The response of microbial heterotrophs to warming can

480   partially be explained by kinetic theory, whereby biochemical reaction rates

481   increase with increasing temperature (Davidson and Janssens, 2006). Hydrolytic

482   and oxidative extracellular enzymes, secreted to depolymerize complex organic

483   matter (Allison et al., 2010), are sensitive to temperature (German et al., 2012).

484   Structural modifications in cold ecosystems maximize their specific activity under in

485   situ temperatures relative to temperate ecosystems (Hochachka and Somero, 2002),

486   which may result in significantly enhanced activity under warming (Koch et al.,

487   2007). This theory fits with the short-term (<2yr) data from the current meta-

488   analysis showing increasing belowground respiration despite no increase in

489   microbial biomass.

490   However, we also identified a drop in belowground respiration in studies

491   lasting longer than 2 years and shorter than 5 years (Fig. S1b). Belowground

492   respiration has consistently been reported to decline under prolonged warming

493   (Rustad et al., 2001) and attributed to substrate limitation (Hartley et al., 2008) or a

494   community-level response of microbial populations to warmer temperatures

495   offsetting the kinetic response of individual microbes (Bradford, 2013; Bradford et

496   al., 2008). Given the increased GPP found in our meta-analysis, belowground

497   communities are unlikely to be substrate limited. Therefore, we hypothesize that the

498   community-level response is likely responsible for the drop in belowground

499   respiration under 2 – 5 years of warming.

500   The subsequent increase in belowground respiration over prolonged

501   warming (> 5 years) could represent either the decomposition of leaf litter driven

502   by changes in microbial community composition, or thawing subsurface organic

503 matter (Dorrepaal et al., 2009). This latter hypothesis is relevant to the long-term

504 fate of high-latitude carbon. In the current analysis, NEE appears balanced, with no

505 change in SOM. However, temporal patterns of vegetation response to warming

506 show a transient response to warming, with nutrient limitation reducing plant

507 productivity on longer time scales (Arft et al., 1999; Chapin and Shaver, 1996). It is

508 possible, given the large nitrogen immobilization under warming, that belowground

509 respiration may continue longer than productivity, unbalancing NEE and leading to

510 net carbon loss.

511 Temperature is a key factor influencing biogeochemical mechanisms in the

512 model. CLM models belowground respiration using a static Q_{10} and fixed carbon use

513 efficiencies (CUE) for different SOM pools size. This approach may result in the large

514 modeled increase in belowground respiration. In reality, both Q_{10} and CUE vary on

515 spatial and temporal scales, and respond non-linearly to changes in temperature

516 (Janssens & Pilegaard, 2003; Sinsabaugh et al., 2013, Tang & Riley, 2014). Recent

517 microbe-explicit models (MEMs) that consider basic microbial physiology (e.g.,

518 Lawrence et al., 2009) introduce direct biological control over soil carbon cycling

519 and different conclusions on soil carbon pool size and dynamics under warming

520 (Allison et al., 2010; Lawrence et al., 2009; Wieder et al., 2013). For example, by

521 scaling the CUE value with temperature, in accordance with published observations

522 (Luo et al., 2001; Melillo, 2002), the MEMs show a decline in soil carbon turnover

523 under warming (Li et al., 2014; Wieder et al., 2013). Recent work using a MEM with

524 explicit representation of internal physiology, extracellular enzymes, and mineral

525 surfaces (Tang and Riley 2014), demonstrates that both decomposition temperature

526   sensitivity and CUE are hysteretic and cannot easily be represented by a simple

527   function of soil temperature. However, it is also important to note that microbial

528   CUE is not solely temperature-dependent, and other factors, some of which are

529   already present in CLM-CN and CLM-Century (including nutrient and soil moisture

530   limitations), may uncouple growth and respiration and change CUE (Manzoni et al.,

531   2008; Sinsabaugh et al., 2013). The predictions of the microbe-explicit models

532   (MEM) provide further impetus for greater representation of the structure and

533   function of belowground biomass.

534   Other aspects of belowground ecology in high-latitude tundra that are not

535   included in the models can have a significant impact on the stability of soil carbon

536   (also see discussion below on barriers to benchmarking). For example, while there

537   is little evidence that fungal:bacterial ratios are altered by warming, either in our

538   observational meta-analysis or in previous work (Strickland and Rousk, 2010), the

539   community composition may change without altering fungal:bacterial ratios

540   (Strickland and Rousk, 2010). Certain traits that separate the main decomposing

541   functional guilds, such as biomass stoichiometry, nutrient use efficiency, substrate

542   utilization, and response to environmental variables (e.g., temperature or soil

543   moisture) (Six et al., 2006), can bring about changes in decomposition rates. These

544   factors are arguably more important than climate when modeling decomposition at

545   local and regional scales (Bradford et al., 2014).

546

547   **4.2 Response of belowground carbon cycling to nitrogen addition**

548 Our meta-analysis of field observations found that the addition of inorganic nitrogen

549 to traditionally nitrogen limited ecosystems enhances the carbon sink, consistent

550 with previous studies (Luo et al., 2012; McGuire et al., 2012). Interactions between

551 the carbon and nitrogen cycles resulting in soil carbon accumulation in different

552 ecosystems have been reported previously (Magnani et al., 2007; Thomas et al.,

553 2013b), and have been attributed to an increased carbon allocation to woody tissue

554 (Ciais et al., 2008; Tummers, 2006) and reduction in the SOM decomposition rate

555 (Olsson et al., 2005). Overall, our data-synthesis is largely consistent with the

556 overarching conclusions of previous meta-analyses (Janssens et al., 2010; Knorr et

557 al., 2005).

558   A question remains, however, about the value of the responses synthesized

559 from studies that add fertilizer (NH_4NO_3 or NPK) as a source of nitrogen far in

560 excess of anticipated global change scenarios for high-latitude ecosystems. The

561 average concentration of nitrogen added to the soils in the tundra studies ($\sim$ 72 kg

562 ha^{-1} yr^{-1}) is extremely high when compared with (1) estimates of nitrogen fixation

563 (< 10 kg ha^{-1} yr^{-1}, Cleveland et al., 1999); (2) nitrogen deposition (both current rates

564 of deposition 0.2 – 0.24 kg ha^{-1} yr^{-1}, (Jones et al., 2005) and projections of future

565 deposition (Galloway et al., 2004)); and (3) potential nitrogen availability from

566 organic matter mineralization under a warming climate (Harden et al., 2012).

567 Consequentially, we question whether such data lends itself to understanding the

568 response of the ecosystem to realistic chronic incremental changes in nitrogen

569 availability, and the benefit of benchmarking the ecosystem models against such a

570 dataset. On the other hand, if the models include the relevant underlying

571   mechanisms, then they should reproduce the field studies, regardless of the amount

572   of nitrogen added. We give further examples below of where the high nitrogen

573   concentrations may confound the interpretation of the experiments with respect to

574   the model predictions.

575

576   *4.2.1 SOM dynamics:* SOM accumulation under nitrogen addition experiments is a

577   common feature of both the field experiments and the model simulations. However,

578   the underlying mechanisms leading to SOM accumulation are very different, adding

579   uncertainty to the model predicted soil carbon fate over longer timescales. In both

580   versions of CLM, the alleviation of nitrogen limitation stimulates a number of

581   ecosystem processes including aboveground primary productivity, litter

582   decomposition, and organic matter decomposition. The accumulation of SOM

583   indicates the stimulation of GPP and litter decomposition (as a source into the SOM

584   pools) must outweigh losses from increased belowground respiration.

585   The observations, on the other hand, show a significant decline in

586   belowground respiration and litter decomposition under nitrogen addition.

587   Belowground respiration depends on the decomposition and substrate utilization

588   capabilities of the microbial (i.e., bacterial and fungal) community to mineralize root

589   exudates and litter. A drop in belowground respiration may, therefore, be

590   attributable to several mechanisms not included in either version of CLM. A recent

591   meta-analysis examined the response of Boreal forest ecosystems to added nitrogen

592   (Janssens et al., 2010), and concluded that the internal reallocation of carbon in

593   plants and trees reduced the rate of exudation to belowground ecosystems,

594 resulting in microbial biomass becoming carbon limited with a concomitant decline

595 in biomass and belowground respiration (Janssens et al., 2010). Our empirical data

596 shows increased GPP and vascular plant biomass, possibly indicating a reallocation

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

598 belowground exudation.

599

600 *4.2.2 Belowground Ecology:* Overall, the current observational meta-analysis found a

601 non-significant increase in microbial biomass (i.e., bacterial and fungal) but a

602 significant increase in fungal biomass under nitrogen addition. This response

603 appears contrary to previous studies that have recorded a drop in microbial

604 biomass under nitrogen addition (Treseder, 2008), but in line with fertilization

605 studies in tundra ecosystems (Clemmensen et al., 2006). We also note that microbial

606 biomass (and belowground respiration) are inversely related to the amount of

607 nitrogen added to the soils (Fig. 4a, b). At low nitrogen concentrations, microbial

608 community activity can be stimulated (Allison et al., 2009) and decomposition

609 elevated, as indicated by the models (Fig. 2b) and some of the observations (Fig. 4b).

610 Elevated nitrogen concentrations, however, have a negative impact on microbial

611 biomass (Treseder, 2008) and decomposition (Janssens et al., 2010). This response

612 can occur through the inhibition of lignin-degrading enzymes produced by

613 saprotrophic fungi (Sinsabaugh et al., 2002); but see (Hobbie, 2008), or the

614 increased chemical recalcitrance of soil carbon undergoing condensation reactions

615 with inorganic nitrogen (Dijkstra et al., 2004), increasing the physical protection of

616 organic matter from decomposition. Therefore, under the high nitrogen inputs used

617   in the present field studies, the coupling between above- and belowground

618   ecosystems can decrease belowground respiration and litter decomposition

619   resulting in an accumulation of SOM.

620   Whereas the warming meta-analysis yielded results that could be used to

621   constrain model mechanisms, the same cannot be concluded for the nitrogen-

622   addition studies due to the uncertainty of how high-latitude soils will respond to

623   lower concentrations of nitrogen. However, we suggest two potential model changes

624   that could rectify the different conclusions derived from the observations and

625   models. (1) A dynamic vegetation approach sensitive to changes in nitrogen

626   inventory could represent compositional changes across the tundra with important

627   ramifications for root biomass, litter quality, and plant exudates that play a

628   significant role in soil carbon dynamics (Aerts et al., 2005). (2) Representation of

629   discrete belowground biomass functional groups (e.g., heterotrophic and fungal

630   decomposers) alongside their dependencies on soil nitrogen may help to constrain

631   the belowground response to nitrogen addition. Finally, while the model

632   mechanisms should ideally be able to reproduce the observed response to high

633   nitrogen loading, we believe that future manipulation studies in high-latitude soils

634   that use realistic nitrogen additions would be more relevant for understanding the

635   tundra soil response. For example, recent studies have added nitrogen to tundra

636   soils at magnitudes one order of magnitude higher than measured concentrations

637   (Lavoie et al., 2011) or guided by soil mineralization rates (Sistla et al., 2012). The

638   ecosystem response is therefore more likely to reflect future responses under

639   anticipated mineralization or deposition scenarios (Galloway et al., 2004).

640

4.3 Barriers and criteria 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, no general protocol consistent with field experiments is available for setting up model perturbations. Although different land models have different structures and degrees of complexity, a standard approach to establishing perturbations would be beneficial. In our model, atmospheric warming resulted in unrealistic uniform soil warming across the study domain and therefore underestimated the spatial heterogeneity found in passive warming experiments (Bokhorst et al., 2012). On the other hand, solely reducing the wind speed failed to alter the soil thermal regime, indicating a possible problem in the formulation of CLM's surface boundary layer resistance. 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.

Therefore, criteria need to be established to ensure, regardless of the method used, that the experimental manipulation is reproduced in the model with sufficient fidelity that the predicted and observed responses can be reasonably compared. We consider the criterion used here for the warming experiments (i.e., that the mean predicted manipulation soil temperatures are not significantly different from the observations) to be a minimally acceptable criterion. Ideally, the predicted response

663   of soil temperature, soil moisture, and radiation under warming would emerge in a

664   statistically similar manner to the observations. In the current study, this criterion

665   was not met for soil moisture, where the observations found that soil moisture

666   declined (by 8% ± 6%) under warming and the model predicted large increases

667   CLM-CN: 38% ± 42%; CLM-Century: 7% ± 33%).This may be an important given the

668   significant impacts moisture has on decomposition and nitrogen cycling.

669   Second, the spatial discrepancy between the model predictions and

670   observational data is large. This mismatch arises from several sources, including

671   uncertainties: (1) in the climate and environmental forcing data used to drive the

672   models; (2) in soil and plant characterization; (3) caused by spatial heterogeneity in

673   the site and experimental manipulation (e.g., unequal heating within the open-top

674   chambers, energy leaking at the boundary with surrounding soil); and (4) in

675   accurate model characterization of the growing season.

676   Third, while we acknowledge the complexity of interpreting single-factor

677   manipulation experiments, the multifaceted nature of climate change calls for more

678   multifactorial experiments and models that can reproduce any response. The few

679   studies we could find measuring the response of similar variables to combined

680   warming and nitrogen addition (e.g., Shaver et al., 1998) found an even larger

681   warming response than for the single-factor experiments. However, there were too

682   few studies measuring complementary variables to conduct a meta-analysis.

683   Previous studies conducted in high-latitude soils have recorded a stronger response

684   of decomposition following perturbation by a combination of drivers (e.g., elevated

685   temperature and CO_2) than if those factors were considered in isolation (Fenner et

686 al., 2007). In contrast, Leuzinger et al. (Leuzinger et al., 2011) give several examples

687 where the opposite occurs: a combination of multiple drivers lessens the ecological

688 response relative to individual drivers. These contradictory results call for further

689 consideration of the impact of multiple drivers in high-latitude ecosystems that

690 might be used to benchmark model performance.

691   Fourth, the field observational data lacks sufficient spatial coverage to

692 characterize high-latitude spatial heterogeneity accurately. There are many studies

693 that cluster in a few regions, represented in the model by only a few grid cells. While

694 we obtained some insights into the deficiencies of the model from this

695 benchmarking exercise, more work is required to develop confidence in our

696 conclusions given the spatial heterogeneity of high-latitude ecosystems.

697

698 **4.4 Overall Recommendations**

699   We have demonstrated here that despite some experimental drawbacks, the

700 underlying biogeochemical mechanisms of CLM-CN and CLM-Century are

701 insufficient to accurately reproduce the observations of a number of high-latitude

702 perturbation experiments. However, we can identify several metrics from the meta-

703 analyses, including nitrogen mineralization and litter decomposition, which may

704 serve as useful indices of model performance. The sign and magnitude of these

705 response ratios were incorrectly predicted by the models in under both warming

706 and nitrogen addition. This error in the sign of the response also occurred for

707 simulated belowground respiration under nitrogen addition, where the model was

708 unable to capture the detrimental impact of very high nitrogen concentrations. In

709 contrast, the SOM response under temperature and nitrogen perturbations appears

710 to be a poor metric to benchmark the models, possibly owing to the large size and

711 undefined composition of the soil organic matter stock.

712   Future development of biogeochemistry representation in CLM should focus

713 on improvements to the nitrogen cycle. Recent work has shown that specific

714 modifications to different nitrogen cycle pathways (e.g., redox cycling, plant-

715 microbial interactions) can improve the correspondence between model predictions

716 and observational data (Thomas et al., 2013a). Development should also may focus

717 on improved kinetics (e.g., equilibrium chemistry approximations, (Tang and Riley,

718 2013) to regulate competition for nutrients between biotic and abiotic sinks (e.g.,

719 plants, microbes, minerals) as an alternative to the current allocation schemes of

720 CLM-CN (Thornton et al., 2007). In addition, the integration of dissolved organic

721 nitrogen cycling as a nutrient source for microbes and plants appears to be an

722 important source of nitrogen in high-latitude soils (Hobbie et al., 2009; Weintraub

723 and Schimel, 2005). However, insufficient data were available to include DON as a

724 response factor in the meta-analysis.

725   The lack of explicit coupling between plant functional types (PFT) and

726 belowground microbial ecosystems in the model fails to capture the importance of

727 this interaction for carbon and nutrients cycling and SOM stability. The PFT concept

728 could be further extended to characterize differential belowground carbon

729 allocation (Street et al., 2013). In addition, symbiotic relationships between

730 different plants and mycorrhizal fungi can increase nutrient acquisition (Hobbie et

731 al., 2009), by facilitating nitrogen fixation (Nasto et al., 2014), and phosphorus

732   acquisition (Smith et al., 2011), thereby increasing photosynthetic rates (Jia et al.,

733   2004). Improving and expanding the definition of the PFT to include these

734   associations may serve to improve coupling between nutrient cycling with

735   belowground biogeochemistry.

736   Finally, while the magnitudes of nitrogen added to tundra soils were very

737   high, the threshold relationship (Fig. 4) that describes the alleviation of nitrogen

738   limitation and stimulation of ecosystem processes at low concentrations from their

739   inhibition at high nitrogen concentrations has support from previous studies (Knorr

740   et al., 2005). However, mechanisms have not yet been integrated in the model to

741   capture this range of responses. The model should be able to reproduce the impact

742   of high nitrogen concentrations associated with agriculture soils, and more work is

743   required to further characterize this threshold effect. It is unlikely, however, that the

744   model-predicted linear relationship between nitrogen availability and ecosystem

745   processes will, in general, be true.

746

747   **5 Summary and conclusions**

748   We have shown that certain mechanisms poorly represented in land models,

749   as highlighted by ecological meta-analysis, can undermine conclusions regarding the

750   stability of high-latitude soil carbon. We found that two versions of CLM

751   biogeochemistry (1) poorly replicated coupling of the aboveground and

752   belowground components of the carbon cycle; (2) poorly represented nitrogen

753   cycling; (3) inaccurately grouped belowground processes, and (4) insufficiently

754   represented plant community dynamics.

755   The use of a meta-analysis to benchmark models has a distinct advantage of

756   aggregating the response of a number of different climate change experiments

757   across spatial and temporal scales to converge upon an average ecosystem or biome

758   response. This aggregation reduces the weight that any one study has on the

759   development of a model benchmark metric. This approach is particularly valuable in

760   ecosystems in which a large number of studies have been performed (e.g.,

761   temperate systems, (Lu et al., 2013). However, we also caution that the field

762   experiments used in a benchmarking meta-analysis must be carefully chosen. We

763   demonstrated the utility of benchmarking land models using studies and

764   measurements that attain a realistic ecosystem response to warming, and the

765   difficulties associated with comparing model performance against nitrogen addition

766   studies that do not replicate conditions under current, or anticipated future climate.

767

768   **Author contribution**

769   NJB and WJR designed the experiment. NJB develop the meta-analysis. JYT
770   developed model perturbation approach and carried out the simulations. NJB
771   analyzed the results and wrote the manuscript with input from WJR and JYT.
772
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1142   Figure 1: Study sites included in the meta-analysis.

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1144   Figure 2: Response ratio of select variables under (a) warming and (b) nitrogen
1145   addition. The figures show the average response to perturbation derived from the
1146   observations (blue circles or squares), CLM-CN (orange squares), and CLM-Century
1147   (red squares). Also shown is the variance either side of the average. Under

1148 circumstances where the variance could not fit on the axis, a numerical value
1149 indicates the limits of variance. In figure 2b, R_B is given as the response to the
1150 average nitrogen concentration and also to lower, more realistic concentrations
1151 (represented by the green square). The modeled response in Figure 2b is the
1152 collated response following the addition of low nitrogen concentrations (i.e., 0.2, 1.0,
1153 2.0 and 3.0 kg-N ha^{-1} yr^{-1}) and high concentrations (20, 60 and 100 kg-N ha^{-1} yr^{-1}).
1154 Note the axis change in fig. 2b following the break. The number of individual studies
1155 and data points (in brackets) used in calculating the observation response ratio are
1156 given in blue on the right-hand side of the figure.
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1158 Figure 3: Relationship between GPP and heterotrophic respiration in warmed plots.
1159 Data points from the graph also represent the duration of warming. Each point
1160 represents the effect size expressed as a percentage and the calculated bootstrapped
1161 variance (across the x and y axis).
1162 Figure 4: The effect of increasing N-addition on (a) Belowground respiration, and
1163 (b) microbial (i.e., bacterial + fungal) biomass.
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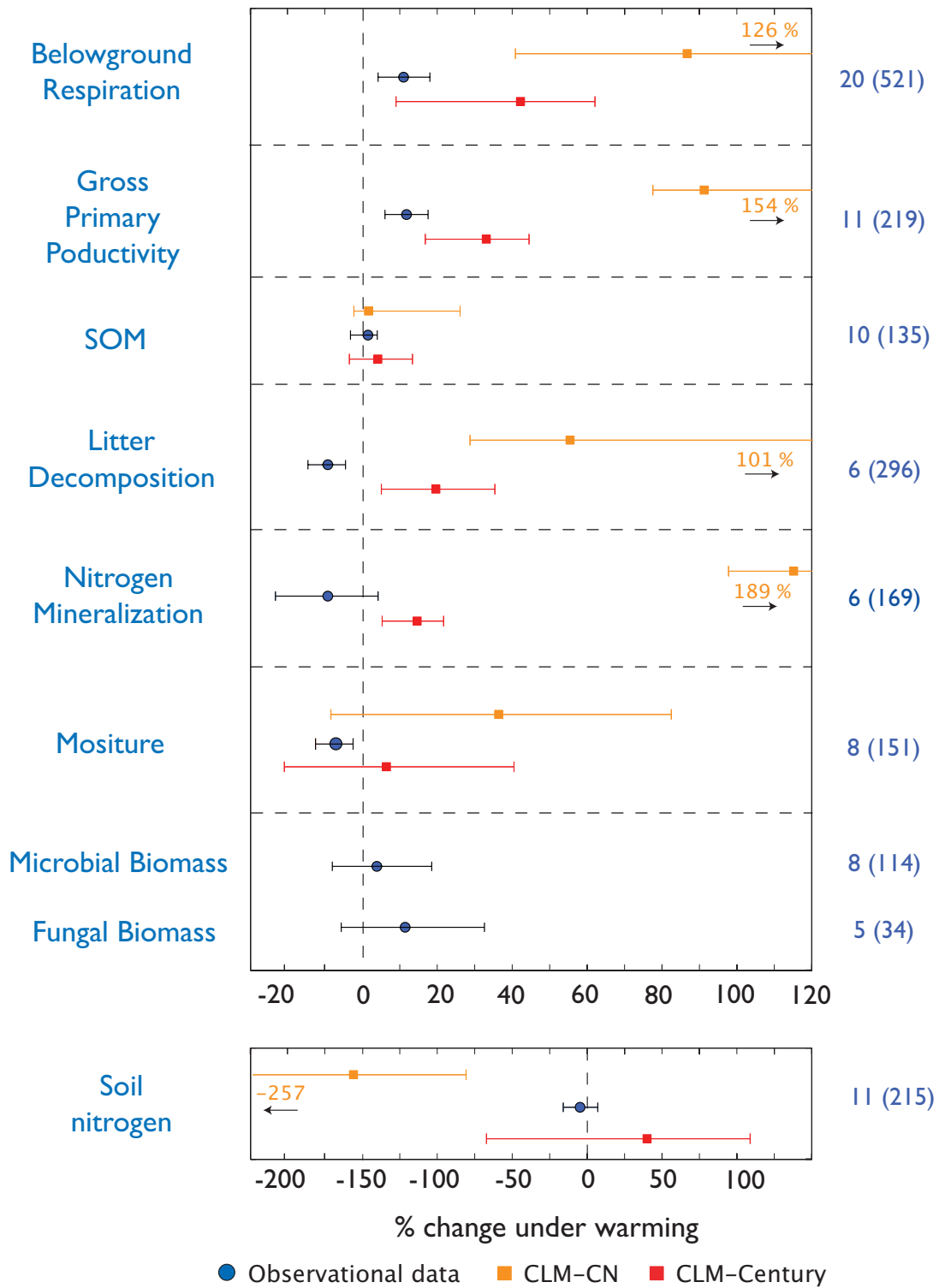1186
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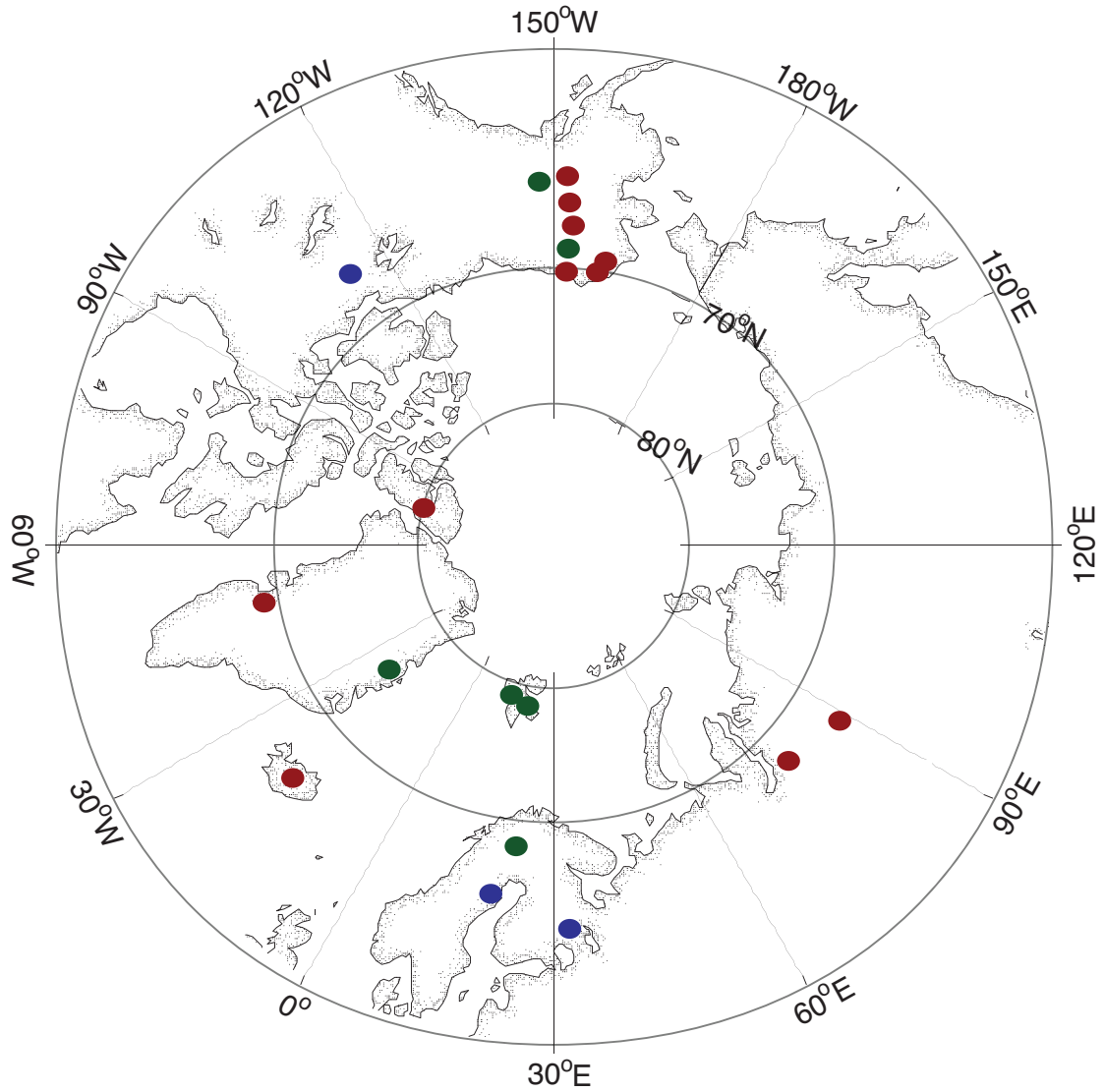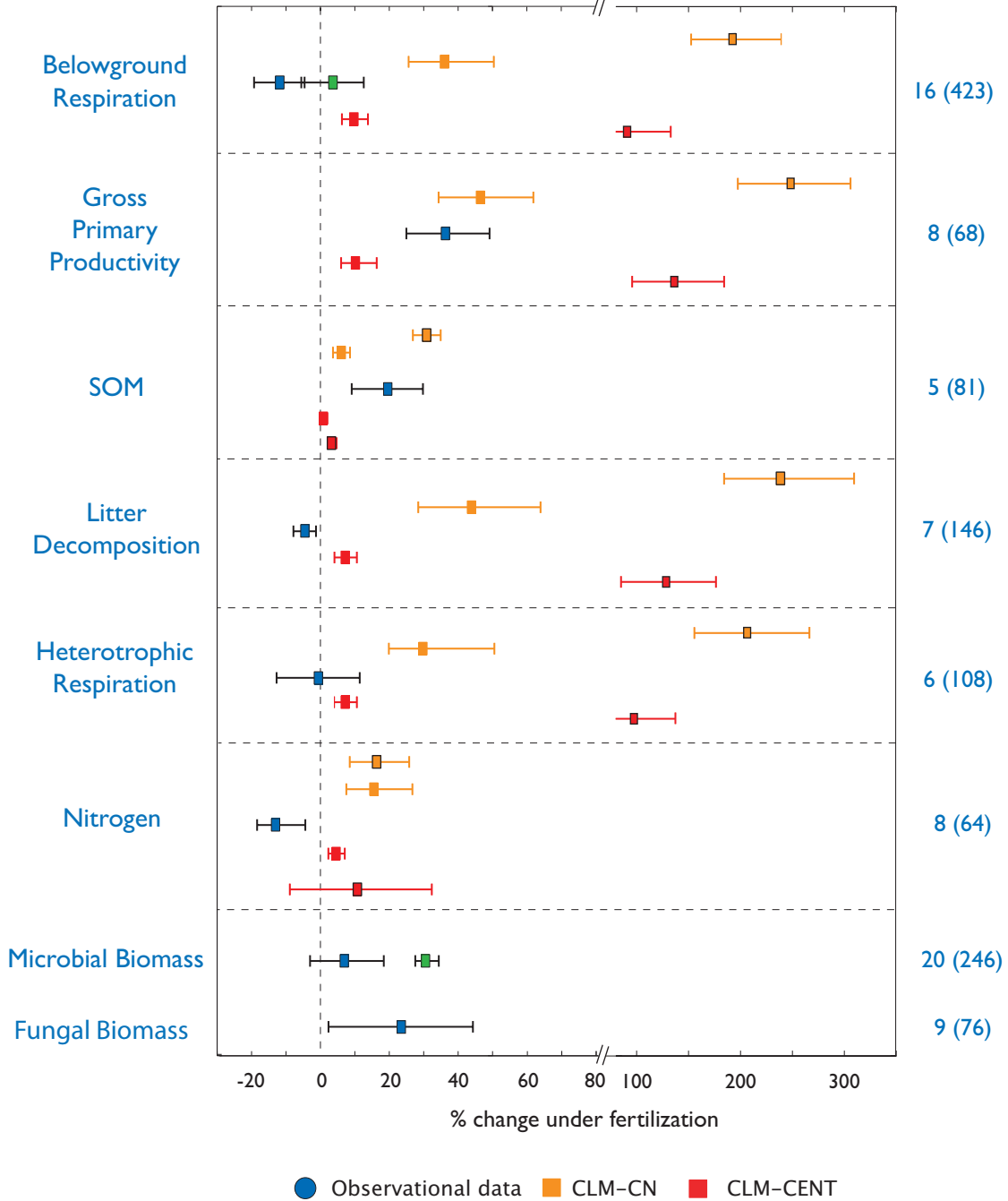
Figure 1

Figure 2a

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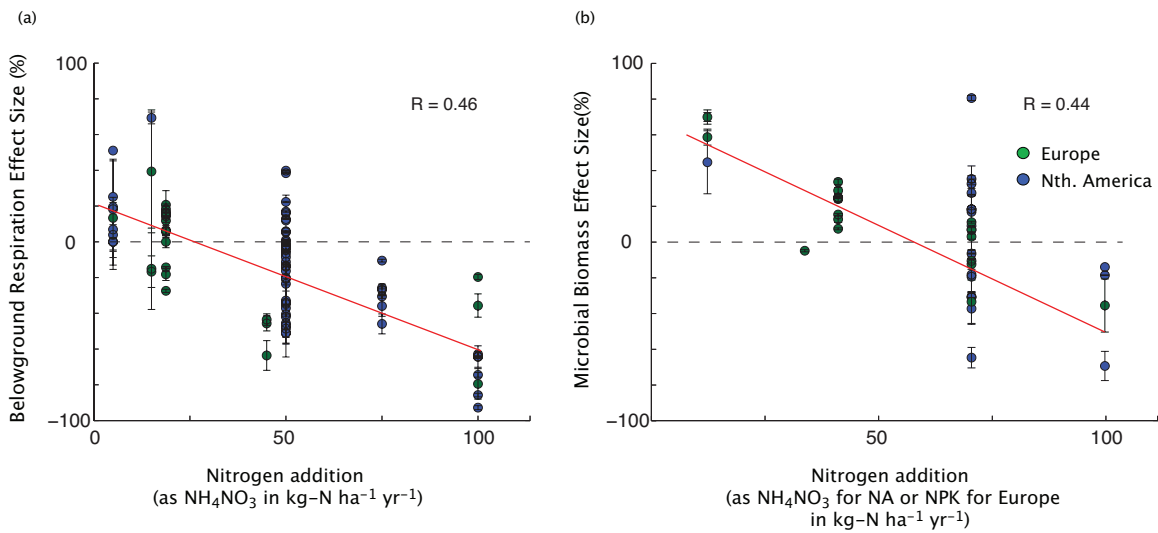1251
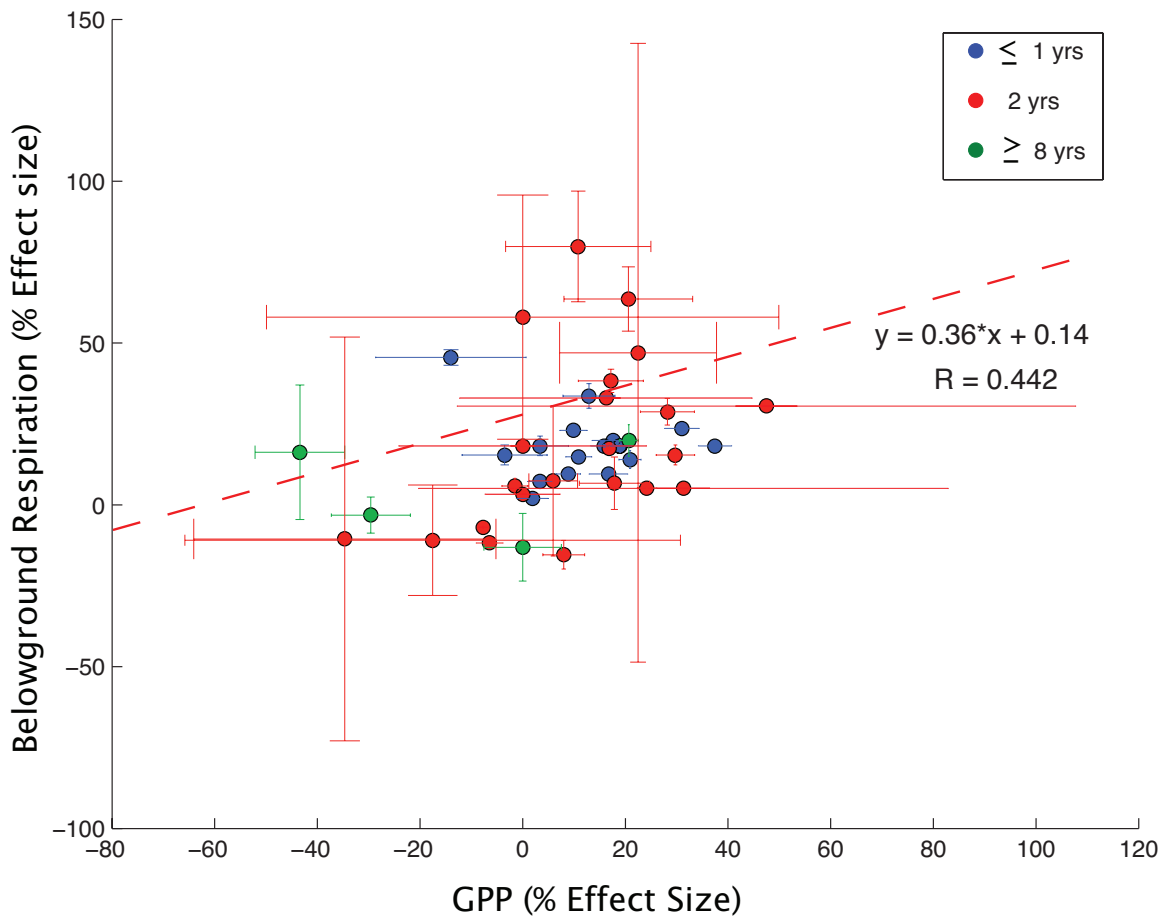
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(a)

(b)

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1288   Figure 4
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